THE UNIVERSITY OF HULL

The efficacy of back calculation methods for determining length at age data and the use of such data to determine growth standards, national growth patterns and recruitment dynamics of roach (*Rutilus rutilus* (L.)), dace (*Leuciscus leuciscus* (L.)) and chub (*Leuciscus cephalus* (L.)) in UK rivers.

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By

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ABSTRACT

The efficacy of back calculation methods for determining length at age data and the use of such data to determine growth standards, national growth patterns and recruitment dynamics of roach (*Rutilus rutilus* (L.)), dace (*Leuciscus leuciscus* (L.)) and chub (*Leuciscus cephalus* (L.)) in UK rivers.

The use of fish scales to age and back-calculate previous lengths at age and gain age and growth information has long been used as a management tool in fisheries. Calcified structures from fish, including otoliths, fin rays, and vertebrae have been used to gain length at age data. Scales however, are the most common structure used for aging freshwater fish (Borkholder and Edwards 2001). In order to gain accurate back-calculated length at age data gained from fisheries surveys, an appropriate method of back-calculation was sought. A number of back-calculation methods were found from the literature and applied to data from fish surveys. Back-calculated lengths at age from specific cohorts were compared to observed mean lengths at age from historic surveys, revealing the method proposed by Hile (1941) as being the most consistent method for providing accurate length at age data from fisheries surveys.

Comparative assessments of population mean growth rates remain important aspects of stock assessment in river fisheries (Britton 2007). Standard growth curves were originally produced for roach, dace, chub and bream (Hickley and Dexter 1979) and later expanded to include pike (Hickley and Sutton 1984). Habitat rehabilitation (Quinn 1994) and water quality improvements (Environment Agency 2001; 2006) are among a number of factors that have changed in rivers since the inception of the standard growth curves. Comparison of standard growth curves produced in this study and those produced by Britton (2007) against the original growth standards affirm the suggestion that the observed growth of these species has changed. Standard growth curves were produced and proposed for use as an updated comparative data set and an update to these standard growth rates is made on a regular basis.

Riverine fish communities are highly structured and follow non-random patterns along a longitudinal profile (Jackson *et al.* 2001). Plasticity in the growth of fish along the longitudinal gradient of rivers has been demonstrated (Cowx 1988; Zelt *et al.* 1999). This study affirms the longitudinal plasticity in the growth of roach, dace and chub along the longitudinal gradient and reveals areas where conditions are conducive to better growth in these species, namely the downstream areas for roach and the upstream areas for dace and chub. Many studies have demonstrated growth rates as being dependent on geographical variation (Pyron 1999), with evidence that some fish species attain larger sizes at lower latitudes (Modde and Scalet 1985) while other studies demonstrate increased growth at higher latitudes (Isley *et al.* 1987, Conover and Present 1990). Latitudinal variation of fish growth characteristics from rivers throughout England and Wales revealed the growth rate of dace as being strongly related to latitudinal position, with the growth of dace showing a preference toward the cooler temperatures in the higher latitudes. Roach were found to prefer the lower latitudes where temperatures were higher, while chub were found to prefer the high latitudes and easterly longitudes.

The year class strength of fish is an important index in the management of freshwater fisheries (Cowx and Frear 2004) with early developmental stages representing a crucial period in cyprinid fishes where variations in mortality during this period are critical in determining year class strength (Cowx 2001). A number of specific periods, where elevated flows occurred, were found to be related to the year class strengths of roach, dace and chub and identified as being important in playing a role in determining year class strength. The Gulf Stream was demonstrated as having a relationship with the flow regimes of a number of rivers which in-turn related to variances observed in the year class strengths and mean lengths at the end of the first year of life, of the fish species analysed. Northerly shifts in the Gulf Stream were found to have a positive influence in the growth characteristics and consequently the year class strengths in a number of the populations tested. A lag phase in the influence of the Gulf Stream on year class strengths was also identified in roach, dace and chub from a number of rivers. In this instance it was postulated that northerly shifts in the Gulf Stream produced conditions conducive to the growth of the adult fish stock which may in turn relate to an increased fecundity and/or the production of higher quality gametes from an increased condition of the adult stock.

CHAPTER ONE

INTRODUCTION

1.1 – Overview

The goal of fisheries science is to provide information for the appropriate management of fisheries (Musick and Bonfil 2004), of which age determination is an essential tool (Jiménez *et al.* 2001). Fish ageing increases the understanding of how both individuals and populations of fish grow and how numbers of fish within a fishery change over time. This information is vital in the production of growth rates, life history traits, mortality rates and year class strengths (Environment Agency 2007), information vital for management decision making. For example, where stunted populations are identified within a freshwater fishery the decision to 'crop' the population, and therefore reduce the potential competition for resources could enable an increase in growth rate in the remaining population (Environment Agency 2007).

Growth characteristics have been related to various physical, geographical and environmental variables, including species in specific regions (Williams 1967; Cragg-Hine and Jones 1969; Shafi and Maitland 1971; Pitcher and MacDonald 1973; Cowx 1988) and with respect to temperature (Le Cren 1958), diet (Jezierska 1974; Lammens 1982), density (Linfield 1979) and limnological features (Marciak 1972). River fish have been described as useful for characterizing environmental conditions, with biotic diversity and natural characteristics of the fish communities being directly related to the variety and extent of natural habitats within a river basin (Cowx and Welcomme 1998).

1.2 – Factors affecting the growth of fishes

1.2.1 - Zonation patterns

Fish have preferred physico-chemical requirements, and because longitudinal physico-chemical gradients exist in rivers, they can be translated into zonation patterns of fish species assemblages, where species with same or similar habitat requirements are grouped. Huet (1949, 1959) found the distribution of fish in rivers fell into four zones, the trout, grayling, barbel and bream zones, which related to areas of river moving from the headwaters downstream toward the mouth of the river. Gradient is described as the primary feature, with width of the stream also characterising these zones. A number of authors have related the variability in growth of fish to their distribution within the respective catchments and concluded growth as being characterized by the physical nature of the habitat in which the fish were found (Cowx 1988; Przybylski 1996; Osmundson 1999). For example, Cowx (1990) described the distribution of roach, *Rutilus rutilus* (L.) and dace, *Leuciscus leuciscus* (L.) within the River Exe catchment; dace were numerically dominant in the middle reaches and roach dominated the fish assamblage of the lower reaches. The growth parameters of these species displayed faster growth within 'preferred' areas of their distribution and slower growth outside of these 'preferred' areas, for example where the river topography portrayed characteristics in the habitat which best suited the species preferences, namely the faster flowing middle reaches for dace and the slower flowing lower reaches for roach.

1.2.2 – The influence of temperature on growth

Fish growth is an indeterminate, plastic process that can change considerably in response to environmental factors (Weatherley and Gill 1987). Temperature is known to influence both the rate of ingestion and the metabolic processes of fish, with metabolic rate increasing with concurrent rises in temperature (Jobling 1995). Le Cren (1958) working with perch, *Perca fluvitalis* (L.) in Lake Windermere, demonstrated the growth of all ages to have considerable year to year variation, which was attributed to temperature differences, and described annual growth to begin in the spring when water temperatures reached between 13° and 14°C. 14°C also initiated growth in the roach populations of the River Hull (Broughton and Jones 1978). Considerable annual variation was observed in growth of R. Hull roach and related to water temperatures above 14°C, suggesting water temperature, acting through the food supply, was the dominant factor governing the growth of roach in this river and an adjacent gravel pit (Broughton and Jones 1978). However, 14°C is not considered by a number of authors to be the temperature above which somatic growth is observed. Mann (1997) showed 11.5° – 12°C to be the temperature below which growth was not observed in River Great Ouse roach, a view supported by Mann (1973), Mills and Mann (1985) and Mooij and van Tongeren (1990).

Seasonal variances have been observed in the growth patterns of fish and scale check formation. Cragg-Hine and Jones (1969) discussed seasonal variances between annual cycles in the growth of dace, roach and chub (*Leuciscus cephalus* (L.)). Inter-annual differences in growth were found, especially in roach, and were attributed to differing temperatures between years (Cragg-Hine and Jones 1969). Comparisons were also made between the growth of the fish from Willow Brook and fish from other British and Continental waters for example; dace from the Hampshire Avon (Berry, 1935); River Funshion (Healy 1956); River Cam and Shepreth Brook (Hartley, 1947) and the River Thames (Williams, 1967), while roach growth rates were compared to roach from Lake Glaningen, Sweden (Kempe, 1962); Pool Mala and Velka Arazimova, Czechoslovakia (Frank, 1961); Elbe region, Czechoslovakia (Frank, 1961) and Lake Halmsjon, Sweden (Kempe, 1962). Cragg-Hine and Jones (1969) showed the growth regimes of roach and dace from Willow Brook to be average in some areas and poor in other areas when compared to other water bodies. Where poor growth was observed it was attributed to density dependant factors, such as competition for resources in the stretches of river concerned (Cragg-Hine and Jones 1969).

1.2.3 – The influence of flow velocity on growth

Flow is a key abiotic operator in lotic systems influencing the ecology of the inhabiting fish populations. Water flow can vary between systems, and usually involves a continuum from upstream torrential rapids to deeper, slower flowing lowland areas. The velocity of water can vary within and across systems and is typically based upon rainfall inputs, variability of friction with the bottom or sides of the channel, sinuosity, obstructions and gradient (Allan 1995). Seasonal changes in flow rate also influence growth rates of fish, with specific growth rates being as a response to river flow rate (Smith 1991). Energy use due to metabolic demands constitutes a large proportion of the energy budget of a fish, with energy costs being attributed to basic bodily functions, typically to digestion, absorption, the processing of food and those associated with activity (Jobling 1995). Current velocity has the ability to reduce the potential growth rate of fish, as the energy that is expended while maintaining its position or swimming against a current, is not available for somatic growth (Wootton 1990; Penczak 2007).

1.2.4 – Density dependant factors and growth

Fish populations with high densities have a reduced growth rate as a result of increased competition for available resources, compared with populations of the same species where population densities are lower (Goldspink 1978). Stock numbers are a function of birth rate, recruitment rate and the effects of a mortality rate, which are themselves under the control of density-dependent and density independent factors (King 1995). Density dependant effects include competition for food and space as well as changes in the rate of predation and incidence of parasitism, with decreasing growth rates being as a direct result of increasing population density (Wooton 1990).

Many freshwater habitats support large populations of relatively slow growing fish (Williams 1963; Ylikarjula *et al.* 1999), and as such the growth of the fish is diminished relative to the potential of the species (Burrough and Kennedy 1979). The fish populations of the River Thames at Reading were considered very abundant and as such stunted by Williams (1963). Williams (1967) found that in no British rivers were the roach consistently smaller than those found in the River Thames, and dace were found to exhibit extremely poor growth compared with other rivers. However, a slight improvement was observed in the growth of older individuals, which was attributed to a specialisation of diet. Competition for food resources was also demonstrated between dace and roach in the River Exe Catchment where considerable dietry overlap resulted in a decline in the growth rate of one or both species, suggesting the existence of competition (Cowx 1988).

1.2.5 – The influence of growth on life history traits

The rate at which a fish grows is highly dependant on the environment within which it lives, which in turn has a profound effect upon a number of life history traits. Faster growing fish have the potential to reach sexual maturity at an earlier age, being larger and therefore more fecund than smaller, slower growing fish of the same species. In many cases, YCS appears to be highly influenced by the growth of fish in the first year of life (Mills & Mann, 1985). YCS being determined through the contribution of a number of factors, which ultimately either increases or decreases a fish's chance of survival, such as favorable or unfavorable environmental conditions for that species, predation and or fishing pressure.

Growth rate can also influence YCS via reproductive output; female fecundity in fish is a function of the fish's length (Schemske, 1974). In less than ideal conditions, where, through increased fishing pressure or where environmental conditions are less than ideal an increased growth rate can be observed (Diana, 1983). This increase in growth rate enables the fish to reach sexual maturity in a time period that is shorter than would normally be observed. When these fish then pass through their first spawning event they are larger, having the potential to produce a greater number of offspring, increasing the numbers of young of the year fish and therefore increasing the potential for stronger year classes. Growth rate that are slower than normal, due to less then ideal environmental conditions, can also be advantageous. Slower growing individuals tend to invest a greater portion of their available energy into producing oocytes that are of a higher quality, although fewer in number. The increased energy input per oocyte, gives them a greater chance of survival, and contributing to the YCS of that species in that particular year.

Fast growth rates are not always observed when prevailing conditions are optimal for that species and according to current life-history theory a high, variable or unpredictable juvenile mortality rate will lead to a decreased reproductive effort each year and a long reproductive life span (Steams, 1983). Thus, in iteroparous species, reproductive effort is sacrificed for a long reproductive life in order to increase the chance at least once to be successful in reproducing (Fenchel, 1987; Philippi & Seger, 1989). This bet hedging strategy is expected, provided that there is a causal relationship between reproductive effort and the natural mortality rate of mature individuals (Roff, 1992). Empirical and theoretical studies demonstrate that environmental uncertainty can strongly influence the evolution of life histories. Organisms adapt their life histories to temporally uncertain environments with life-history delays, variable age at maturity, and iteroparity, and they adapt to spatially uncertain environments with dispersal. Such strategies were called "spreading of risk" by den Boer (1968), "escape in time and space" by Janzen (1971), and "bet hedging" by Slatkin (1974). Distributing reproduction in time has been visited by many studies since Cole (1954) coined the terms "semelparity" and "iteroparity" as he posed the paradox that iteroparity should not evolve in a constant environment. Many vertebrate species exhibit both variable age at maturity and iteroparity, and most populations also experience density-dependent population regulation (Wilbur and Rudolf 2006).

1.3 – Age and growth of fish

1.3.1 - Age determination

Ageing of fish is the basis for the derivation of growth rates, mortality rates and production, which ranks it among the most influential of biological tools (Campana 2001), as it is integral to the formulation of many fisheries management strategies (Britton *et al.* 2004a). Several calcified structures in fish produce features that can be used to determine age and hence growth increments (Campana 2001). The use of calcified structures used in the determination of age in fish include: scales (Cragg-Hine and Jones 1969; Mann 1971, 1973; Mathews and Williams 1972; Gee 1978; Linfield 1979; Frost and Kipling 1980; Hickley and Bailey 1982: Cowx 1983, 1988; Lorenzoni *et al.* 2002); otoliths (Geffen 1985; Holmgren 1996: Panfili and Tomás 2001; Xie *et al.* 2005); vertebrae (Wintner 1999; MacNeil and Campana 2002); fin rays and spines (Metcalf and Swearer 2005); cleithra (Laine and Momot 1991; Johal *et al.* 2000) and opercula (Guma'a *et al.* 1984), with scales being the most popular means of age determination from freshwater populations throughout England and Wales (Environment Agency 2007).

The determination of age from scales is achieved by counting the number of annuli present on the scales based on the assumption that annulus formation occurs once per year (Graham 1928). Check formation has been described as an annual occurrence and the method validated by a number of authors (Mathews and Williams 1972; Fukuwaka and Kaeriyama 1997). Cragg-Hine and Jones (1969) examined the seasonal growth pattern of dace scales from Willow Brook and concluded there was a definite annual cycle of scale growth in young dace, whereby checks were laid down during May and June, after which scale growth was rapid until mid-autumn when scale growth almost ceased until the following spring. Validation of scale reading from the scales of roach, dace and bleak, *Alburnus alburnus* (L.), was achieved by Williams (1967). Examining scales from monthly samples of fish from the River Thames, it was concluded that check formation was an annular event with April to June, April to May and June to July being the time of check formation in roach, bleak and dace, respectively.

Scales are widely used to determine the age and growth rate of fish, their use, however, is complicated by the occurrence of false checks (Ottaway and Simkiss 1977) and is prone to errors from the subjective interpretation of the scales features (Mann and Steinmetz 1985) or from the readability of the hard structure used (Britton *et al.* 2004b). False checks form on the scale because of a general temporary cessation in growth rather than as part of the annual growth cycle, and have been attributed to the effects of handling (Coble 1970; Bilton 1974), low oxygen levels occurring from elevated temperatures caused by dry, hot weather (Hofstede 1974), starvation and changes in food supply (Bhatia 1931) and light and temperature changes (Ottoway and Simkiss 1977). The effects of misinterpretation in the determination of a fish population's age structure can, and has been shown to, have serious repercussions for management decision making. For example the *Sebastes* spp fisheries of eastern and western Canada, where an underestimation of the age structure led to the fishery being over-fished (Campana 2001).

To further complicate the ageing process, the first annuli to be laid down on the scale may not be that of the first year of life. Spawning strategies adopted by fish species are a combination of a range of adaptive traits to maximize the number of offspring (Mills 1991). Species that adopt multiple spawning strategies, such as chub, bleak, bream (*Abramis brama* (L.)), gudgeon (*Gobio gobio* (L.)) and minnow (*Phoxinus phoxinus* (L.)), are more likely to have a greater size range of young at the end of the first year, since the later progeny have less time to grow before the end of the growing season (Nunn *et al.* 2007c). Smaller progeny may not lay down an annulus because they are of a size at which scale squamation commences, identified for chub as 15.9 mm (Economou *et al.* 1991). Fish not yet or only just reaching a length at which scale squamation begins, have been shown to persist through the winter period, (Nunn *et al.* 2007c) in the Yorkshire Ouse (chub 16 mm) and River Trent (chub 18 mm). A potential for the misinterpretation of these scales therefore exists, as the first annuli may be very small or missing. However, as no guidance currently exists for determining the exact year class of these fish, scales have to be read to the conventional scale reading methodology.

1.3.2 - Back-calculation of fish length from hard structures

Back-calculation models are important tools in fisheries research and management, which infer historic lengths and growth rates from the bony structures of fish (Klumb *et al.* 1999a). Specifically, when the dimensions of one or more marks in some hard part of the fish, together with its current body length, are used to estimate the length of that fish at the time of formation of each of the marks. The often strong relationship between body length and scale radius leaves little doubt that the dimensions of marks on the scale, contain some information on the growth history of that fish (Klumb *et al.* 1999a). However, this still leaves the question of how precise is the information and which back-calculation procedure best extracts it? (Francis 1990).

Many different bony structures have been used to determine the ages of fish for many years, and several back-calculation models have been developed (Johal *et al.* 2001).

These fall into one of two categories, the proportional methods and those based on regression techniques (Francis 1990). The first technique proposed was the directly proportional method of Dahl-Lea (Dahl 1907; Lea 1910), based on investigations on herring, it was formed around the hypothesis that "the scale grows in exact proportion to the total length of the individual" (Francis 1990). This hypothesis assumes direct proportionality between the fish length and scale radius.

This was followed by the Fraser-Lee method, also known as the intercept corrected direct proportional method (Johal *et al.* 2001). After examining plots of scale radius against fish length from a number of species, Lee (1920) concluded that the relationship was not a straight line passing through the origin as suggested by Lea (1910). From this, the hypothesis that "the growth increment of the scale is on average a constant proportion of the growth increment of the fish" was formulated, and instead of passing through the origin, the line must pass through the point where scale radius equals 0 and the length of the fish is a constant (c) (Francis 1990). Francis (1990) described c as the length of the fish at the time of scale formation and stated that it is the current practice of many authors to set the constant (c) value as the length intercept of the regression line, and not from observations of juvenile fish. He recognised that it is the derivation of the constant (c) that is of utmost importance, and stated this subject was the focus of many of the associated literature after this time.

1.3.3 – Standard growth curve

Hickley and Dexter (1979) devised a method, whereby the growth in length of fish in the UK, could be assigned a value, to which comparisons of fish from differing locations or populations at the same geographic location at different sampling dates could be made. Comparisons of the growth in length of fish is achieved by a growth index, calculated from a standard growth curve, where slow, normal and fast growth gives indices less than, equal to or greater than 100 respectively. Using values gained from published data from various locations around the British Isles, Hickley and Dexter (1979) derived a growth curve for a number of species that reflected the mean lengths at age. Initially four species were considered, bream *Abramis brama* (L.), roach, chub and dace. The number of species was later expanded to include pike *Esox lucius* (L.) (Hickley and Sutton, 1984). Standard growth curves for barbel (*Barbus barbus* (L.)) and perch were later derived by Cowx (2001) and growth curves later updated for a proportion of these species by Britton (2007).

1.3.4 – Year class strength (YCS)

Year class strength (YCS) is an important index in the management of inland fisheries, which demonstrates the dominance of particular cohorts within a fish population and the possible influences they can have on the fishery at the present time or in the future (Cowx and Frear 2004). A number of environmental influences have been attributed to the formation of year class strength in fish, and has been the attention of many authors. The determination of year class strength in relation to such factors as temperature (Summerfelt and Shirley 1978; Sarvala and Helminen 1996; Tolonen *et al.* 2003), temperature and food availability (Mann 1997), water discharge rate (Bonvechio and Allen 2005; Rand *et al.* 2006), density dependant processes (Grenouillet *et al.* 2001) position of the Gulf stream (Nunn *et al.* 2003; Britton *et al.* 2004b), and in relation to predation pressure (Mooij *et al.* 1996) have all been demonstrated.

Temperature has been positively related to the formation of strong year classes in a number of species (Summerfelt and Shirley 1978; Tolonen *et al.* 2003). Aprahamian and Aprahamian (2001) found July temperature to be positively related to year class strength and explained the greatest variance for year class strength in twaite shad, *Alosa fallax fallax* (Lacépède) in the River Severn. Temperatures below 16^0C at this time of year, acting through physiological responses controlled the population by affecting the hatching success and/or growth rates, causing mortality of eggs and poor condition. Difficulty in emergence from the egg was also demonstrated at temperatures below 18^0C (Aprahamian and Aprahamian 2001).

Water temperature acting through the growth rate of fish can also play an important role in the formation of strong year classes. High survival rates of roach fry have been related to rapid growth rates associated with warmer summer temperatures (Mann 1973). Roach that grew rapidly were less susceptible to predation by small piscivores such as perch and pike, increasing the number of surviving fish. Survival of young cyprinid fishes through the first year of life is dependant upon their growth during the first summer of life (Cowx 2000). This view was supported by data on the growth of juvenile fish within the Yorkshire Ouse, where enhanced growth rates relating to warm summers translated into the formation of strong year classes (Cowx 2000).

Nunn *et al.* (2003), however, found stronger relations between river discharge rate and recruitment success than they did for water temperature. Negative relationships between water temperature and discharge rate were identified, with reduced temperatures being related to periods of high discharge and vice versa. The effects of elevated discharge at critical periods during early life history were described as being a direct cause of high mortality rates, or by a reduction in the growth rate due to reduced temperatures. Temperature was recognised as determining the potential year class strength, although discharge determines the realised year class strength. Discharge velocity rate at critical periods was also demonstrated by Daufresne *et al.* (2005) when examining the downstream displacement of brown trout, *Salmo trutta* (L.) in experimental channels. Young-of-year brown trout were highly sensitive to velocity changes during the first few days after emergence. An average displacement rate of 80% was recorded in all of the experimental channels. In the channels where low velocities occurred, displacement timing was between 5 and 6 days, which was accelerated in channels where increased flow velocity occurred. The importance of discharge was also shown by Smith *et al.* (2005) while examining smallmouth bass (*Micropterus dolomeiu* Lacepède 1802) recruitment. They suggested mean June flows were a reasonable predictor of abundance at the end of the year, with the strongest year classes being formed in years where flow was moderate in the period during and immediately after spawning.

1.3.5 - Environmental influences – position of the Gulf Stream

The ocean is increasingly seen as a vital component of the Earth's climate, as exchanges of large quantities of heat, water, gases, particles and momentum within the atmosphere play an important role in the global redistribution of heat from the tropics to polar regions (Brigg *et al.* 2003). Concentrations of nitrate recorded in Irish lakes during the winter were related to a sequence of factors initiated by the latitudinal position of the Gulf Stream (Jennings and Allott 2006). A negative relationship between wind speeds, cloud cover and precipitation in relation to Gulf Stream position was described, with lower values recorded the more northerly the position of the Gulf Stream's North Wall. This was positively related to an increase in maximum daily air temperature (Jennings and Allott 2006).

Summer weather patterns observed in England are strongly influenced by the position of the North Wall of the Gulf Stream (Willis *et al.* 1995). If large scale global weather patterns are impacting upon a population, then any change in the position of the Gulf Stream should manifest itself in terms of a change in fish recruitment, with higher recruitment observed the further north the North Wall of the Gulf Stream is positioned (Aprahamian and Aprahamian 2001), which coincides with warmer and drier than average years (Nunn *et al.* 2003). Positive relationships were demonstrated between year class strength and the position of the North Wall of the Gulf Stream. Nunn *et al.* (2003) suggested a relation between year class strengths of roach, dace and chub and the mean annual position of the North Wall of the Gulf Stream, where increased year class strength estimates were found to coincide with northerly shifts in the North Wall.

1.4 - Objectives of this study

A number of methods have been developed to calculate the length at age of fish from measurements of annular marks on a number of bony structures in fish. These methods have been validated by various authors using data gained from mark recapture of pond studies where the data were paired to the same fish. To date, however, no study has demonstrated which of the back-calculation techniques best describes data gained from routine surveying where paired data from specific individual fish are not always available. The most appropriate method of back-calculation for general use in the determination of length at age from fisheries data describing age data collected during routine fisheries surveys conducted throughout England and Wales will be sought, using data derived during these surveys.

The use of standard growth indices has been used as a comparative tool for length at age data since their inception. These growth standards were based on limited data that may now be outdated due to changes in the growth rates of a number of species that have occurred over the ensuing years in relation to changing population characteristics, generally improving water quality (such as reduced serious pollution incidents, decreased concentrations of phosphates (P) and nitrate (NO_3)) and physical habitat. These standards will be updated for as many of the species that the data allow and tested for variance from the existing standards.

Zonal patterns of fish growth have been described at both the catchment and national levels for many species in many countries. The influence environmental parameters have at the national level, however, has not been examined in England and Wales. Abiotic and biotic data from rivers throughout England and Wales will be used to demonstrate the factors influencing the pattern of growth of roach, dace and chub with respect to longitudinal variation along a rivers course, but also to investigate the patterns of growth observed for these species at the national level.

Many factors combine to determine year class strength in fish. These include the timing of spawning and hatching events in relation to critical periods when increased flows and reduced thermal regimes lead to the displacement of eggs and larvae thus reducing the potential for strong year classes. To test the hypothesis that high flow events at critical periods in time affect YCS, flow data from a number of rivers at specific times will be tested along side year class strength estimates of roach, dace and chub to determine critical periods affecting year class strength. The position of the North Wall of the Gulf Stream has been shown to influence the climate of the British Isles with northerly shifts producing a warmer British climate and southerly shifts producing a cooler climate. To determine any affect on year class strengths of fish populations in rivers throughout England and Wales, year class strengths of roach, dace and chub will be tested against the mean annual position of the North Wall of the Gulf.

1.5 – Structure of thesis

Chapter Two - Describes the methods for determining the most appropriate method of back-calculation of fish lengths gained from fisheries data collected from throughout England and Wales. A number of back-calculation methods were chosen from the literature and used to compare back-calculated mean length at age data to observed mean lengths from earlier surveys conducted in the same area. Mean length at age data was then tested to determine how each method describes the data in relation to an observed mean value, and the most appropriate method chosen as the method that most accurately and consistently described the data.

Chapter Three – Standard growth curves for a number of species found in rivers throughout England and Wales were derived and a comparison made between these standard growth curves and those previously published. An investigation into the relationship between asymptotic length and the growth coefficient was made and phenotypic plasticity discussed in relation to these parameters.

Chapter Four – The role of such factors as latitudinal position and flow regime plays in influencing growth rates, length at age and longevity is examined. Statistical analysis is used to show how biotic and abiotic variables change in relation to the position of the site along a longitudinal gradient. Canonical correspondence analysis and multiple regression is used to show the distribution of growth parameters of roach, dace and chub from rivers throughout England and Wales and the factors that most influence this distribution.

Chapter Five – The influence of prevailing climate and flow regime play in influencing year class strengths of roach, dace and chub from rivers throughout England and Wales is examined. Specific emphasis is given to hydraulic regimes and the role the Gulf Stream in structuring the British climate and how these influence fish growth, especially in the first year of life, which ultimately influences the ability of the young of the year fish to overwinter and contribute to their year class strength.

Chapter Six – The knowledge gained from the previous chapters is integrated and recommendations made for future work.

CHAPTER TWO

ASSESSMENT OF THE EFFICACY OF BACK-CALCULATION METHODS FOR DETERMINING LENGTHS FOR AGE DATA IN RIVER FISHES IN ENGLAND AND WALES

2.1 - INTRODUCTION

Back-calculation of fish length has been widely used to increase the number of observations in length-at-age data or to estimate lengths at ages, and is based on the assumption that somatic growth in fish is proportional to the growth of its bony structures (Horpilla and Nyberg 1999). Given the relationship between body length and scale radius, there can be little doubt that characteristic marks on scales contain information on the growth history of fish, the question is how precise is the information and which method best extracts it? (Francis 1990).

Dahl and Lea (1910) proposed the first model assuming a direct proportional relationship between body and scale growth (Klumb *et al.* 1999a; Klumb *et al.* 1999b). Whitney and Carlander, (1956) recognised that this method gives an approximation, since the body scale regression rarely, if ever, has a zero intercept. Fraser (1916) and Lee (1920), proposed the need for a correction to account for body growth before scale formation (Klumb *et al.* 1999a). The current practice of most authors is to set the correction as the intercept of the regression of fish length against scale radius (Francis 1990).

Hile (1941) was the first to give a mathematical basis to the derivation of the constant value. Francis (1990) explained that in its linear form, the equation proposed by Hile, is the same as that of the Fraser-Lee equation, except that the constant value, c, is replaced by $-(a/b)$, the length intercept (where a is the intercept and b is the slope, determined from the regression of fish scale radius on fish length). The derivation of this constant in back-calculation formulae is important, and is described as the length of the fish at the time of scale formation (Smedstad and Holm 1996), loosely representing the beginning of the juvenile period when metamorphosis has come to an end and scales appear on the body (Urho 2002).

Many authors have validated the use of calcified structures as a technique for the derivation of age in fish (Cragg-Hine and Jones 1969; Mathews and Williams 1972; Hubert *et al.* 1987; Fukuwaka and Kaeriyama 1997). Francis (1990) discussed the validation of back-calculation applications and used several data sets to argue that using different back calculation methods can result in large differences in the estimated lengths at age. Literature on the subject of determining length at age data from fish scales uses data from laboratory reared fish (Holmgren 1996) or from mark recapture methods (Smedstad and Holm 1996; Panfili and Tomás 2000). These techniques use paired data from the same fish to test various back-calculation methods to a known length, which is determined on the hard parts of the fish by marking them with chemical dyes such as oxytetracycline. In this study, scales were taken from wild populations of fish from rivers throughout England as part of the Environment Agency's core monitoring programme and from various research projects. Therefore, unlike the laboratory and mark recapture methods, the scale data are not paired to the same animal, but instead used population data of fish taken from the same location at different times. Therefore, the possibility exists that the population structure may have changed in the interim period between the initial and subsequent surveys due to such factors as immigration, emigration and the effect of mortality. The aim of the present chapter is to test a number of back-calculation methods with standard data derived from scale reading to determine the most accurate method for use on data from fisheries surveys and to elucidate sources of error associated with each method.

2.2 – METHODS AND MATERIALS

2.2.1 – Determination of an appropriate back-calculation method

To determine the most appropriate method of back-calculation, a number of criteria were formulated to which survey data must conform to gain robust observed and back-calculated mean length at age estimates for comparison. First, the survey data must have a set of historic data, from which observed mean lengths at age can be extracted, containing specific cohorts with appropriate numbers of individuals within those cohorts to achieve robust mean length at age estimates, appropriate numbers being that which produces estimators that are not unduly affected by small departures from modal assumptions. Second, the surveys from which mean length at age estimates were to be extracted must be conducted at a time of year when the fish population had completed its seasonal growth increment. This ensures the length per individual represents the size of that year class at the time when the annulus is laid down. Mann (1973, 1974) described the end of the growing season in the rivers Stour and Frome as being between October and March for dace and December to April for roach. A number of data sets were available for analysis based on these criteria (Table 2.1).

Table 2.1 – Site, water body, source of data, species and survey dates for evaluation of back-calculation methodologies.

Site (data source)	Species	Historical Survey dates (for length at age data)	Subsequent Surveys (to be back-calculated)
River Exe @ Exwick (Cowx)	dace	December 1974	1975
River Exe @ Trews weir (Cowx)	roach	1976,	1977
Anglian River Stour (EA)	dace	1988,	1991, 1994, 1997, 2000
River Colne sites combined (EA)	chub	April 1984	June-July 87, 1990, Aug 1993, April-May 1996 and 1999
Leven Canal, Hull (HIFI)	bream, roach	December 1998,	December 1999, May 2000
Warwickshire Avon @ Twyford (HIFI)	roach	November 2003, December 2003, January 2004	October 2004
River Trent @ Holme Pierepoint (HPP) (HIFI)	roach	October 1995	June 1997, October 1997, January 1998, June 1998
River Trent @ Trent Bridge (HIFI)	roach	October 1995	March 1996, January 1998, March 1998

2.2.2 – Determination of age from scale reading

Scale samples were derived from surveys conducted around England and Wales by the Environment Agency and supplied through the National Fisheries Laboratory between April 2003 and October 2006, and data sets from surveys conducted by Hull International Fisheries Institute (H.I.F.I.) or Cowx (personal data). Scales from individual fish were supplied in small envelopes inscribed with information, including location of the sampled area (e.g. which river, still-water), sampling date, species and length of the fish (fork length mm), and in some instances site specific data (Figure 2.1).

Scale packets from fisheries surveys were first sorted into the appropriate number of species and number of scales to be read according to the Environment Agency's, Agency Management Strategy (AMS), information which was included in an accompanying survey submission sheet. In most cases, as per AMS, three scale packets from each 10mm length class for each species were randomly selected for reading under a Bell and Howell (ABR-VIII) microfiche projector (20x magnification). For the purpose of this chapter however, the remaining scales from each survey were read to allow a clearer view of the age structure of the population and to provide sufficient numbers for the calculation of robust mean lengths at age.

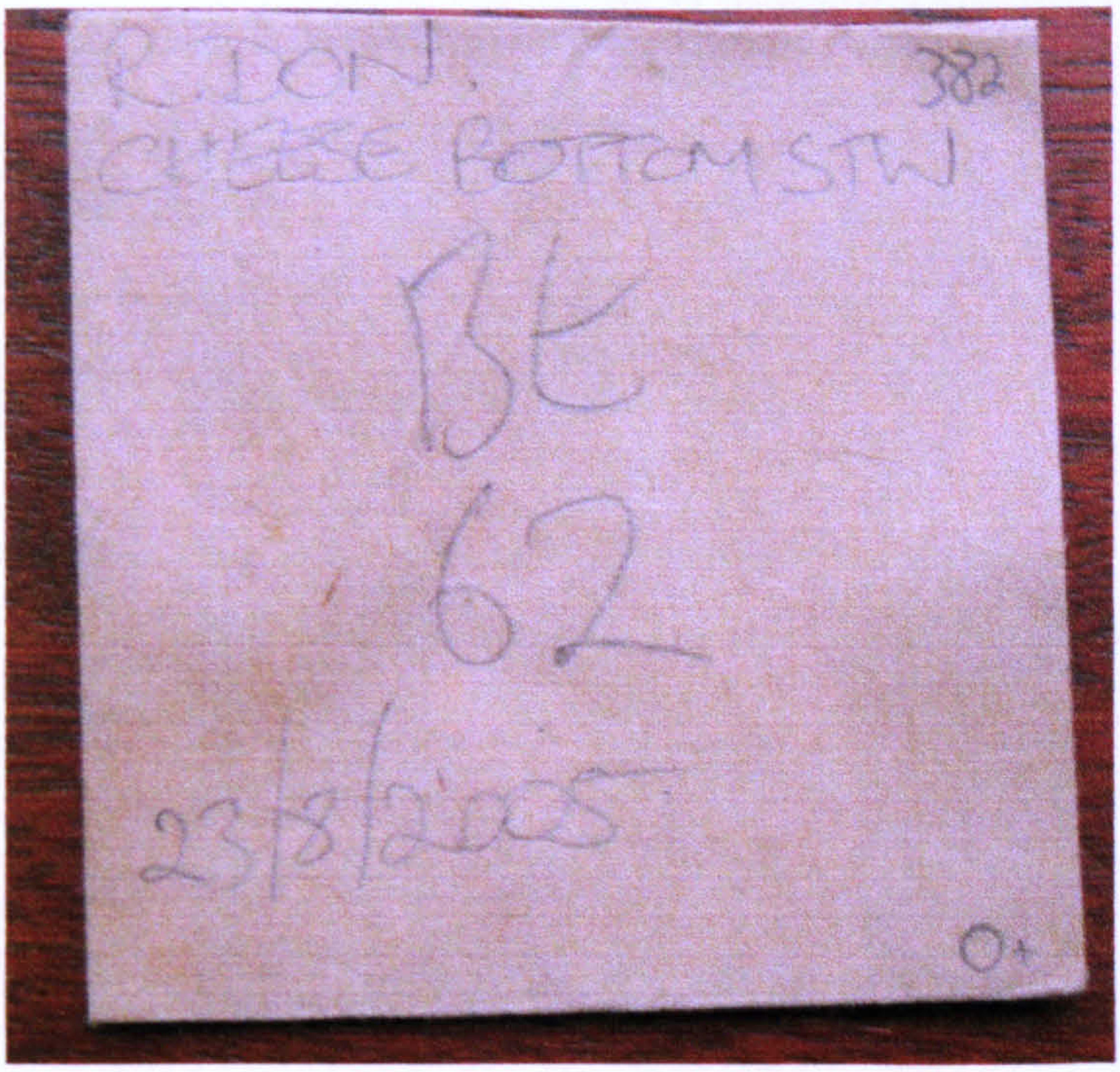


Figure 2.1 - Example of scale packet with all information provided.

All scale samples were subjected to a quality control procedure, whereby a percentage of the scales from each survey (usually 10%) were read by the primary reader, and the age, species and length of the fish recorded. A second reader then read the same scales independently and again a record of the age of each fish was made. A comparison of the findings was then made. If any disagreements as to the age of a fish occurred, the scales were again read by both parties to discuss their findings and allow an agreement as to the age of the fish. As the reading of fish scales was performed under contract from the Environment Agency, then contractually there had to be a greater than 80% agreement upon the ages of the fish. If there was less than 80%

agreement, an additional number, equivalent to the number of non agreements, was read by both parties until an 80% agreement was reached. However to increase the accuracy of the primary reader, additional scales were read by both parties until a 100% agreement in the ages of fish being examined was achieved.

The interpretation of features found on fish scales is very subjective and, as such, prone to errors (Mann and Steinmetz 1985). When viewed, fish scales consist of a number of concentric rings, which are normally laid down in a regular sequence. This regular pattern is broken, when irregular, closely spaced rings are laid down on an annual basis (Cragg-Hine and Jones 1969). These features on fish scales are known as annuli and are characterised by a region of cutting over of previously laid down rings in the latero-posterior region of the scale (Figure 2.2). The formation of annuli result from a slowing in the growth of the fish usually attributed to, in temperate regions, the reduction in temperature and the slowing or cessation of feeding and the associated metabolic processes during winter (Cragg-Hine and Jones 1969).

The use of scales to determine age is complicated by the occurrence of false checks (Ottaway and Simkiss 1977) (Figure 2.3) or from the readability of the hard structure used (Britton *et al.* 2004) (Figure 2.4). False checks form on the scale because of a general temporary cessation in growth rather than as part of the annual growth cycle, and have been attributed to the effects of handling (Coble 1970; Bilton 1974), low oxygen levels due to elevated temperatures caused by dry, hot weather (Hofstede 1974), starvation and changes in food supply (Bhatia 1931) and light and temperature changes (Ottoway and Simkiss 1977). Difficulty in reading scales from older fish also occurs when the growth rate slows to an extent that annuli are laid down in close proximity to each other (Musk *et al.* 2006) and the erosion of one annuli, as they are so close, can effectively remove the whole or a portion of the previous annular marks (Figure 2.4). When eroded scales, often encountered when reading scales from larger fish, were found the procedure to deal with them was to firstly seek another scale from the same fish, not always supplied, and if no alternative was found the scales and all information from that fish were discarded and, where possible, replaced by the scales and information from a different fish.

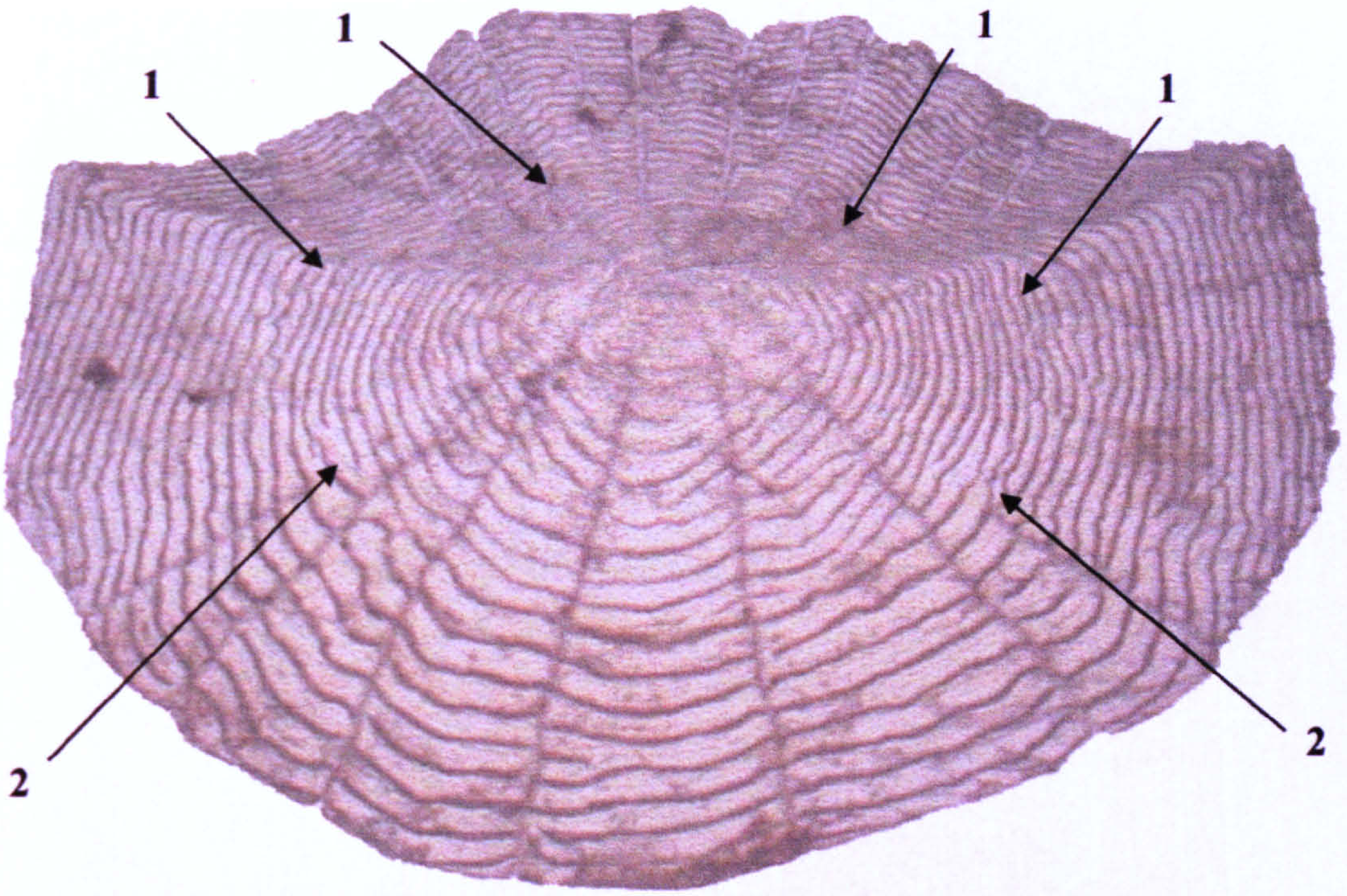


Figure 2.2 – Scale of a dace from the R. Exe at Fortesque, showing how annuli can be followed around the entire scale (1), and the region of cutting over (2).

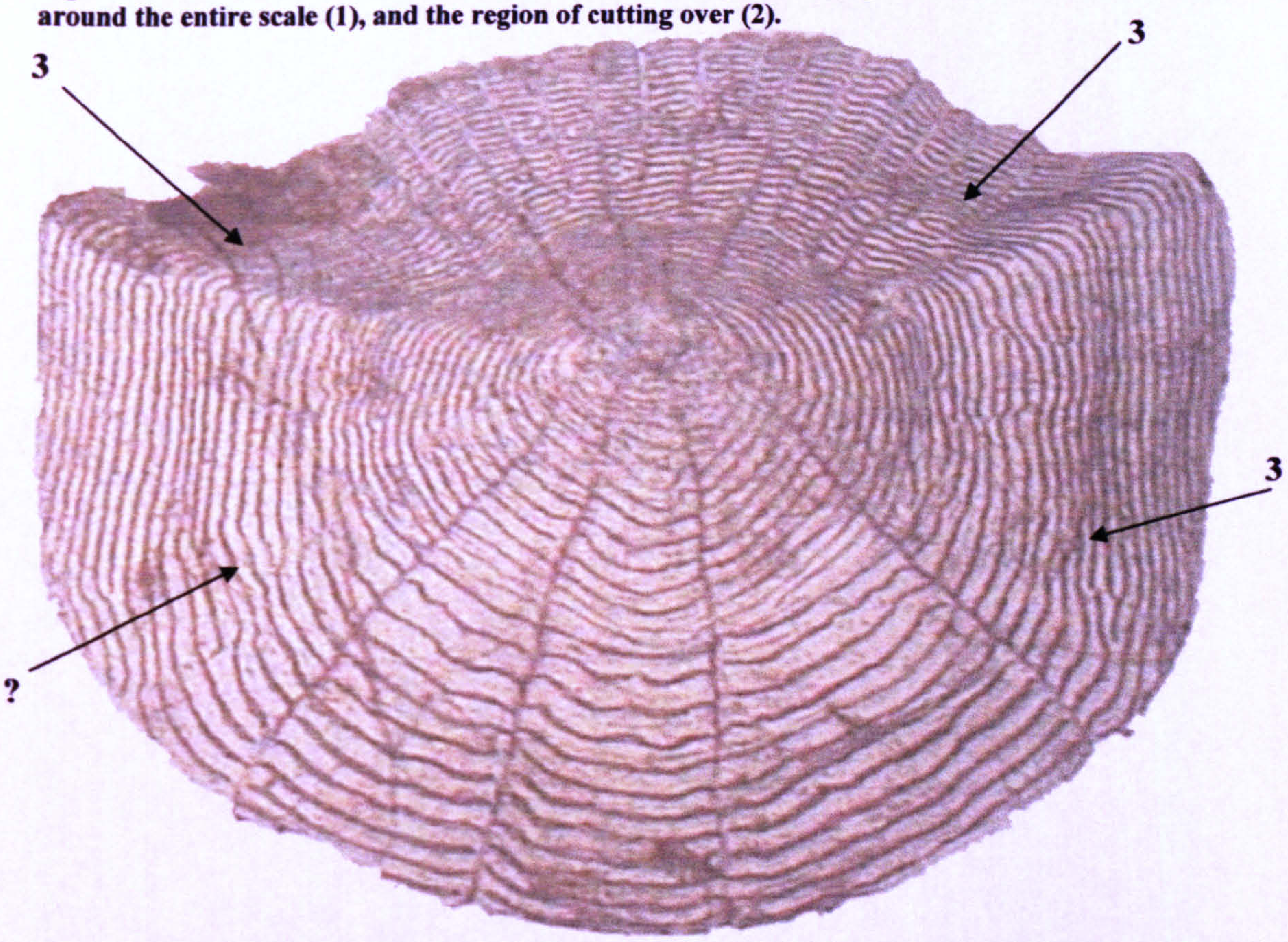


Figure 2.3 – Scale of a dace from the R. Exe at Fortesque, showing the position of a false check (3), with little cutting over on the left hand side of the scale (?).

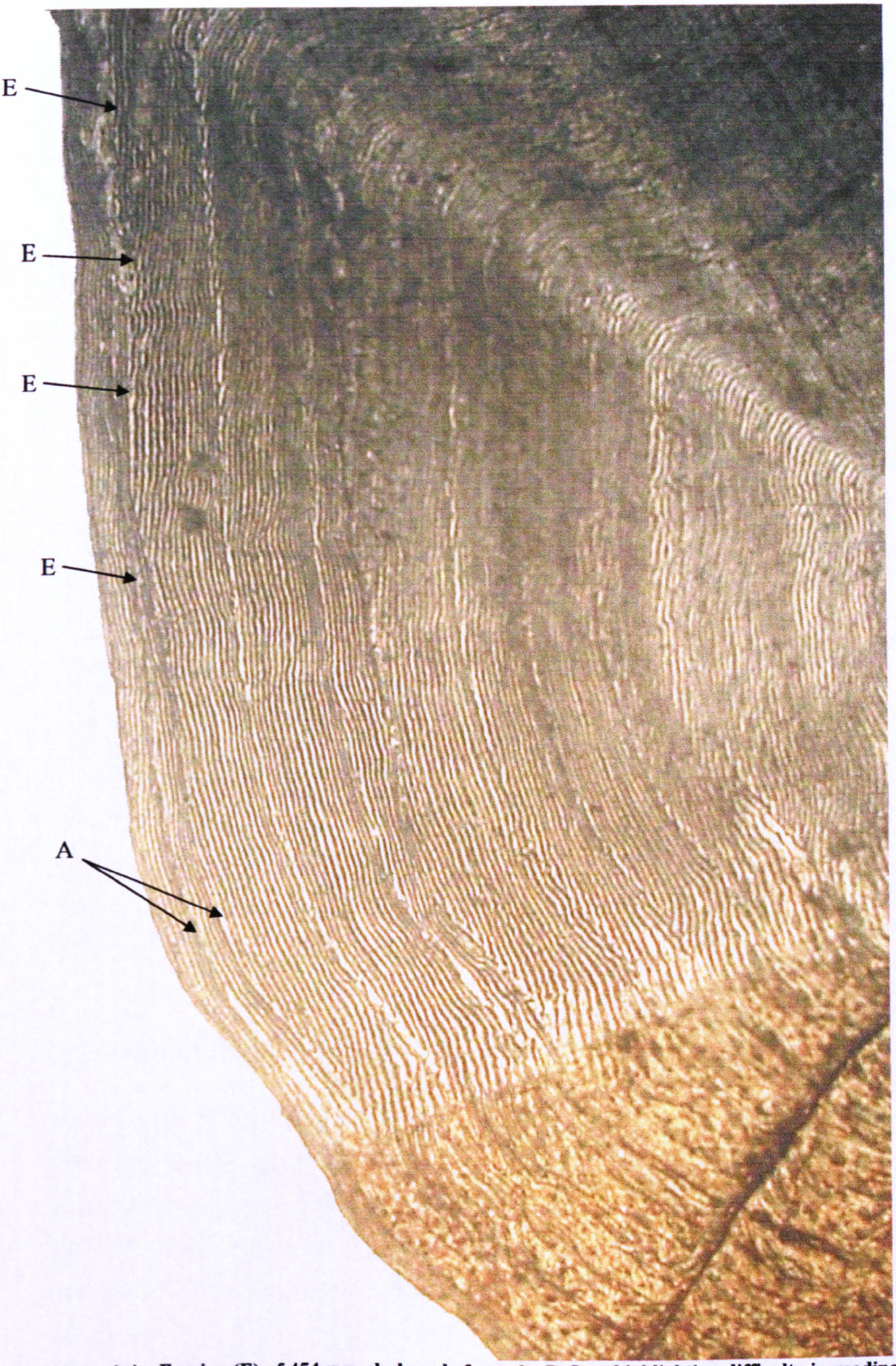


Figure 2.4 – Erosion (E) of 454 mm chub scale from the R. Lee, highlighting difficulty in reading annuli (A) of older chub.

The remaining scales from each survey were then read to determine the population's age structure. Measurements were taken from the focus of the scale to each annulus and the total scale radius (Figure 2.5), and a record made within an appropriate Excel spreadsheet (Appendix 1). Additional information provided on the submission sheet and the individual scale packets, which included the location, species, fork length (mm), year class and age in years, and where appropriate, site specific details were recorded in the spreadsheet.

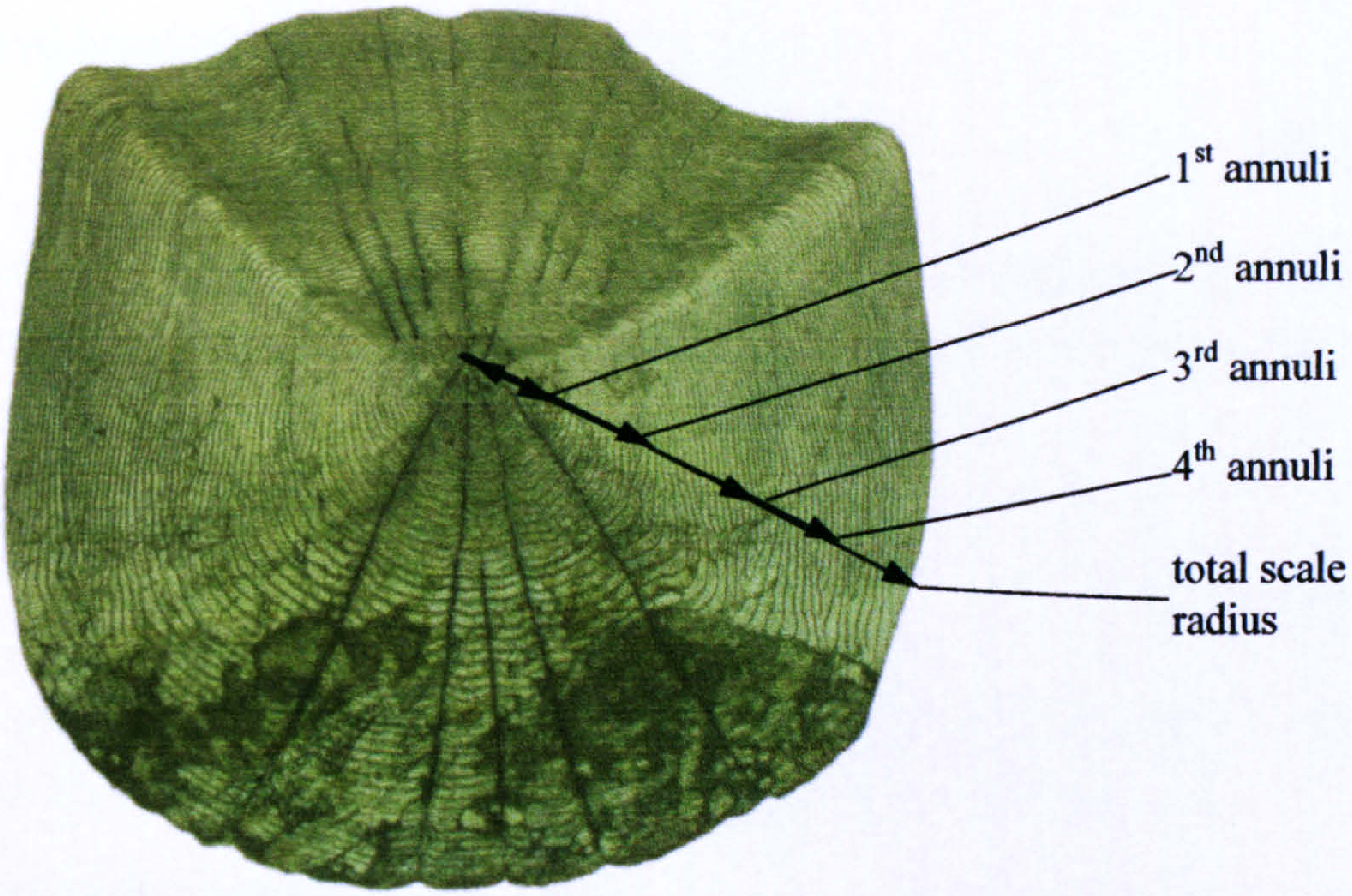


Figure 2.5 – Example of a dace scale from the R. Mole, indicating the position of four annular checks and the total scale radius.

2.2.3 – Relationship between fish length and scale size

Growth rings on bones and scales are used to back-calculate lengths of fish at age to provide information on growth histories. Virtually all back-calculation procedures are based on the assumption of proportionality between the size of the fish and the size of the bony structure in question (Campana and Jones 1992). However, Whitney and Carlander (1956) argued that it is doubtful that the body-scale regression is ever strictly linear, and that caution should be exercised when fitting any regression to the sample. To test the relationship between fish length and scale size, a number of regressions were made of scale radius on fish length from the surveyed populations identified in section 2.2.1 using curve estimation analysis in SPSS (V14) and the various regression model forms available. The regression models used for this test were; linear, logarithmic, inverse, quadratic, cubic, power, compound, S, logistic, growth and exponential.

2.2.4 – Methods of back-calculation

To determine the most appropriate model for back-calculation of fish length from routine fisheries survey data, a number of methods were chosen;

The directly proportional Dahl-Lea (1910) model:

$$L_i = (S_i/S_c)\, L_c \qquad \text{Equation 2.1}$$

where L_i and S_i are the length and scale radius at the formation of the $_i$th scale mark respectively, and L_c and S_c are the length and scale radius of the fish at the time of capture respectively.

The Fraser-Lee (1920) model,

$$L_i = c + (L_c - c)(S_i/S_c) \qquad \text{Equation 2.2}$$

where c is a constant set as the L intercept of the regression of scale radius upon length, the length of the fish at which scale formation commences.

The method proposed by Hile (1941),

$$L_i = -(a/b) + (L_c + a/b)(S_i/S_c) \qquad \text{Equation 2.3}$$

where a and b are the intercept and the gradient of the regression of scale radius on length respectively.

Whitney and Carlander's body proportional hypothesis (1956), which in its linear form, is expressed as

$$L_i = [(c + dS_i) / (c + dS_c)]L_c \qquad \text{Equation 2.4}$$

where c and d are the y axis intercept and slope of the regression of fish length on scale radius respectively.

The final method chosen was that proposed by Ricker (1992) where the recommended use of geometric mean regression is used to determine the length intercept for use in another back-calculation method. Geometric means is the antilog of the mean of the logged data (Dytham 2005). This method involves the transformation of the fish length and total scale radius measurements ($\log_{10}$) and a mean value taken for each age class. The mean values are then transformed again (power^{10}) and the values for each age class used to plot a linear regression, the intercept (a) and slope (b) of which are used to calculate the length intercept value to be used with the Hile model of back-calculation (equation 2.3).

2.2.5 – Calculation of length at age data using all back-calculation methods

A number of templates were constructed in Excel spreadsheets to compare observed mean lengths at age from historic observed data against mean lengths at age derived from back-calculated data. Observed lengths at age for each year class were first sorted from the observed data sets, as were the data to be back-calculated. Templates for each back-calculation method contained links to the data to be back-calculated and performed the appropriate calculation. With the Dahl-Lea method (equation 2.1) no further modification was made to the data, with the exception of the calculation being performed. Regressions of length on scale radius were performed on the data for the Whitney-Carlander method, to gain estimates of c and d for use in equation 2.4. Regressions of scale radius on length were performed for both the Fraser-Lee and Hile methods to gain estimates of a and b for use in equation 2.3. The Ricker method was achieved as outlined in section 2.2.4.

2.2.6 – Comparison of observed and back-calculated mean length at age using ANOVA and Tukey's post hoc analysis

Where appropriate numbers of fish per year class where identified, comparisons were made between the mean lengths at age from specific year classes at specific ages from the observed and back-calculated data sets. For example, from the historic data set of roach from the River Trent at Holme Pierepoint, the observed lengths of the 1995 year class at age 1 were used to estimate an observed mean length at age 1. From the subsequent survey conducted during 1998 the first annular increment and total scale radius was used to back-calculate a mean length at age 1 for the 1995 year class. Mean values for observed lengths and the variance around the mean value were compared against mean values from each of the back-calculation methods using

ANOVA in SPSS (ver. 14) under the hypothesis that back-calculated mean lengths and the variance around the mean lengths are the same as the observed mean length at age.

Back-calculated mean lengths at age were then compared against the respective observed mean lengths at age for significant differences using Tukey's HSD test. If no significant differences were identified between the observed and back-calculated mean length at age values, all mean values were grouped into a single subset. If significant differences were identified between the observed and any of the back-calculated mean lengths at age, they were assigned to different subsets, indicating statistically significant differences.

2.3 – RESULTS

2.3.1 – Scale radius-fish length relationship

Robust relationships between fish length and scale radius were found in all cases ($r^2>0.840$). In the majority of cases the linear relationship was the strongest, (an example of best fit can be seen in Figure 2.5 for roach from the River Don). The exception was the Leven Canal roach where a cubic relationship was fractionally stronger ($r^2=0.845$); a result similar to that of Horpilla and Nyberg (1999) who demonstrated both linear and non-linear relationships occur in roach populations. However, as the cubic relationship was only fractionally stronger than the linear relationship ($r^2=0.843$), all further regressions of fish length against scale radius in this study were considered to be linear.

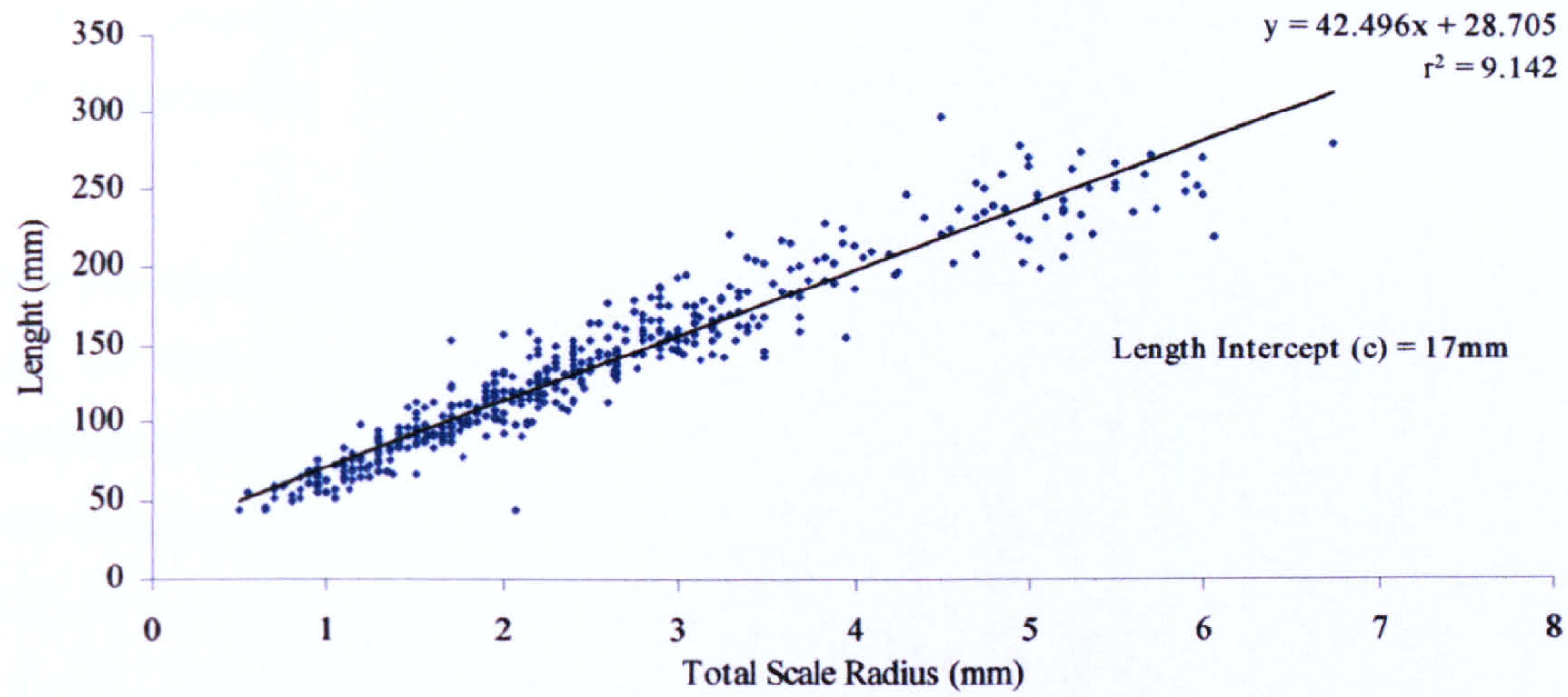


Figure 2.5 – Relationship between total scale radius and length of roach from the River Don.

2.3.2 – Length intercept values (c) from regression analysis in the back-calculation of mean length at age

Variation existed between the length intercept (c) for each regression calculated from the various back-calculation methods (Table 2.2). The Whitney-Carlander method almost consistently returned the largest value of c, with the exception of roach from the R. Trent at Holme Pierepoint (1997 data set). The Ricker method recorded a number of very low c values for bream in the Leven Canal, dace in the R. Exe at Exwick and roach in the R. Exe at Trews weir. Negative values were recorded for both the Fraser-Lee and Hile methods, for dace in the R. Exe at Exwick.

Table 2.2 – Constant Values (c), calculated from the various methods used to compare back-calculated length at age (all measurements in mm).

	Whitney-Carlander	Ricker	Fraser-Lee	Hile
Leven Canal roach 2002 data set	40	34	26	26
Leven Canal bream 2002 data set	38	1	9	9
R. Trent Holme Pierepoint roach 1997 data set	27	41	42	42
R. Trent Holme Pierepoint roach 1998 data set	42	32	34	34
R. Colne chub 1999 data set	37	33	13	13
R Exe Exwick dace 1975 data set	11	0	-3	-3
R. Exe Trews weir roach 1977 data set	40	0	25	25
R. Trent, Trent Bridge roach 1998 data set	52	34	44	44
Warwickshire Avon Twyford Farm roach 2004 data set	15	10	13	13

2.3.3 – Comparison between observed and back-calculated mean length at age (MLA) estimates

Fifty year classes had sufficient data to produce robust mean length at age estimates in both the observed and back-calculated data sets. ANOVA and Tukey's test found significant differences between the observed mean length at age and at least one of the back-calculated mean length at age estimates in 19 of these data sets ($P<0.05$; Tables 2.3-2.6).

All back-calculated MLA estimates of the 1994 year class of chub from the R. Colne at age 2 were significantly different from the observed MLA (Tukey's test $P<0.05$; Table 2.3). The observed MLA was assigned to subset a, while all back-calculated MLA estimates were assigned to subset b, as they were considerably larger than the observed MLA.

In the remaining tests from this data set, all back-calculated MLA estimates were assigned to the same subset as their respective observed MLA, as no significant differences existed ($P>0.05$). However, despite no statistically significant differences between MLA estimates, all back-calculated MLA estimates for the 1991, 1990 and 1989 year classes were greater than the observed MLA. Conversely, all back-calculation methods for the 1992 year class were less than the observed MLA. A slightly different situation was observed for the 1993 year class at age 3. In this case the Whitney-Carlander, Dahl-Lea and Ricker methods were less than the observed MLA, while the Fraser-Lee and Hile methods were slightly greater than the observed MLA.

Within these tests the Whitney-Carlander method produced the closest estimate to the observed mean length on four occasions. The Dahl-Lea method produced the closest estimate to the observed on two occasions and the Fraser-Lee, Hile and Ricker methods produced the closest estimate on just one occasion.

Table 2.3 – Mean length at age estimates of chub, from ANOVA and Tukey's comparison of observed mean length at age against the mean length at age from each back-calculation method. All measurements in mm, brackets contain subset assignment from Tukey's testing (yc=year class).

	Observed mean length	Whitney-Carlander	Dahl-Lea	Ricker	Fraser-Lee	Hile	P
Age 2, 1994 yc R. Colne	68 (a)	85 (b)	86 (b)	88 (b)	93 (b)	93 (b)	<0.01
Age 3, 1993 yc R. Colne	125 (a)	120 (a)	119 (a)	97 (a)	126 (a)	126(a)	>0.05
Age 4, 1992 yc R. Colne	193 (a)	168 (a)	168 (a)	181 (a)	173 (a)	173 (a)	>0.05
Age 5, 1991 yc R. Colne	223 (a)	239 (a)	240 (a)	249 (a)	243 (a)	243 (a)	>0.05
Age 6, 1990 yc R. Colne	269 (a)	281 (a)	281 (a)	288 (a)	284 (a)	284 (a)	>0.05
Age 7, 1989 yc R. Colne	308 (a)	329 (a)	329 (a)	334 (a)	331 (a)	331 (a)	>0.05

All back-calculated MLA estimates of the 1975 year class of dace at age 1 and the 1971 year class at age 5 from the R. Exe were significantly different to their respective observed MLA estimates (Tukey's test $P<0.05$; Table 2.4). In these tests, all back-calculated MLA estimates were significantly less than their respective observed MLA estimates.

In the remaining tests on R. Exe dace, all back-calculated MLA estimates were assigned to the same subset as their respective observed MLA estimates, indicating no significant differences between the observed and back-calculated MLA estimates ($P>0.05$). Despite no statistically significant differences, the 1974 year class at age 2 and the 1972 year class at age 4 both produced back-calculated MLA estimates that were larger than the observed MLA. Conversely, the back-calculated MLA estimates of the 1973 year class at age 3 were less than the observed MLA. With the exception of the 1971 year class at age 5, the Whitney-Carlander, Dahl-Lea and Ricker methods all produced greater MLA estimates than the Fraser-Lee and Hile methods.

In these tests, all methods recorded the closest estimate to the observed MLA on three occasions each.

Table 2.4 – Mean length at age estimates of dace, ANOVA and Tukey's comparison of observed mean length at age against the mean length at age from each back-calculation method. All measurements in mm, brackets contain subset assignment from Tukey's testing.

	Observed mean length	Whitney-Carlander	Dahl-Lea	Ricker	Fraser-Lee	Hile	P
Age 1, 1975 yc R. Exe	67 (b)	52 (a)	52 (a)	52 (a)	50 (a)	50 (a)	<0.05
Age 2, 1974 yc R. Exe	109 (a)	118 (a)	118 (a)	118 (a)	117 (a)	117 (a)	>0.05
Age 3, 1973 yc R. Exe	156 (a)	154 (a)	154 (a)	154 (a)	153 (a)	153 (a)	>0.05
Age 4, 1972 yc R. Exe	172 (a)	176 (a)	176 (a)	176 (a)	175 (a)	175 (a)	>0.05
Age 5, 1971 yc R. Exe	194 (b)	179 (a)	179 (a)	179 (a)	179 (a)	179 (a)	<0.05

The 1998 year class of bream at age two from the 1999-2002 dataset from the Leven Canal was the only test to show significant differences between the observed MLA and the back-calculated MLA estimates (Tukey's test $P<0.05$; Table 2.5). In this case, estimates produced by each of the back-calculation methods were considerably less than the observed MLA.

Of the remaining tests, no significant differences were recorded between the observed and back-calculated MLA estimates (Tukey's tests $P>0.05$) and all back-calculated MLA estimates were assigned to the same subset as their respective observed MLA. However, all back-calculation methods from the 1996 year class at age 3 (1998-2002 data), the 1996 year class at age 4 and the 1995 year class at age 5 (1999-2002 data), produced estimates that were greater than the observed MLA. All back-calculation methods used in the 1999 year class at age 1 and the 1997 year class at age 3 (1999-2002 data) were less than the observed MLA. In the 1995 year class at age 4 (1998-2002 data) the Whitney-Carlander, Dahl-Lea and Ricker methods produced estimates that were larger than the observed MLA while the Fraser-Lee and Hile methods produced estimates that were less than the observed MLA.

In these tests the Hile model produced the closest estimate to the observed MLA on three occasions, with the 1996 year class at age 4 being identical to the observed MLA estimate. The Fraser-Lee method produced the closest estimate on four occasions, while the remaining methods produced the closest estimate on just one occasion each (Table 2.5).

Table 2.5 – Mean length at age estimates of bream, ANOVA and Tukey's comparison of observed mean length at age against the mean length at age from each back-calculation method. All measurements in mm, brackets contain subset assignment from Tukey's testing.

	Observed mean length	Whitney-Carlander	Dahl-Lea	Ricker	Fraser-Lee	Hile	P
Age 3, 1996 yc (98-02 data) Leven Canal	99 (a)	108 (a)	108 (a)	108 (a)	110 (a)	112 (a)	>0.05
Age 4, 1995 yc (98-02 data) Leven Canal	143 (a)	152 (a)	152 (a)	152 (a)	139 (a)	135 (a)	>0.05
Age 1, 1999 yc (99-02 data) Leven Canal	44 (a)	38 (a)	38 (a)	38 (a)	40 (a)	40 (a)	>0.05
Age 2, 1998 yc (99-02 data) Leven Canal	91 (b)	74 (a)	73 (a)	74 (a)	75 (a)	73 (a)	<0.05
Age 3, 1997 yc (99-02 data) Leven Canal	120 (a)	110 (a)	110 (a)	110 (a)	111 (a)	105 (a)	>0.05
Age 4, 1996 yc (99-02 data) Leven Canal	152 (a)	157 (a)	156 (a)	157 (a)	158 (a)	152 (a)	>0.05
Age 5, 1995 yc (99-02 data) Leven Canal	187 (a)	221 (a)	221 (a)	221 (a)	222 (a)	206 (a)	>0.05

The roach examples proved more complex with 16 of the tests showing significant differences between the observed and back-calculated mean length age estimates (P<0.05; Table 2.6). The Whitney-Carlander and Dahl-Lea methods were generally less than their respective observed MLA estimates while the Ricker, Fraser-Lee and Hile methods were generally larger than their respective observed MLA estimates.

In the tests where no significant difference was recorded between the observed and back-calculated MLA estimates, back-calculated estimates were generally larger than the observed MLA. However, the Ricker method from the 2002 year class at age 2 from the Warwickshire Avon was identical to the observed MLA. The Hile method also produced an identical MLA estimate to the observed MLA on one occasion as did the Fraser-Lee method.

A more complex pattern was found in the tests where significant differences occurred between the observed and back-calculated MLA estimates. In a number of cases, not only were the back-calculated MLA estimates significantly different to the observed MLA estimate, significant differences were also found between the back-calculated methods. For example, the Whitney-Carlander and Dahl-Lea estimates were considerably less than the observed MLA of the 1998 year class of roach at age 2 from the Leven Canal (1999-02 data), assigning these methods to subset a. Subset b consisted of the observed MLA and the estimates produced by the Fraser-Lee and Hile methods. Although these methods were less than the observed MLA, they were significantly different to the Whitney-Carlander and Dahl-Lea methods. The Ricker method produced an estimate that was greater than the observed MLA, showing the Ricker method to be significantly different not only to the observed MLA but also to the other back-calculation methods.

The Ricker method produced the closest estimate to the observed MLA in 13 of the tests while the Whitney Carlander gave the closest estimate in 12. The Dahl-Lea method produced the closest estimate in 10 of the tests while the Hile method produced the closest estimate in nine of the tests and the Fraser-Lee eight.

Table 2.6 – Mean length at age estimates of roach, ANOVA and Tukey's comparison of observed mean length at age against the mean length at age from each back-calculation method. All measurements in mm, brackets contain subset assignment from Tukey's testing.

	Observed mean length	Whitney-Carlander	Dahl-Lea	Ricker	Fraser-Lee	Hile	P
Age 1, 1995 yc (95-98 data) HPP	78 (b)	52 (a)	51 (a)	52 (a)	77 (b)	77 (b)	<0.01
Age 2, 1994 yc (95-98 data) HPP	132 (d)	68 (b)	53 (a)	55 (a)	79 (c)	79 (c)	<0.01
Age 4, 1992 yc (95-98 data) HPP	206 (c)	155 (b)	82 (a)	84 (a)	105 (a)	105 (a)	<0.01
Age 2, 1996 yc (97-98 data) HPP	131 (a)	132 (a)	132 (a)	134 (a)	134 (a)	134 (a)	>0.05
Age 3, 1995 yc (97-98 data) HPP	189 (b)	194 (b)	161 (a)	161 (a)	161 (a)	161 (a)	<0.01
Age 1, 1995 yc (95-97 data) HPP	78 (b)	56 (a)	55 (a)	81 (b)	82 (b)	82 (b)	<0.01
Age 4, 1992 yc (95-97 data) HPP	186 (b)	113 (a)	113 (a)	203 (b)	206 (b)	203 (b)	<0.01
Age 2, 1997 yc (98-02 data) Leven Canal	64 (b)	50 (a)	50 (a)	61 (b)	65 (b)	65 (b)	<0.01

Table 2.6 (continued) – Mean length at age estimates of roach, ANOVA and Tukey's comparison of observed mean length at age against the mean length at age from each back-calculation method. All measurements in mm, brackets contain subset assignment from Tukey's testing.

	Observed mean length	Whitney-Carlander	Dahl-Lea	Ricker	Fraser-Lee	Hile	P
Age 3, 1996 yc (98-02 data) Leven Canal	89 (b)	82 (a)	81 (a)	89 (b)	92 (b)	92 (b)	<0.01
Age 4, 1995 yc (98-02 data) Leven Canal	109 (a)	(a) 114 (b)	(a) 114 (b)	(b) 119 (c)	121 (c)	121 (c)	<0.01
Age 5, 1994 yc (98-02 data) Leven Canal	135 (a)	138 (a)	137 (a)	142 (a)	144 (a)	144 (a)	<0.05
Age 6, 1993 yc (98-02 data) Leven Canal	155 (a)	153 (a)	153 (a)	157 (a)	158 (a)	158 (a)	>0.05
Age 7, 1992 yc (98-02 data) Leven Canal	159 (a)	187 (b)	187 (b)	190 (b)	192 (b)	192 (b)	<0.01
Age 8, 1991 yc (98-02 data) Leven Canal	188 (a)	199 (a)	199 (a)	202 (a)	203 (a)	203 (a)	>0.05
Age 1, 1999 yc (99-02 data) Leven Canal	42 (b)	30 (a)	29 (a)	53 (d)	47 (c)	47 (c)	<0.01
Age 2, 1998 yc (99-02 data) Leven Canal	66 (b)	51 (a)	50 (a)	69 (c)	65 (b)	65 (b)	<0.01
Age 3, 1997 yc (99-02 data) Leven Canal	91 (c)	75 (a)	75 (a)	90 (c)	86 (b)	86 (b)	<0.01
Age 4, 1996 yc (99-02 data) Leven Canal	122 (c)	106 (a)	106 (a)	(b) 117 (c)	115 (b)	115 (b)	<0.01
Age 5, 1995 yc (99-02 data) Leven Canal	(a) 146 (b)	139 (a)	139 (a)	148 (b)	146 (b)	146 (b)	<0.05
Age 6, 1994 yc (99-02 data) LevenCanal	169 (a)	160 (a)	159 (a)	167 (a)	165 (a)	165 (a)	<0.05
Age 7, 1993 yc (99-02 data) Leven Canal	180 (a)	171 (a)	170 (a)	177 (a)	176 (a)	176 (a)	>0.05
Age 8, 1992 yc (99-02 data) Leven Canal	209 (a)	212 (a)	212 (a)	217 (a)	216 (a)	216 (a)	>0.05
Age 9, 1991 yc (99-02 data) Leven Canal	230 (a)	210 (a)	210 (a)	216 (a)	214 (a)	214 (a)	>0.05
Age 2, 1994 yc (96-98 data) Trent Bridge	95 (b)	85 (a)	84 (a)	100 (b)	104 (b)	104 (b)	<0.01
Age 3, 1993 yc (96-98 data) Trent Bridge	125 (a)	119 (a)	118 (a)	130 (a)	133 (a)	133 (a)	>0.05
Age 4, 1992 yc (96-98 data) Trent Bridge	143 (a)	145 (a)	144 (a)	154 (a)	156 (a)	156 (a)	>0.05
Age 5, 1991 yc (96-98 data) Trent Bridge	167 (a)	170 (a)	169 (a)	177 (a)	179 (a)	179 (a)	>0.05
Age 6, 1990 yc (96-98 data) Trent Bridge	189 (a)	194 (a)	194 (a)	200 (a)	202 (a)	202 (a)	>0.05
Age 7, 1989 yc (96-98 data) Trent Bridge	216 (a)	219 (a)	219 (a)	224 (a)	225 (a)	225 (a)	>0.05
Age 2, 2002 yc, Warwickshire Avon	72 (a)	69 (a)	69 (a)	72 (a)	73 (a)	73 (a)	>0.05
Age 3, 2001 yc, Warwickshire Avon	104 (a)	97 (a)	97 (a)	100 (a)	100 (a)	100 (a)	<0.05
Age 4, 2000 yc, Warwickshire Avon	130 (a)	134 (a)	134 (a)	135 (a)	136 (a)	136 (a)	>0.05

2.4 – DISCUSSION

Accurate ageing of fish is central to fisheries evaluation as it forms the basis for a wide range of techniques that are applicable to fish resource assessment (Lyle *et al.* 2000). Most of the literature on this subject uses data from laboratory reared fish (Holmgren 1996) or from mark recapture methods (Smedstad and Holm 1996; Panfili and Tomás 2000). These techniques use paired data to test various back-calculation methods to a known length, which is determined on the hard parts of the fish by marking them with chemical dyes such as oxytetracycline. In this study, scales were taken from wild populations of fish from rivers throughout England and the R. Severn, which rises in Wales and flows into England as part of the Environment Agency's core monitoring programme and from various research projects. Therefore, unlike the laboratory and mark recapture methods, the scale data are not paired to the same animal, but instead used population data of fish taken from the same location at different times. Therefore, the possibility exists that the population structure may have changed in the interim period between the initial and subsequent surveys due to such factors as immigration, emigration and the effect of mortality. The aim of this study was therefore not to provide definitive evidence for the validation of the technique or use of a single back-calculation method, but to demonstrate which method best describes survey data collected from wild populations of fish from rivers throughout England.

It was anticipated that one method would be prevalent so this could be adopted as the most appropriate method for the back-calculation of fish length from routine surveys. However, from the analysis all back-calculation methods have their own merits, but as the objective was to decide upon one method for general use; the method chosen was that of Hile. This method showed a degree of consistency between the back-calculated mean length at age and the observed mean length at age. For example, on two occasions the Hile method produced back-calculated mean lengths for age that were identical to the observed mean length for age. On a number of occasions, the Hile method produced mean length at age estimates that were closer to the observed mean length at age than any other method. Mean length at age estimates produced by the Hile method were also most often included in the same subset as the observed mean length at age estimate after testing, while other methods were found to be significantly different.

The decision to accept the Hile method as the most appropriate method was difficult, as no one back-calculation method excelled over the entire range of calculations made. However, there were occasions when the other back-calculation methods fell short of the consistency of the Hile method. The Fraser-Lee and Ricker methods were both seen to generally produce estimates that were greater than the observed mean length at age estimates. However, on a number of occasions the Ricker method produced length estimates that were considerably less than the observed mean length at age while the Hile method produced an estimate close to that of the observed. The Fraser-Lee method was found to produce an identical estimate as that of the Hile method on a number of occasions. However, the Hile method gives a calculation for the derivation of the length intercept (c), whereas the length intercept in the Fraser-Lee method is derived from the examination of the plot of scale radius and fish length.

The Whitney-Carlander and Dahl-Lea methods generally underestimated the observed mean length at age estimate. For example, mean length at age 4 from the 1992 year class of roach from Holme Pierepoint calculated by the Whitney-Carlander and Dahl-Lea methods was considerably lower than the observed mean length at age while the remaining back-calculation methods were slightly above the observed MLA. The Whitney-Carlander method also produced the largest length intercept (c) values, suggesting the regression of length on scale radius is perhaps not the best method for the determination of the length intercept. The Whitney-Carlander and Dahl-Lea methods were also significantly different from the observed mean length at age on the most numerous occasions.

The underestimation of observed mean length at age by the Whitney-Carlander method was similar to that found by Roemer and Oliveira (2007) for bluefish (*Pomatomus salatrix* (L.)) and related it to changes in the body size/otolith size relation during different life stages. Significant differences in the growth rate between different ontogenetic stages during the larval period were demonstrated by Hare and Cowen (1997). They stated these differences explain why the regression of otolith radius and fish length did not predict a biologically reasonable length intercept, because the ratio of otolith size and fish length changed during the juvenile and larval stages. This change in growth rate was also observed between juvenile and adult brook trout. Hutchings (1993) stated that from a life history perspective, the growth rate is probably best expressed separately. If the growth rate is faster during the juvenile period than in the adult, an underestimation of the length intercept would result. However in this study the Whitney-Carlander method produced length intercept values that were consistently larger than those produced by the other methods. If the growth rate was slower during the juvenile period than the adult growth rate, the length intercept values may have been overestimated, leading to increased length at age estimates. The changes in growth rate between the juvenile and adult phases may, however, explain the noticeably low and negative length intercept values calculated for the dace populations of the River Exe by all back-calculation methods. In the case of the Dahl-Lea model, the general underestimation of the observed mean lengths at age by this technique may be due to the need of a correction factor, which would ultimately increase the length estimate and possibly account for the underestimations found for this method.

Possible reasons for overestimations of back-calculated lengths at age have been described. For instance, it is known that scale readsorption occurs at the edge of the scale, especially in sexually maturing fish (Persson *et al.* 1999). If scale readsorption is high at the time of collection, then an underestimation of the total scale radius would result (Morita 2001), which would in turn lead to an overestimation of the fishes past length. This may be an important factor in this study, as scales were collected at a time when it was presumed that the growth increment had been reached and no further somatic growth was occurring. If readsorption of the scales was occurring at the time of collection, which is possible, overestimation of the mean length at age values would result.

Conversely, if resorption occurred during the period when the specific annulus is being laid down, or a proportion of that annulus is removed through resorption caused through some environmental stressor, then underestimates of the length at age of that mark would be seen if the fish's calcified structures are analysed later in life. Underestimations of the observed mean lengths at age were observed in this study. It may therefore be that the underestimations of lengths at age were the result of the annuli being measured at a radius that was smaller than it should have been and an annulus with the correct radii would have given a larger length intercept and therefore a larger length at age.

Many of the methods used in this study provided greater mean length at age compared with the observed MLA. This was consistent with Panfili and Tomás (2000) where back-calculated fish lengths were greater than observed fish lengths and was related to a divergence in the rates of somatic and otolith growth. The actual lower or greater back-calculated MLA seems to depend on the coupling between the specific growth rates of the calcified structure and the fish (Panfili and Tomás 2000). An uncoupling between somatic and scale growth rates would explain the deviation of the back-calculated length from the observed value. If the specific growth rates in fish length and the calcified structure size are identical, back-calculation gives a very good approximation of the observed length. Whereas if the growth rate of the calcified structure is higher than the somatic growth rate, then back-calculated MLA is lower than the observed length. Inversely, if the somatic growth rate is higher than the growth rate of the calcified structure, back-calculation will give a greater MLA. Moreover, when the uncoupling between growth rates increases, the greater the back-calculated MLA (Panfili and Tomás 2000).

Changes in the population structure from that of the observed population may also be the cause of lower or greater MLA. Schlosser (1991) stated that four factors are critical in regulating the population dynamics of any animal, fecundity, mortality, immigration and emigration rates. Lucas & Baras (2001) demonstrated the widespread existence of spatio-temporal variations in the distribution and abundance of freshwater fish. Movements are often seen on a seasonal or ontogenetic basis, for spawning, feeding and refuge, and in many cases are fundamental to the successful completion of lifecycles. Although fisheries surveys were conducted at the same location, only a proportion of the fish that made up the historic survey may have been present in any subsequent survey. A proportion of the fish from the historic survey, large enough to change the mean length values, may therefore have moved away or were lost from the system causing a change in the back-calculated MLA.

Inaccurate determination of the length intercept, a constant value used in back-calculation, would also produce inaccurate mean length at age estimates. It is only the increment in the length of the fish and in the size of the scale that are proportional, and not their actual sizes. The main factor that disturbs the proportionality between the length of the fish and that of the scale is the scale is not laid down at the birth of the fish, but somewhat later, when the fish has already attained a certain length (Nikolsky 1963). Garner and Copp (1997) argued that development during the first year of life comprises a number of steps, with growth following the attainment of a given threshold size by periods of development. Ontogenetic changes, reflecting fundamental changes in the fish's behaviour are representative of this, with the onset of scale formation being a part of one of these steps.

Fraser (1916) and Lee (1920), proposed the need for a correction to account for body growth before scale formation (Klumb *et al.* 1999a). The body length at scale formation has been the cause of much discussion since the proposal by Fraser in 1916, advocating its use as the correction factor in the formula for the back-calculation of lengths (Everhart 1949). The current practice for the derivation of the correction factor, c, described as the length of the fish at the time of scale formation, is from the length intercept of the regression line, rather than from observations on juvenile fish (Francis 1990). The biological intercept has been observed for a number of species. Tong (1986) found squamation of scales in roach began at 39-40 days, to be that at which, with scale growth beginning at the tail and covering the entire body after the fish achieved 19 – 22.5 mm total length. Studies on the morphological development of chub, found the first evidence of scale development after 68 days and a length of 15.9 mm (Economou *et al.* 1991). The onset of scale formation in bream was shown to be around 17 mm (Kucharczyk, *et al.* 1998) and at around 18 – 28 mm for perch (Spanovskaya and Grygorash 1977).

The need to examine juvenile fishes to determine the length at which scale formation begins is well founded. In this study it can be seen that considerable variation exists in the correction factors returned for each species. Roach showed a range of values returned for the length intercept, between 12 and 44 mm (Table 2.7). The lower end of the range observed in the correction factors for the roach in this study was close to that of Tong (1986), but the higher end of this range merits the need to check these figures against a known length at the time of scale squamation, taken from observations of juvenile fish from the populations in question. The dace example, where a negative length intercept was returned from calculation only serves to increase the need for a comparison between the calculated length intercept and a known length at the time of scale squamation from the examination of juvenile fish. The negative length intercept values observed in these populations may be due to different growth rates between the juvenile and adult stages, where a slower growth rate during the adult stages produces a regression that underestimates the length intercept.

Lee's phenomenon of an apparent change in the growth rate is the tendency for back calculated length at any age to be smaller than the fish from which they were calculated (Ricker 1992). Various explanations have been advanced for this, including selective mortality of the more rapid growing individuals of a population, errors in the back-calculation process, non-random sampling of the stock, the presence of false checks, which increase in frequency as the individual ages, or from the contraction of the scale annuli toward the scale nucleus (Duncan 1980; Ricker 1992; Pierce *et al.* 1996). Lower MLA's than the observed values were found in the back-calculated data, and on these occasions it may be held that Lee's phenomenon may be acting on these populations. However, in the majority of cases, greater MLA's than the observed mean length at age were seen. Ricker (1992) states that Lee's phenomenon occurs whenever the K (the growth coefficient) value is less than the "best one", estimated biologically or from a symmetrical regression line. Conversely if the K value is greater than the "best one" then an 'inverse Lee's phenomenon' will result, where the back-calculated lengths will tend to be larger than the fish from which they are calculated. Unfortunately, Ricker (1992) does not describe which growth coefficient is the 'best one', and it may be that all fast growing populations will produce overestimated mean lengths at age, if the 'best' growth coefficient is not set as the fastest.

Good growth years can also be a possible cause of the lower than expected back-calculated mean lengths at age. The criteria set out for the timing of the collection of historic data occurs within the time frame set out to ensure an end of year growth increment had been reached. This does not necessarily mean the growth increment had been achieved. Mann (1997) demonstrated temperatures around 11.5° – 12°C to be the threshold, below which growth in fish does not occur. Although the surveys for the historic data were collected at a time when growth was presumed to have ceased, if water temperatures above this threshold persisted for any appreciable length of time and sufficient resources were available, somatic growth may still have occurred. Back-calculation of subsequent survey data would overestimate the observed length at age data as the fish lengths in the historic data set would not have reached the annual growth increment.

CHAPTER THREE

STANDARD GROWTH

3.1 – INTRODUCTION

One method of comparing the growth parameters between different populations of the same species requires the development of standard growth models. Britton (2007) stated standard growth tools are often basic indices to assess population mean growth parameters, but remain valuable to fishery managers because of their ease of interpretation and their role in identifying growth performance. The comparison of growth performance can then be used to identify causal factors behind observed differences in growth rates (Britton 2007). Standard growth curves were first produced for roach, dace, chub and bream from populations in England and Wales by Hickley and Dexter (1979) and later expanded to include pike (Hickley and Sutton 1984). Standard growth curves for these species were later updated and further species added to by Cowx (2001) and Britton (2007). However, the standard growth rates do not account for any of the factors that combine to influence the growth rate, for instance differences in latitude and altitude and the associated differences in temperature, trophic status and the occurrence of pollutants.

Intraspecific variation in fish growth is particularly intriguing because it suggests strong associations between an organism's size and its environment (Angilletta and Dunham 2003). Phenotypic plasticity has been demonstrated by a number of authors who related observed growth differences to a number of factors. Longitudinal variation in growth characteristics along a rivers course was observed by Cowx (1988) and Przbylski (1995), where fish in specific areas of the river matching their preferred habitat had faster growth rates than fish outside of these areas. Temperature changes growth rates by inducing changes in the metabolic processes (Broughton and Jones 1978). Changes in the growth rate can be influenced through density-dependant, intra- and interspecific competition for limited resources (Linfield 1979; Persson and Greenberg 1990) and through changes in food quality (Bowen *et al.* 1995). Latitudinally influenced changes in temperature and length of growing season were demonstrated to change the growth of perch (Karås 1990), with high latitude fish (relating to lower temperatures) having an overall slower growth rate.

Since the original standard growth curves were developed, considerable changes in the quality of the habitat available to fish throughout England and Wales have occurred, as well as improvements in water quality (decreases in both phosphorus (P) and nitrate (NO3) levels (Environment Agency 2005)) and other improvement measures. Thus, given the plasticity of growth of individual species, there may be a need to update continually the standard growth curves to reflect these changes. The original growth standards were determined from a limited number of populations; therefore, there is a need for new standards to be based upon a more robust data set. The aim of this chapter was (1) to produce standard growth curves for as many species as possible using data from scale reading of samples from the Environment Agency's national monitoring programme and (2) to make comparisons between the standard growth curves produced in this study and those produced by Hickley and Dexter (1979) and Britton (2007), and elucidate any changes that may have occurred since the production of the growth standards and therefore justify the need to update the standard growth curves on a regular basis. It is not the intention to discuss the factors influencing variability in fish growth in this Chapter, as this will be discussed later (Chapters 4 and 5).

3.2 – METHODS AND MATERIALS

3.2.1 - Formulation of standard growth curves

Data on the growth of populations of roach, dace, chub, brown trout, pike, perch, bleak and gudgeon from rivers throughout England (Appendix 1) were separated and individually back-calculated according to the Hile method (Chapter 2) while bream were back-calculated using the Dahl-Lea model, due to problems while deriving the value for c, and mean values for length at age of each population recorded. Lengths at age for each population were then modelled using the von Bertalanffy growth model, this linear form of the model was chosen so outputs from Hickley and Dexter (1979) could be directly comparable as it is the same model they employed, which assumes the rate of growth of an organism declines with size so that the rate of change, L, may be described as -

$$L_t = L_{\text{-infinity}} (1 - \exp[-K(t - t_0)]) \qquad \text{equation 3.1}$$

Ford Walford plots for individual samples were constructed, with back-calculated mean length at age t (L_t) plotted against L_{t+1}, to produce a straight line. From this, the intercept on the y axis (a) and slope of the line (b) was calculated and used to estimate the asymptotic length ($L_{\text{-infinity}}$) and the growth coefficient (K) for each sample where

$$L_{\text{-infinity}} = a/(1-b) \qquad \text{equation 3.2}$$

and

$$K = -\ln(b) \qquad \text{equation 3.3}$$

Having calculated these values for each species from each river, length at time 0 (t_o) was estimated, using

$$t_0 = t + (1 / K) (\ln [(L_{\text{-infinity}} - L_t) / L_{\text{-infinity}}]) \qquad \text{equation 3.4}$$

Mean fork lengths at age were then generated according to Hickley and Dexter (1979), where mean values from modelled lengths at age, from each population, were used to construct Ford Walford plots to generate a, b and $L_{\text{-infinity}}$, mean lengths at age were then calculated using

$$l_n = L_{\text{-infinity}} (1-b^n) \qquad \text{equation 3.5}$$

where l_n is the length of the fish at age n.

To demonstrate phenotypic plasticity in the growth of these species, indications of exceptional, fast, mean, slow and stunted growth were estimated, to reflect those developed by Cowx (2001). Average growth was calculated as ± 10% of the mean growth rate and fast growth between 10 and 20% above the mean rate. Slow growth was considered between 10 and 20% below mean. Exceptional growth was defined as values >20% above the average growth rate and stunted growth <20% below the mean rate.

3.2.2 - Relationship between Von Bertalanffy growth parameters ($L\infty$ and K)

Regression analysis was used to demonstrate growth plasticity and to determine any relationship between the von Bertalanffy growth parameters of asymptotic length ($L_{\text{-infinity}}$) and the growth coefficient (K). Values for $L\infty$ and K, for roach, dace, chub, brown trout, pike, perch, bleak and gudgeon populations from throughout England were analysed using the inverse curve estimation regression model in SPSS (ver14).

3.2.3 - Comparison of mean growth rates

The method of comparing fish growth curves proposed by Allen (1976) was used to determine whether any changes in the mean growth curves produced by Hickley and Dexter (1979) and Hickley and Sutton (1984) have occurred since their inception in relation to those calculated in this study and those of Britton (2007). This method avoids the difficulties of non linear estimation by describing the growth of the i^{th} age class by a linear transformation of the data using

$$L(t) = a - b\, r^{t} \qquad \text{equation 3.6}$$

Where

$$a = L_{\text{-infinity}} \qquad \text{equation 3.7}$$

$$b = L_{\text{-infinity}}\, e^{k\, t_0} \qquad \text{equation 3.8}$$

$$r = e^{-k} \qquad \text{equation 3.9}$$

where r is constant chosen to give a suitable shape to the growth curves (Allen 1976) and t is the age of the fish at the $_{i}$th mark.

Original data used by Hickley and Dexter for roach, dace and chub, and data used by Hickley and Sutton (1984) for pike, were sourced from the literature, and mean length values for each age class for each species and estimates of $L_{\text{-infinity}}$, K and t_o calculated. The same values were calculated for these species from the formation of mean growth curves in this study (section 3.2.1) and from Britton (2007). The data were transformed to a linear form according to equation 3.6 and the differences between the resulting regression lines for each species tested using ANCOVA under the hypothesis that individual regressions for the same species were the same. In addition to the tests for differences between all mean growth curves for each species, each growth curve was compared individually to determine which, if any of the curves differed. In addition to these species, comparisons were made of mean growth curves for perch, brown trout, gudgeon and bleak from this study with those of Britton (2007).

3.3 – RESULTS

3.3.1 - Standard growth curves

Bream

Data from 28 populations of bream were compiled in this study. However, the number of individuals used to compile growth curves in a population was often small and consisted of either all large or all small fish. Therefore, the representation of the bream populations across its entire length range was not adequate to formulate a mean growth curve using back-calculated length at age data derived by back-calculating scales with the Hile method. In particular it was not possible to derive the correction factor from the scale radius-fish length relationship accurately as too few small individuals were available for each location and this lead to an error in calculating the correction factor. An example of this pattern can be seen in the bream from the River Medway (Figure 3.1) where a negative length value was derived for the correction factor. Also, in many cases the information provided for "bream" did not differentiate between common and silver bream. On these grounds, length at age for bream was calculated using the directly proportional method of Dahl-Lea (Chapter 2) for the formation of mean lengths at age.

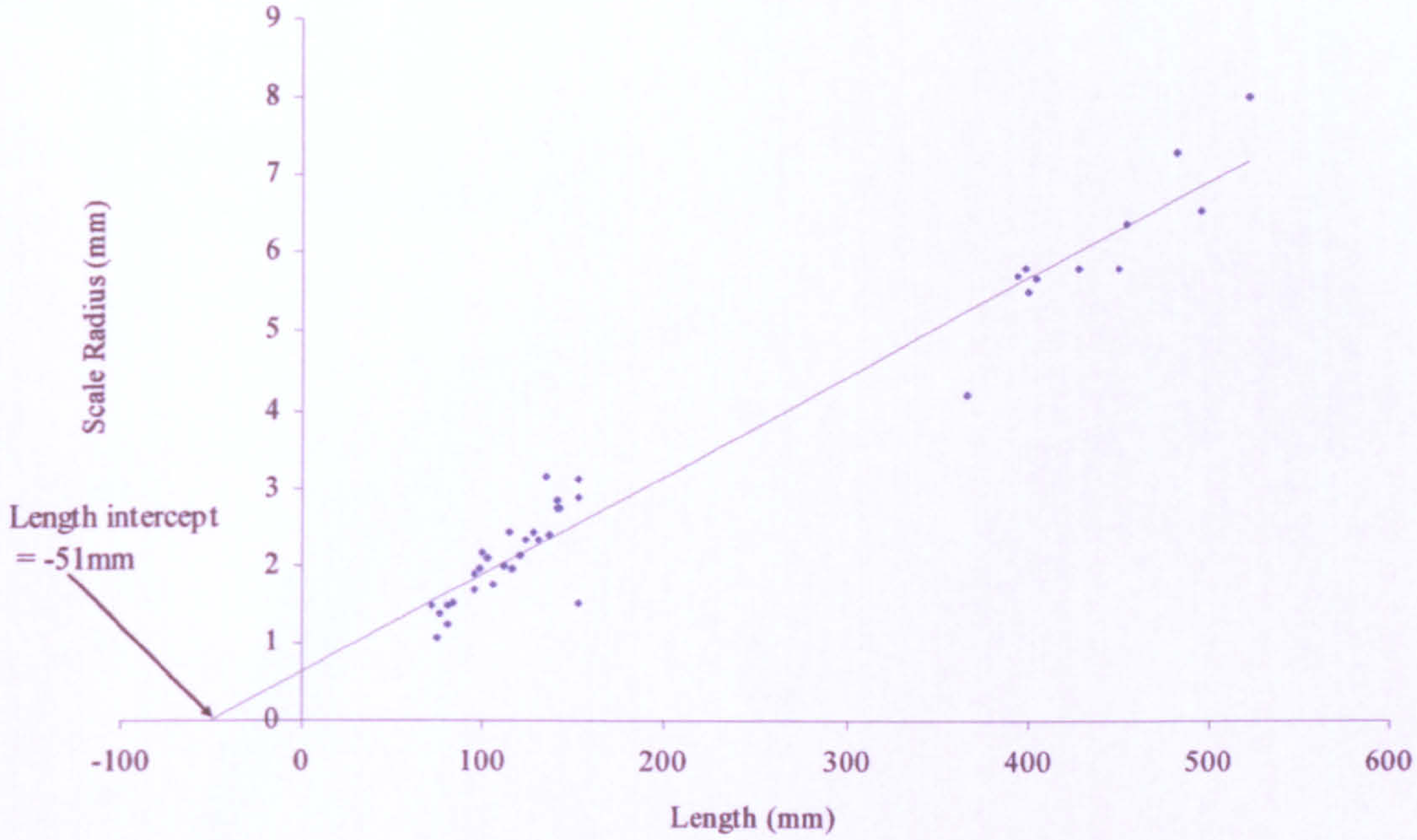


Figure 3.1 – Relationship between length and scale radius of bream from the River Medway, showing position of length intercept.

Growth curves from 28 bream populations were available to calculate the mean growth curve (Figures 3.2a-b; Table 3.1). Mean lengths at age 1, between the slowest and fastest growing bream populations, ranged between 34 and 97 mm, with a mean length at age 1 of 67 mm. At age five, mean lengths of bream ranged between 203 and 322 mm with a mean length of 264 mm. At age ten, mean lengths ranged between 336 and 490 mm, with 404 mm being the mean length. Longevity of the bream populations ranged from 3 to 20 years; 20 years of age was recorded in the River Great Ouse. The fastest growing bream population was in Barton Broad, whereas the slowest growing population was bream from the Old Bedford River. The shortest lived bream were also seen in the Old Bedford River.

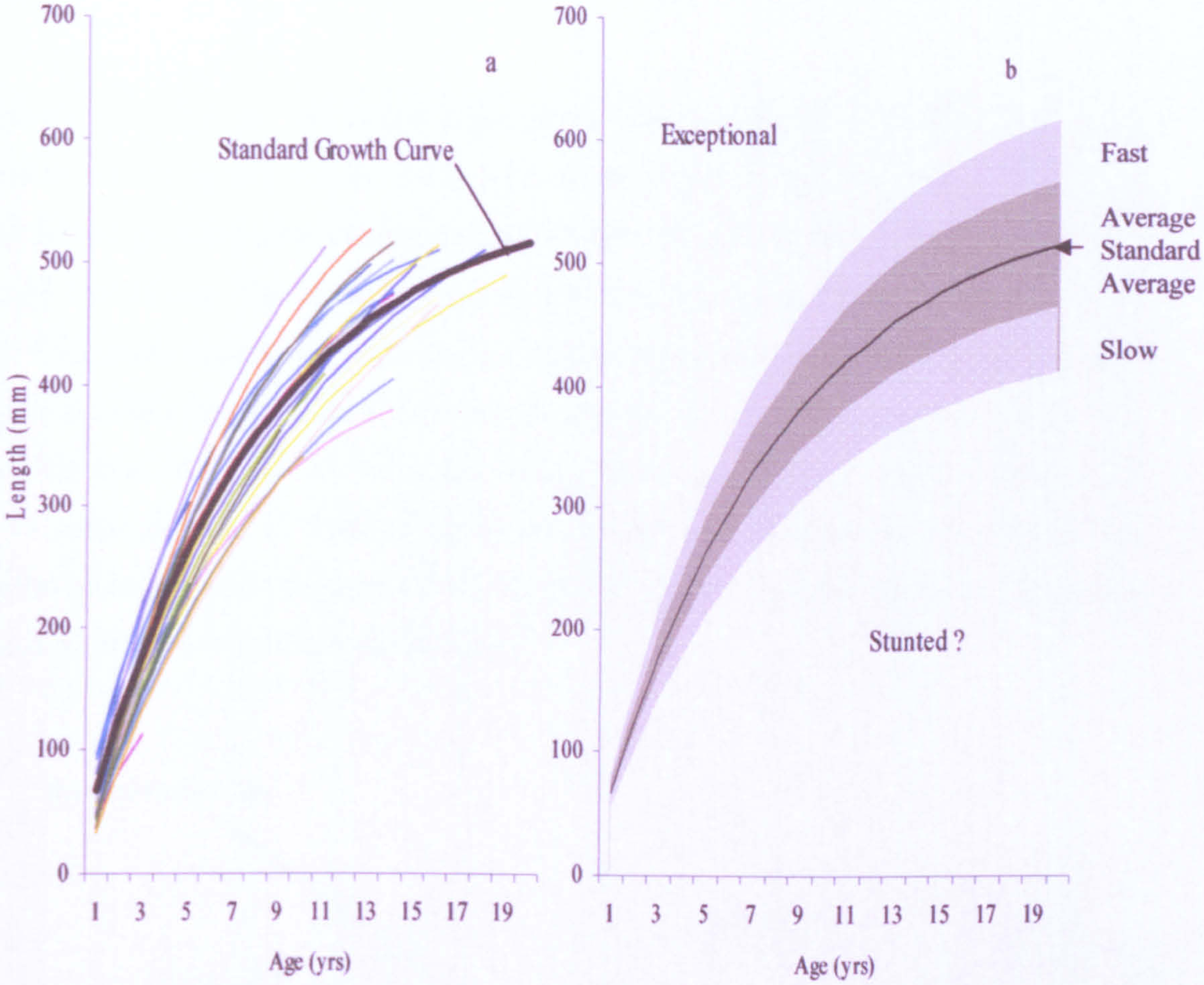


Figure 3.2a-b – Growth curves (a) from bream populations (n=28) and standard growth curve (b) from rivers throughout England and Wales.

Table 3.1 – Mean lengths at age of fish in this study from rivers throughout England and Wales. (all measurements in mm).

age	bream	roach	dace	chub	brown trout	pike	perch	bleak	gudgeon
1	67	35	51	57	104	199	80	41	62
2	126	67	93	108	186	360	143	73	102
3	178	96	129	154	251	490	194	98	128
4	224	123	159	195	301	595	235	117	146
5	264	148	184	232	341	679	268	132	157
6	300	171	205	265	372	747	294	144	164
7	331	192	223	295		802	315	153	
8	358	211	238	322		846	332		
9	382	228	251	346		882	345		
10	404	244	261	368			356		
11	422	259	270	388			365		
12	439	273	278	405			371		
13	453	285	284	421			377		
14	466	296		435					
15	477	307		448					
16	487	317		460					
17	496			470					
18	503			480					
19	510			488					
20	516			495					

Roach

Growth curves from 140 roach populations were available to calculate the mean growth curve (Figures 3.3a-b; Table 3.1). Mean lengths at age 1, between the slowest and fastest growing populations, ranged between 28 and 78 mm, with a mean length at age 1 of 35 mm. The range in mean lengths at age increased with increasing age. At age five, mean lengths of roach from different populations ranged between 126 and 224 mm with a mean length of 148 mm. At age ten, mean lengths ranged between 188 and 329 mm, with 244 mm being the mean length. Longevity of roach ranged from 4 to 16 years; roach of 16 years of age were recorded in the Rivers Trent and Brett. The fastest growing roach population was in the R. Bure, whereas the slowest growing roach population were from the R. Cam.

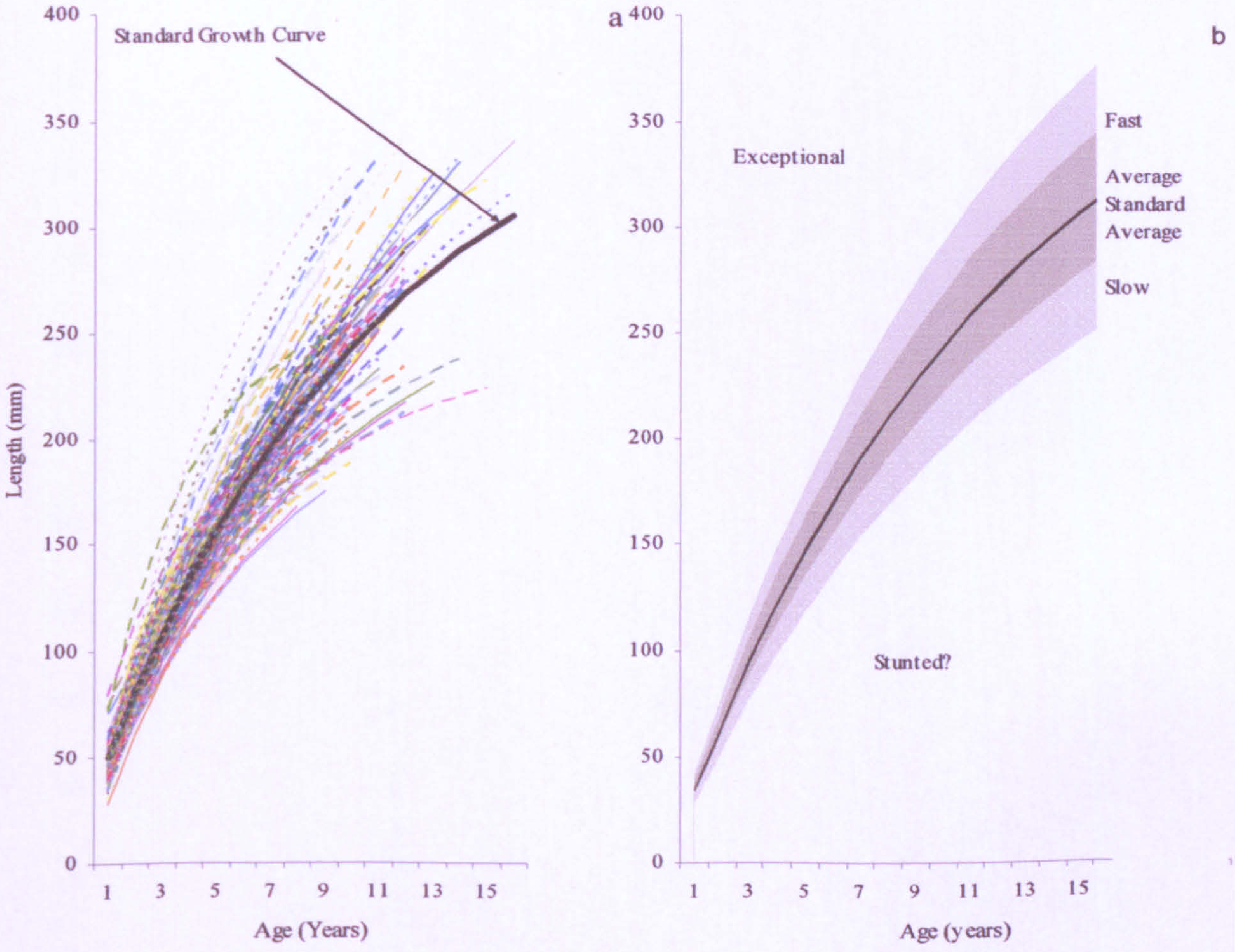


Figure 3.3a-b – Growth curves (a) from roach populations (n=140) and mean growth curve (b) from rivers throughout England and Wales.

Dace

Growth curves from 98 dace populations were available to calculate the mean growth curve (Figures 3.4a-b; Table 3.1). Mean lengths of dace at age 1, between the slowest and fastest growing populations, ranged between 35 and 95 mm, with a mean length at age one of 50 mm. At age five, mean lengths of dace from different populations ranged between 156 and 243 mm, with a mean length of 184 mm. Only eight of the original 98 dace populations had individuals which reached age 10, with mean lengths ranging between 201 and 350 mm. Longevity of dace populations ranged between 3 and 13 years, with the oldest and fastest growing dace being recorded in Yorkshire's River Don, this exceptional growth rate, possibly due to this river recovering from long term pollution and a numerically low population, allowing for fast growth through reduced competition. The slowest growing dace population was in the River Alne.

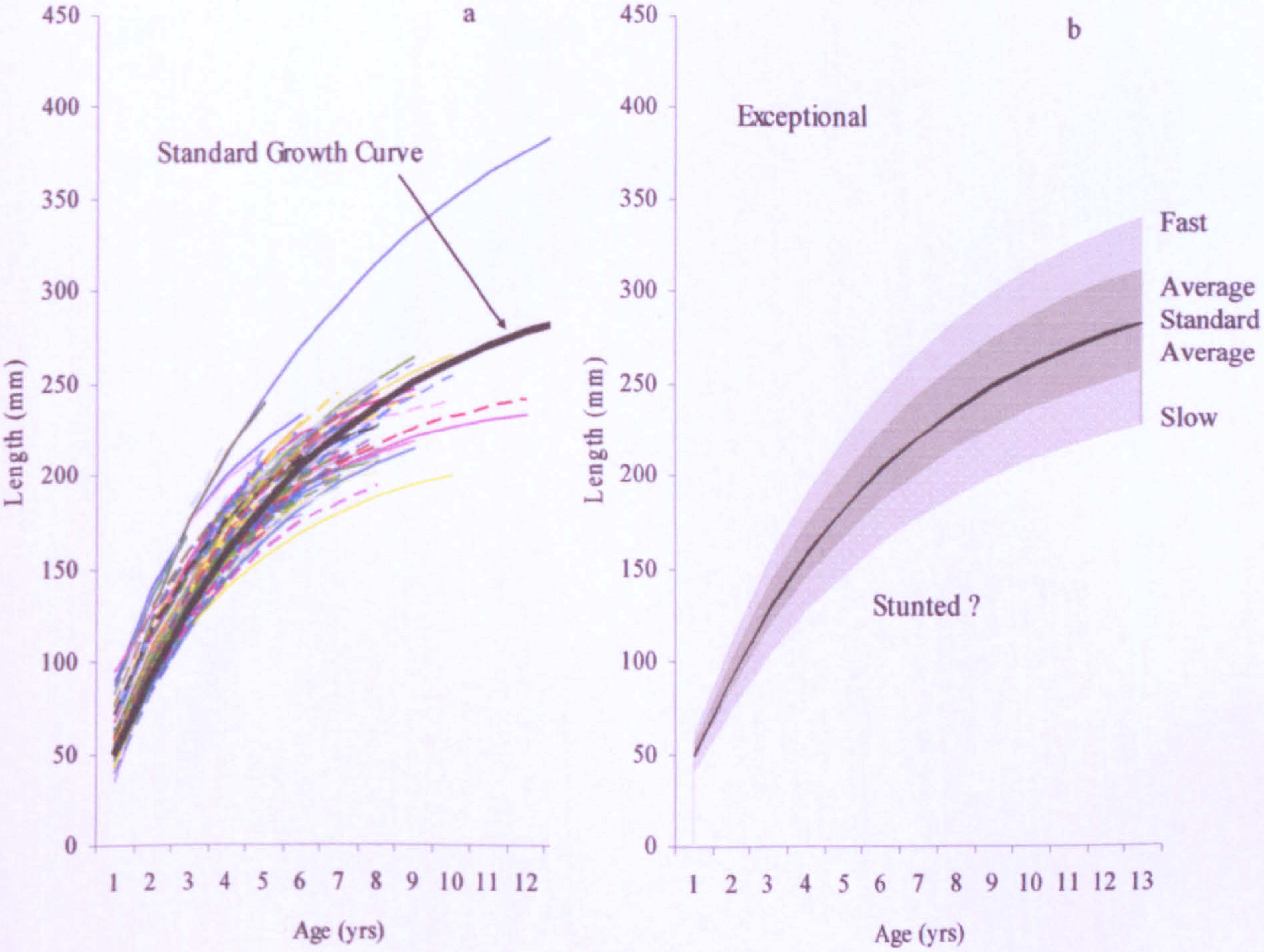
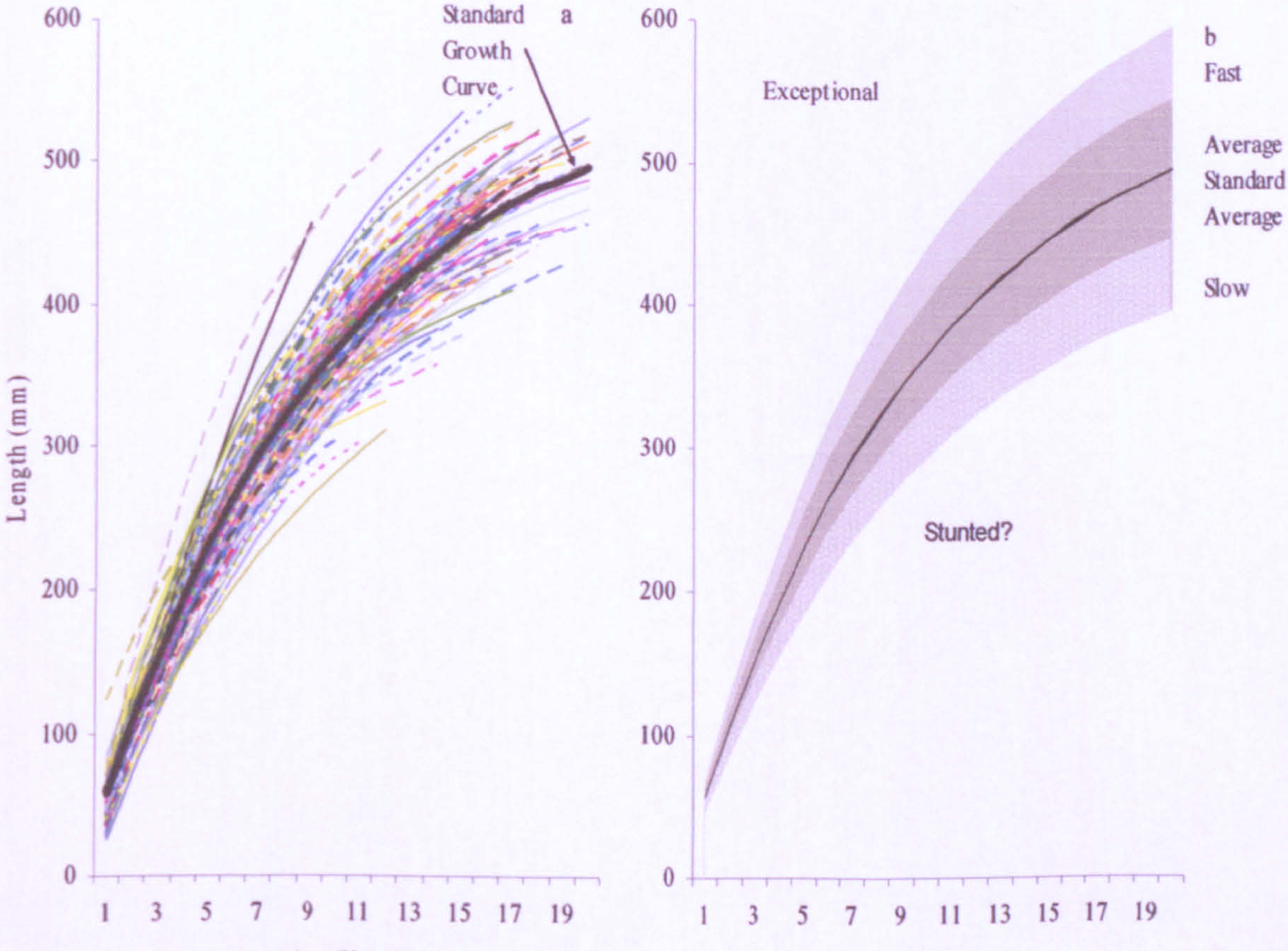


Figure 3.4a-b –Growth curves (a) from dace populations (n=98) and mean growth curve (b) from rivers throughout England and Wales.

Chub

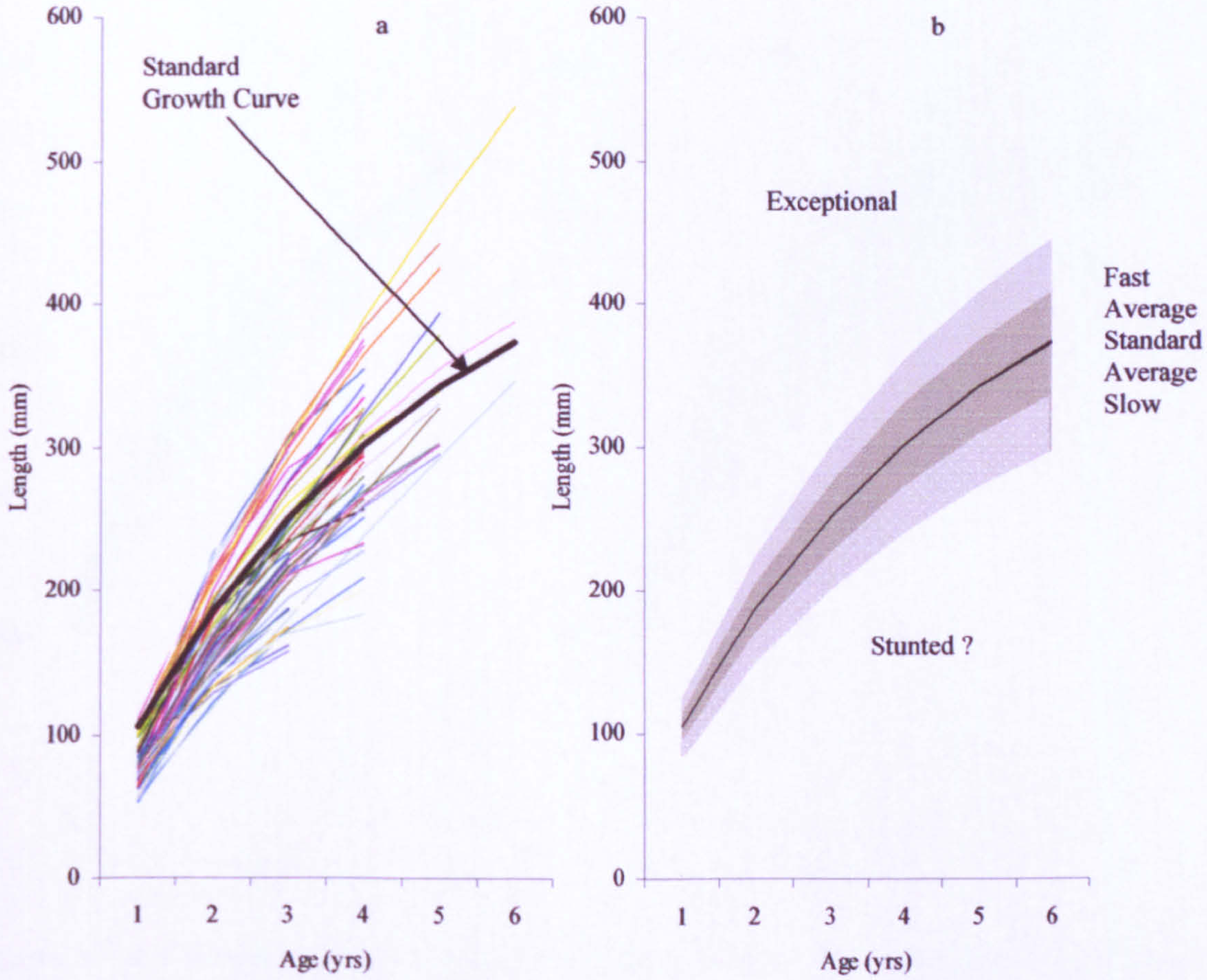
Growth curves from 115 chub populations were available to calculate the mean growth curve (Figures 3.5a-b; Table 3.1). Mean lengths at age 1 ranged between 26 and 123 mm, with a mean length at age 1 of 57 mm, although the individual with the length at age 1 of 123mm was considered to be wrong and left out of the analysis. This high value may be due to exceptional growth but may also be from an absent first year annuli as the fish may have been too small to produce scales in the first year of life. At age 5, mean lengths between the slowest and fastest growing chub populations ranged between 178 and 316 mm, with a mean length of 232 mm. At age 10, mean lengths ranged between 282 and 473 mm, with a mean length of 368 mm. Greater longevity was shown by chub with ages ranging from 5 to 20 years. The fastest growing chub population was from the R. Hull whereas the slowest growing chub population was again from the R. Alne.



Figures 3.5a-b –Growth curves (a) from chub populations (n=115) and mean growth curve (b) from rivers throughout England and Wales.

Brown Trout

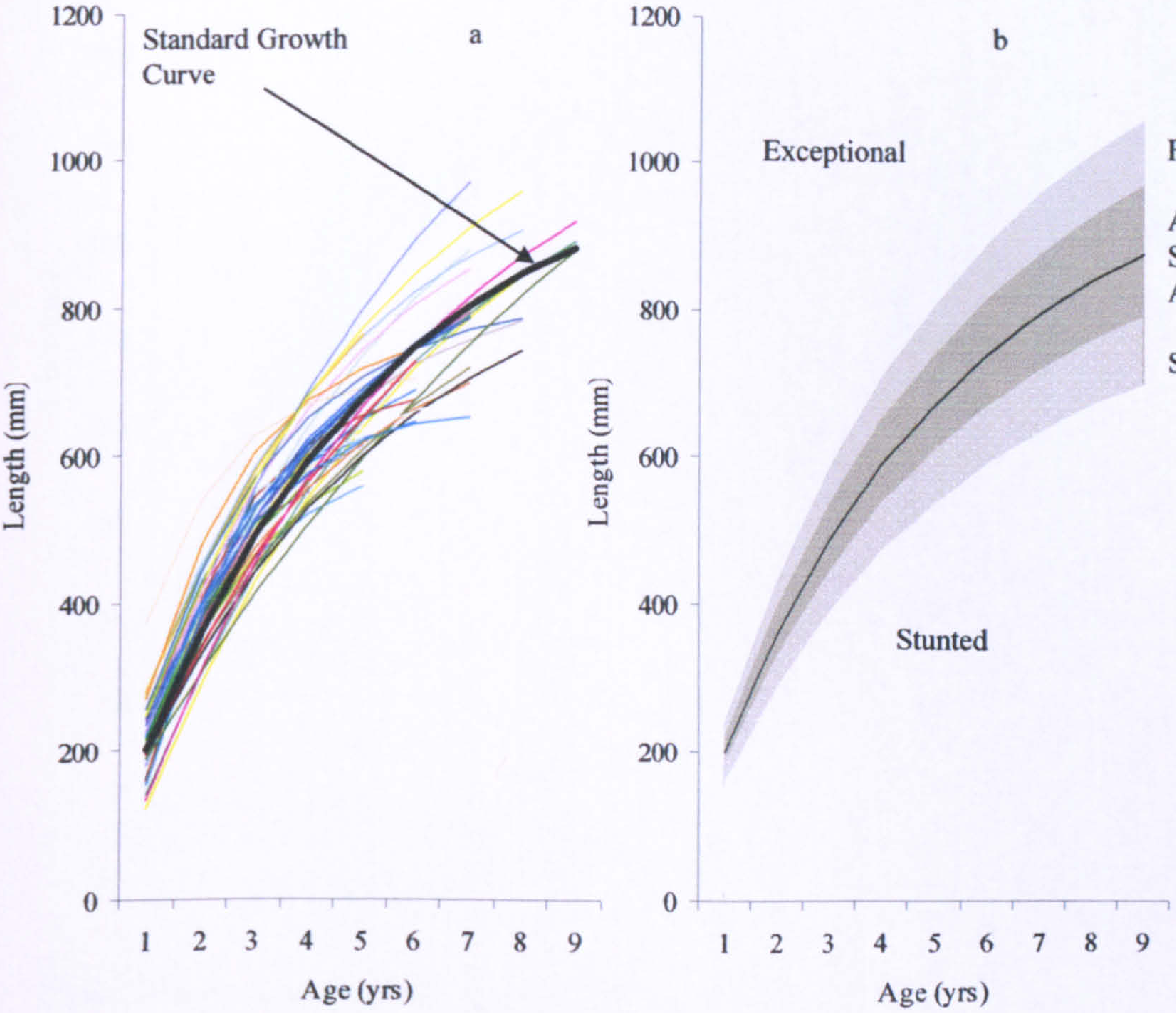
Growth curves from 53 brown trout populations were available to calculate the mean growth curve (Figures 3.6a-b; Table 3.1). Mean lengths of brown trout at age 1 ranged between 53 and 111 mm with a mean length at age 1 of 104 mm. At age 3, mean lengths ranged between 157 and 330 mm with a mean length of 251 mm. Only three of the original 53 brown trout populations were found to live to 6 years of age, where mean lengths ranged between 346 and 536 mm with a mean length of 372 mm. Longevity within the brown trout populations ranged from 3 to 6 years, with 6 years of age being recorded in the Rivers Camel, Aire and Manifold. The brown trout population of the River Aire also had the fastest growth while the brown trout population of the R. Sett, had the slowest growth rate.



Figures 3.6a-b - Growth curves (a) from brown trout populations (n=53) and mean growth curve (b) from rivers throughout England and Wales.

Pike

Growth curves from 39 pike populations were available to calculate the mean growth curve (Figures 3.7a-b; Table 3.1). Mean lengths of pike at age 1 ranged between 121 and 374 mm with a mean length of 195 mm. At age 5, mean lengths of pike ranged between 560 and 801 mm, with a mean length of 679 mm. Only four of the original 39 populations held individuals that reached age 9 where mean lengths ranged between 880 and 915 mm with a mean length of 882 mm. No pike were recorded beyond nine years of age in this study. The pike population with the fastest initial growth rate was from the River Thames. These pike however were shown to live to 6 years of age, suggesting there are not very long lived, showing the live fast, die young strategy. The slowest growing pike were from the Yorkshire Ouse, they had one of the largest asymptotic lengths and lived to 9 years of age, suggesting this population grows slowly but lives a longer life, the opposite of the pike from the R. Thames.



Figures 3.7a-b - Growth curves (a) from pike populations (n=39) and mean growth curve (b) from rivers throughout England and Wales.

Perch

Growth curves from 49 perch populations were available to calculate the mean growth curve (Figure 3.8a-b; Table 3.1). A wide range of lengths were observed in the mean lengths at age 1, with lengths ranging from 29 to 116 mm, with a mean length of 77 mm. At age 5 the range in mean lengths between the fastest and slowest growing populations ranged between 183 and 314 mm with a mean length of 270 mm. Mean Lengths at age 10 ranged between 341 and 402 mm with a mean length of 356 mm. The number of populations containing fish over the age of ten years was just three with the longest lived individual aged at 13 years, caught in the River Great Ouse, and achieved a length of 364 mm. The fastest growing perch population was from the R. Mole. The slowest perch populations were also some of the shortest lived of this species and were from the R. Brue and Peover Eye.

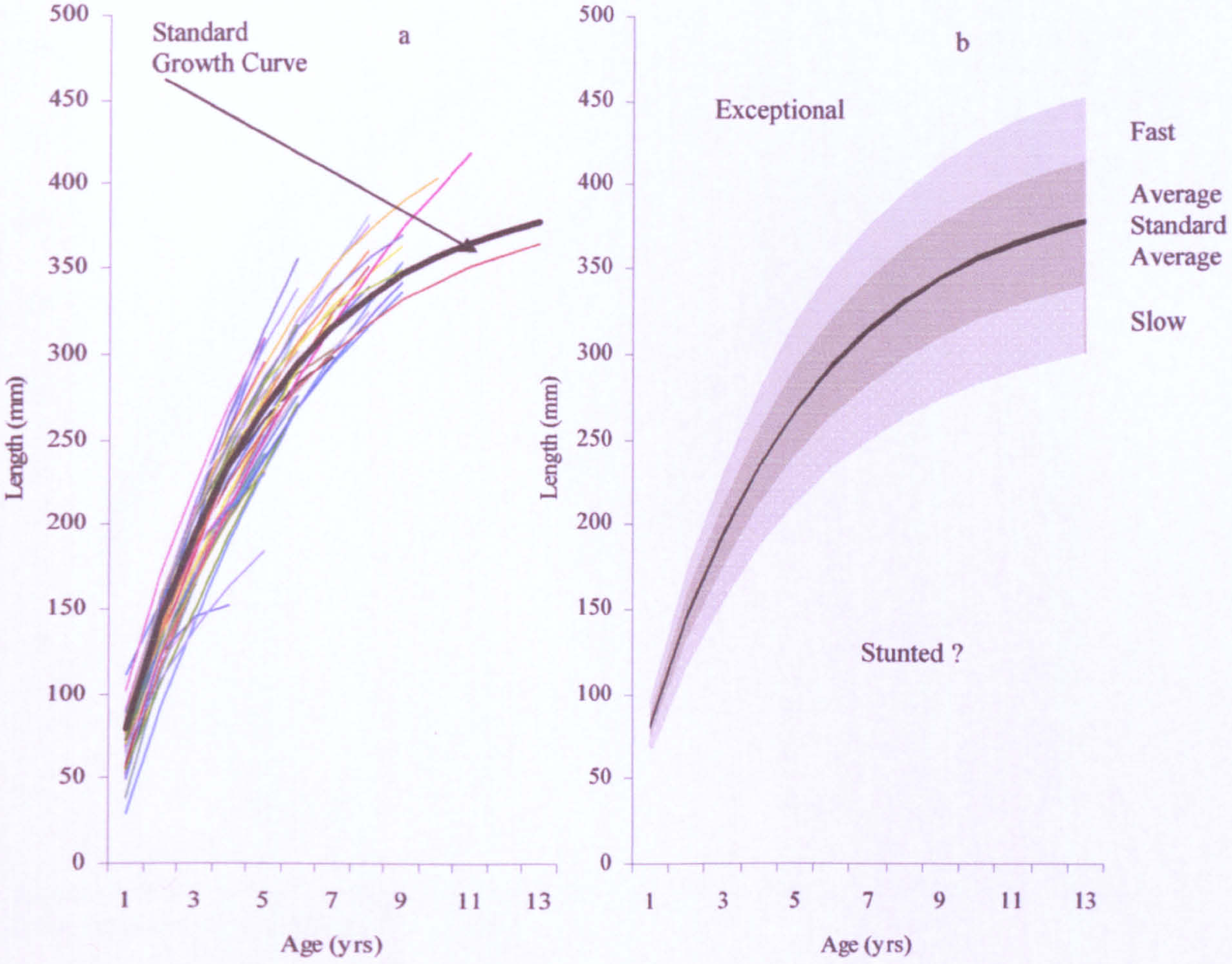
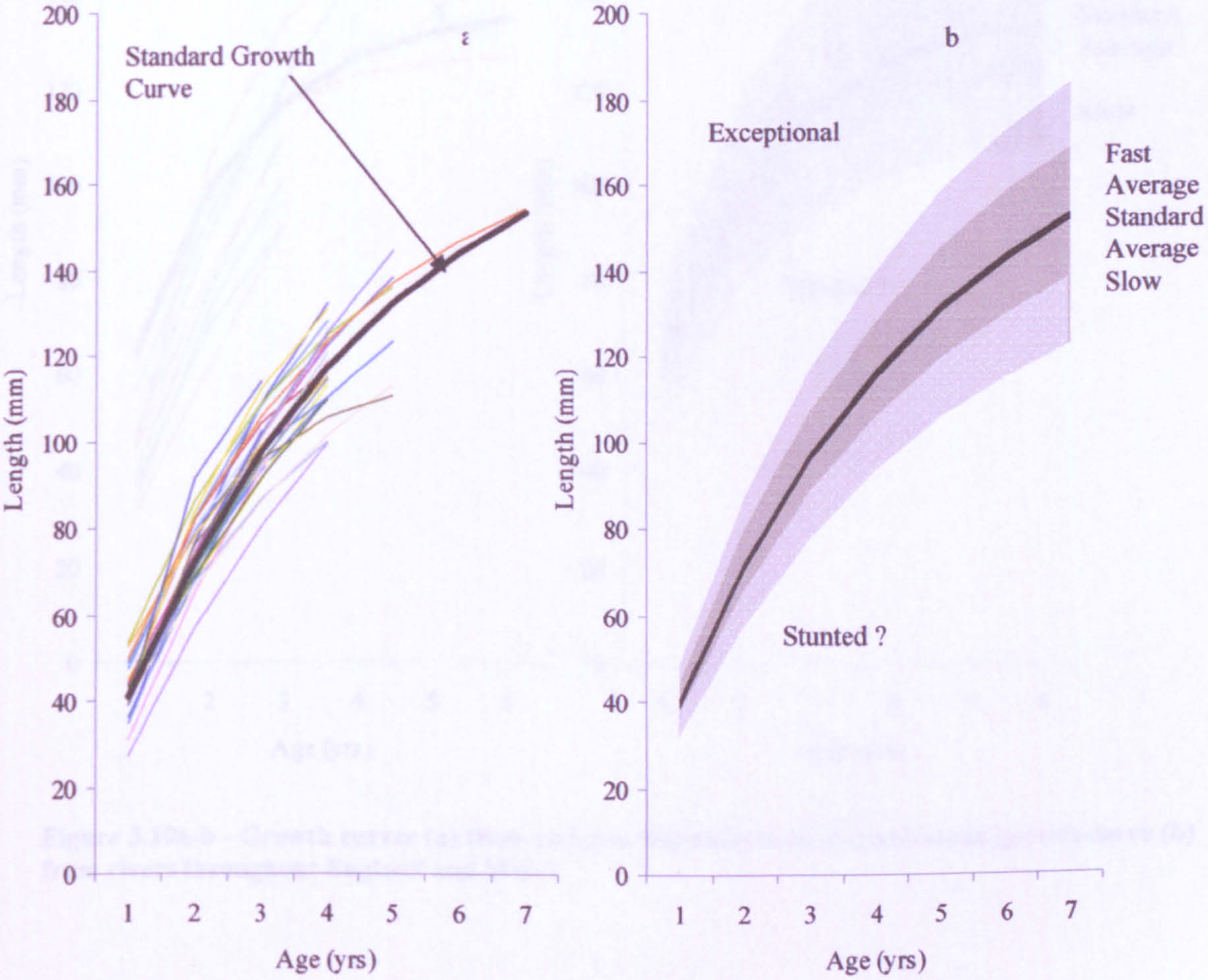


Figure 3.8a-b - Growth curves (a) from perch populations (n=49) and mean growth curve (b) from rivers throughout England and Wales.

Bleak

Growth curves from 28 bleak populations were available to calculate the mean growth curve (Figure 3.9a-b; Table 3.1). Mean lengths of bleak at age 1 ranged between 28 and 54 mm with a mean length of 41 mm. At age 3, the range in mean length increased to between 81 and 114 mm with a mean length of 98 mm. At age 5, mean lengths between the fastest and slowest growing populations ranged between 111 and 144 mm with a mean length of 132 mm. Only one population of bleak showed individuals which lived past five years with 154 mm at seven years being recorded from the River Kennet. The fastest growing population of bleak was from the R. Eden, while the slowest growing bleak population was from the R. Rother, Sussex.



Figures 3.9a-b - Growth curves (a) from bleak populations (n=28) and mean growth curve (b) from rivers throughout England and Wales.

Gudgeon

Growth curves from 14 gudgeon populations were available to calculate the mean growth curve (Figure 3.10a-b; Table 3.1). Gudgeon are a short lived species with no fish recorded beyond six years of age in this study, although older gudgeon have been recorded (Britton *pers comm.*). The range in mean lengths between the fastest and slowest growing populations at age 1 ranged from 31 and 63 mm with a mean length of 62 mm. At age 3, mean lengths at age ranged between 91 and 134 mm with a mean length of 128 mm. Only one population of gudgeon had individuals at six years of age and were from the River Kennet, where the greatest length was 127mm.

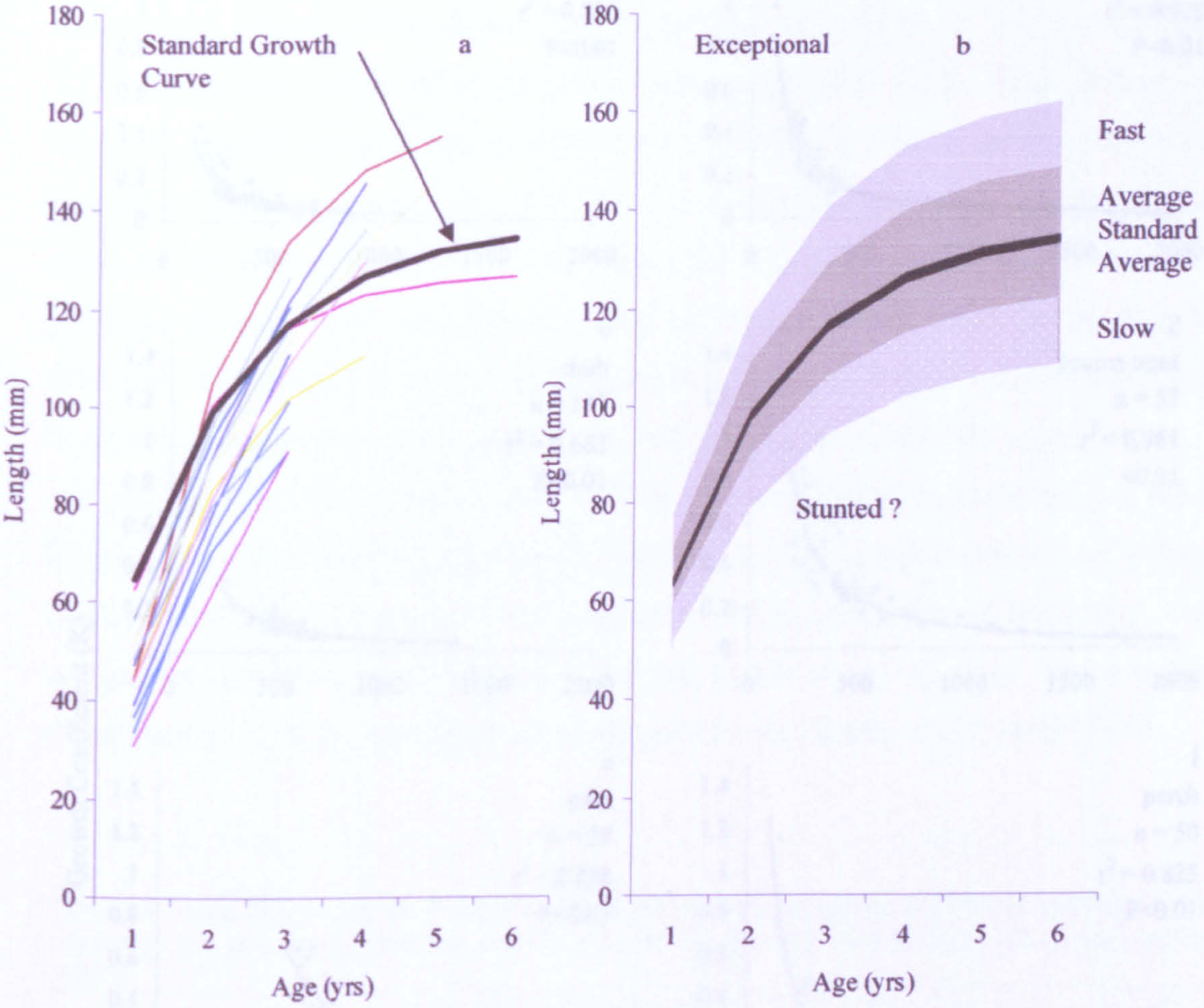
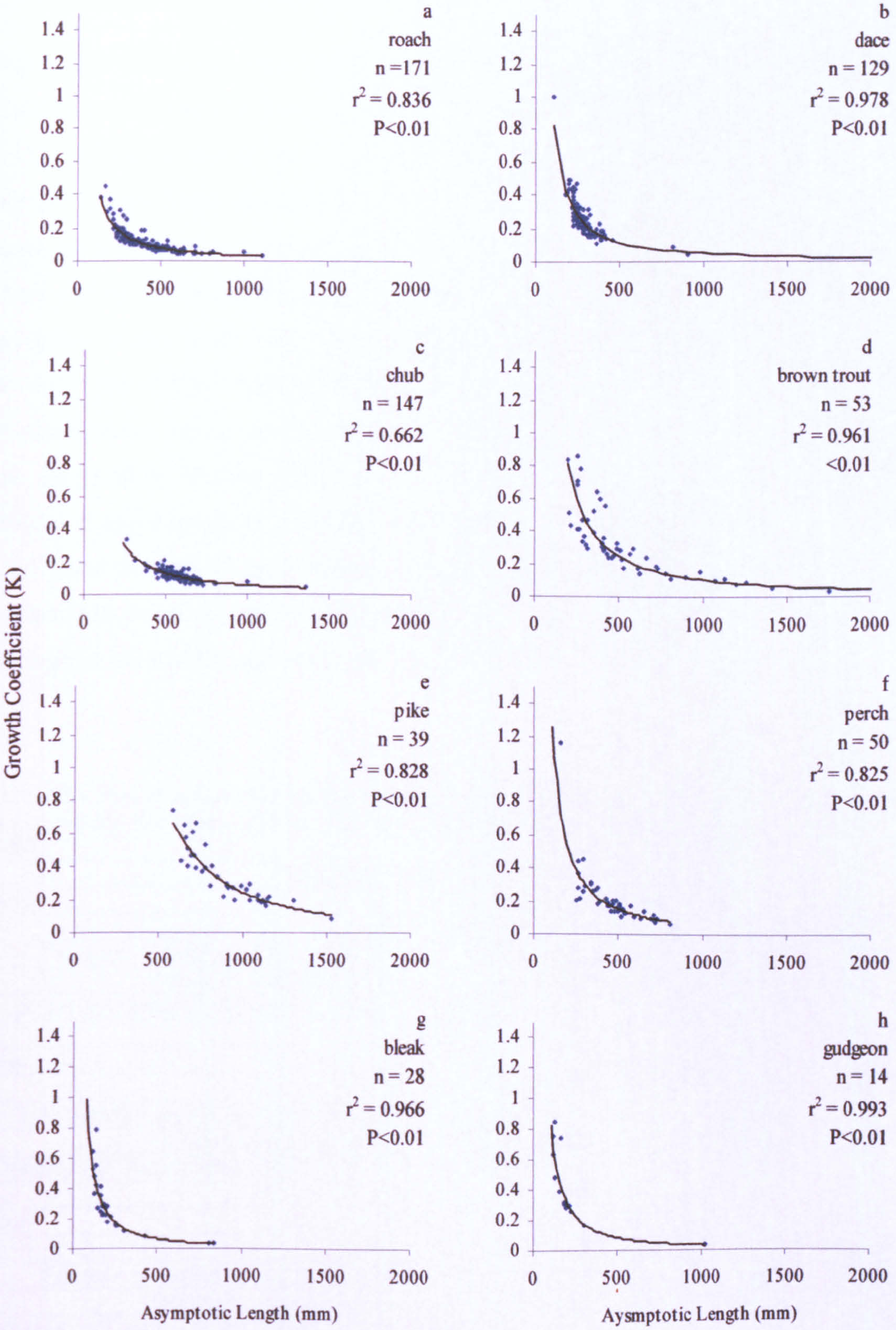


Figure 3.10a-b - Growth curves (a) from gudgeon populations (n=14) and mean growth curve (b) from rivers throughout England and Wales.

3.3.2 - Relationship between asymptotic length ($L_{\text{-infinity}}$) and growth coefficient (K)

An inverse relationship was found between asymptotic length and the growth coefficient of roach, dace, chub, brown trout, pike, perch, bleak and gudgeon populations from rivers throughout England and Wales (Figures 3.11 a-h). The inverse relationship reflected the growth coefficient decreasing with increasing values of $L_{\text{-infinity}}$, suggesting growth of populations that achieved a larger size was slower.



Figures 3.11a-h – Relationships between asymptotic length ($L_{\text{-infinity}}$) and the growth coefficient for various fish species from throughout England and Wales.

3.3.3 - Comparison of mean growth rates

Significant differences were found between the mean growth curves of all roach from Hickley and Dexter (1979), Britton (2007) and this study (P<0.01, Table 3.2, Figure 3.11). Individual testing of mean growth curves revealed where these differences occurred. Significant differences were found between the mean growth curves of roach from Hickley and Dexter (1979) and the mean curves of roach produced in this study and by Britton (2007) (P<0.01; Table 3.2). The mean growth curves for roach produced in this study was similar to that of Britton (2007) in the initial 8 years (P>0.05), the slightly higher growth rate of roach produced in this study however lead to greater mean lengths at age after 8 years of age (Figure 3.12). The mean lengths at age produced by Hickley and Dexter (1979) for roach however, show greater mean lengths at age throughout the entire 15 year range when compared to that of Britton (2007) and the first 12 years when compared to the mean lengths of this study. This comparison therefore reveals a reduced mean length at age of roach has occurred throughout most of the age range when compared with Hickley and Dexter (1979).

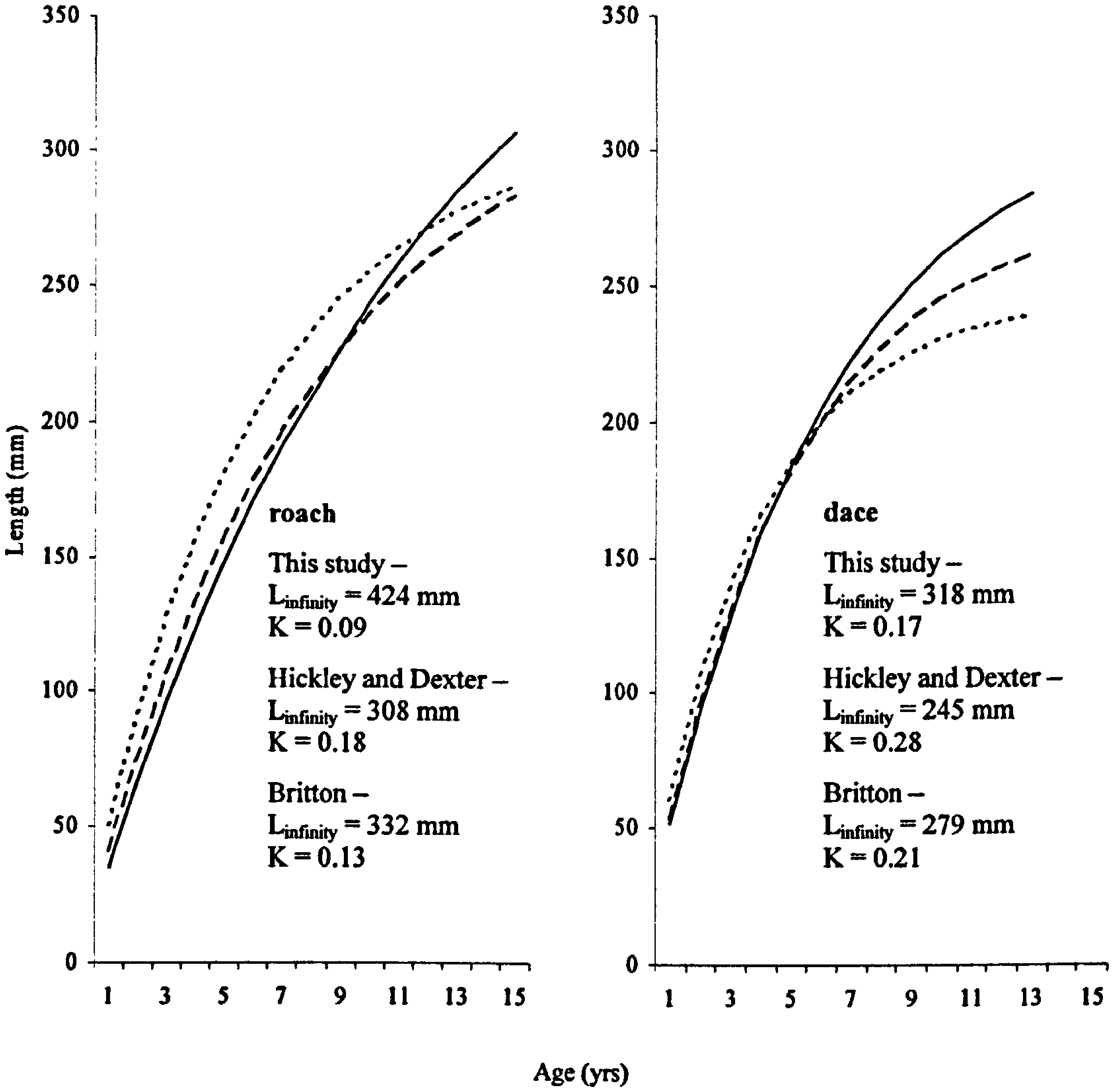
Table 3.2 – Sum of squares, df, F statistic and P values from comparison of Mean Growth Curves calculated for this study, Hickley and Dexter (1979), Hickley and Sutton (1984) and Britton (2007).

Comparison	Sum of Squares	df	F	P
roach				
all	2266.836	2	19.884	<0.01
This study v Hickley and Dexter (1979)	1448.242	1	17.473	<0.01
This study v Britton (2007)	33.063	1	0.661	>0.05
Hickley and Dexter (1979) v Britton (2007)	1918.949	1	101.540	<0.01
dace				
all	1226.276	2	8.145	<0.01
This study v Hickley and Dexter (1979)	1190.110	1	10.449	<0.01
This study v Britton (2007)	504.320	1	16.336	>0.05
Hickley and Dexter (1979) v Britton (2007)	144.984	1	3.682	<0.01
chub				
all	1286.578	2	5.151	<0.01
This study v Hickley and Dexter (1979)	783.971	1	22.566	<0.01
This study v Britton (2007)	29.329	1	0.303	>0.05
Hickley and Dexter (1979) v Britton (2007)	1116.567	1	5.985	<0.05

Table 3.2 (continued) – Sum of squares, df, F statistic and P values from comparison of Mean Growth Curves calculated for this study, Hickley and Dexter (1979), Hickley and Sutton (1984) and Britton (2007).

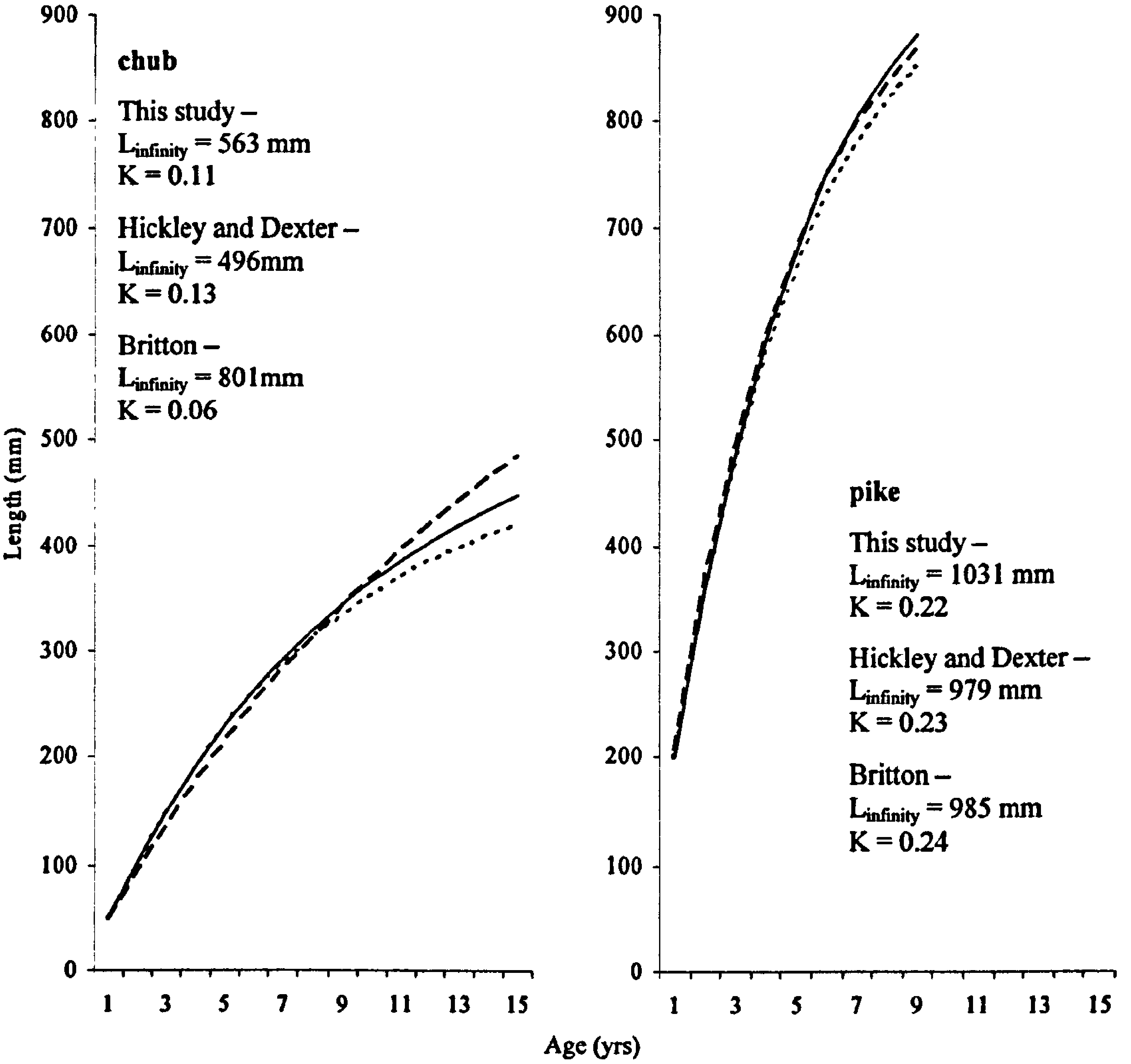
Comparison	Sum of Squares	df	F	P
pike				
all	1513.841	2	34.272	<0.01
This study v Hickley and Sutton (1984)	1181.129	1	40.712	<0.01
This study v Britton (2007)	1.924	1	0.094	>0.05
Hickley and Sutton (1984) v Britton (2007)	1087.708	1	244.759	<0.01
gudgeon				
This study v Britton (2007)	30.508	1	0.618	<0.05
bleak				
This study v Britton (2007)	17.274	1	4.266	>0.05
brown trout				
This study v Britton (2007)	3971.661	1	77.160	<0.01
perch				
This study v Britton (2007)	592.897	1	688.113	>0.05

Significant differences were found between the mean growth curve for dace calculated by Hickley and Dexter (1979) and both of the mean growth curves for dace calculated in this study and Britton (2007) (P<0.01, Table 3.2, Figure 3.13). Growth of dace in the first few years of life determined from this study was lower than that derived by Hickley and Dexter. The mean length at age of dace in this study was on average 10 mm lower until age four; after which the mean length at age was greater than those derived by Hickley and Dexter (1979). Again the mean growth curve of dace calculated by Hickley and Dexter slowed markedly as the asymptote was approached. The greater asymptotic lengths produced by this study and Britton (2007) reflects greater mean lengths at age after 5 years of age. The comparison therefore revealed the initial growth rate of dace has slowed slightly since that produced by Hickley and Dexter (1979) but greater mean lengths are achieved in later life.



Figures 3.12-13 – Mean growth curves of roach and dace from this study ———— , Hickley and Dexter (1979) ·········· and Britton (2007) – – – – – – – .

Mean growth curves for chub from this study and Britton (2007) were both significantly different to that of Hickley and Dexter (1979) ($P<0.01$; Table 3.10, Figure 3.14). However, the mean growth curves calculated in this study and that of Britton (2007) were similar ($P>0.05$). The mean growth curve of Hickley and Dexter had the lowest asymptotic length and the highest growth coefficient (Figure 3.14). Mean lengths at age from Hickley and Dexter (1979) were marginally larger prior to age 9, after which they were the smallest. The asymptotic length of chub calculated from Britton (2007) was much greater than the asymptotic lengths calculated for this study and Hickley and Dexter (1979) and produced the largest mean length estimates after age nine. The mean lengths produced by this study, after age 9, were intermediate to those of Britton and Hickley and Dexter (1979).

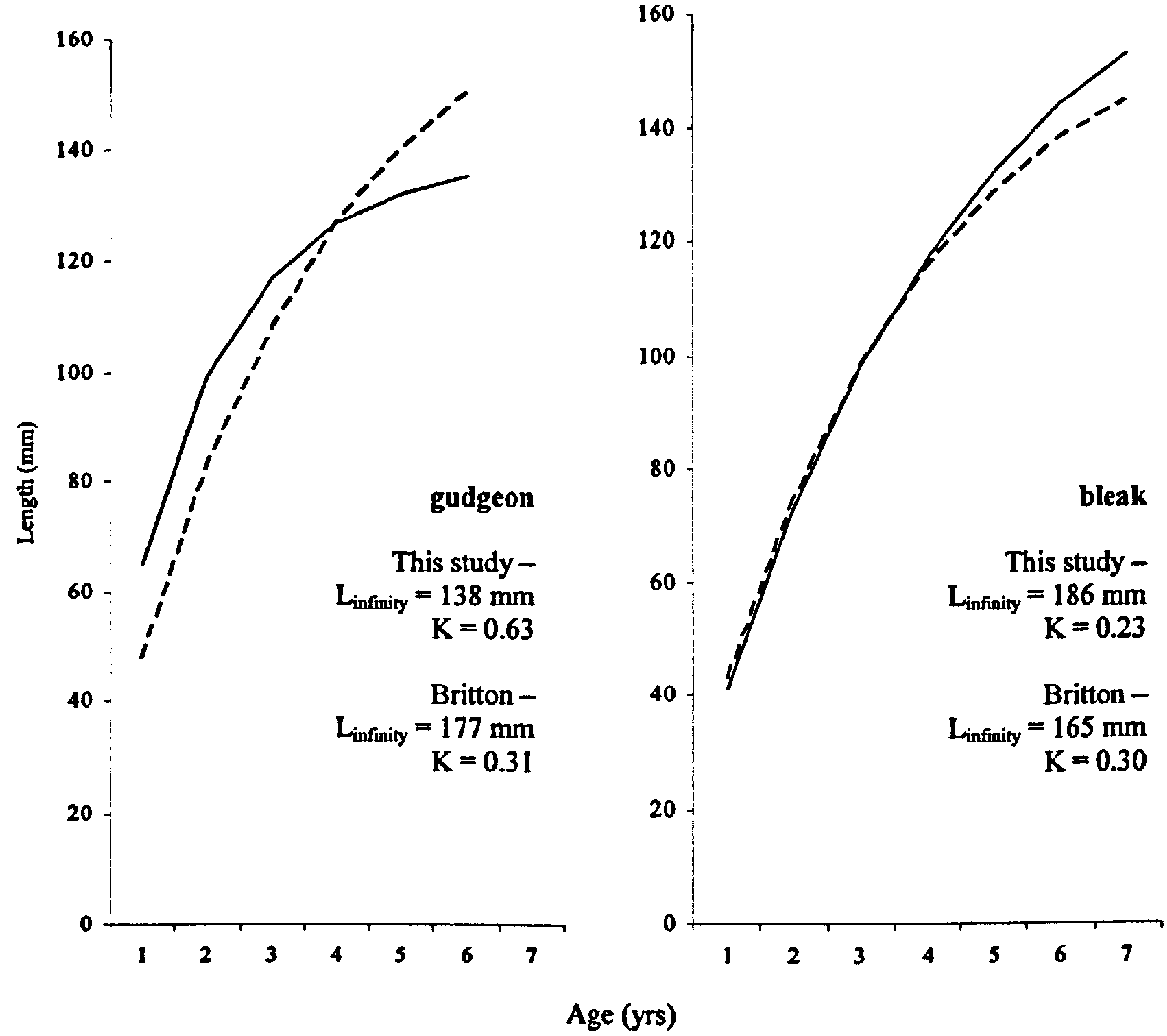


Figures 3.14-15 – Mean growth curves of chub and pike from this study ————, Hickley and Dexter (1979) ········ and Britton (2007) – – – – – – –.

Although the mean growth curves of pike appear to be very similar (Figure 3.15) significant differences were found (P<0.01, Table 3.10, Figure 3.15). Significant differences were again seen between the mean growth curve of pike produced by Hickley and Sutton (1984) when compared against the mean growth curves for pike calculated in this study and Britton (2007) individually (P<0.01, Table 3.10). The growth means from this study and that of Britton (2007) were however found to be similar (P>0.05; Table 3.10). Despite being significant, only small differences were observed between the growth curves (Figure 3.15), suggesting the growth of pike has changed little since the initial growth means for this species were produced by Hickley and Sutton (1984). Sexual dimorphism has been detected in the growth rates if pike (Clark and Stienbach 1959) with female fish growth being more rapid than that if male pike, however as no information as to the sex of the fish being included on each scale packet, no account of the differences between the growth of male and female pike can be given which, as Craig (1996) describes can be between 7% and 40% larger for females.

Comparison of mean growth curves for gudgeon from this study and Britton (2007), revealed a significant difference ($P<0.01$, Table 3.10, Figure 3.16). The growth coefficient was seen to be greater from the mean growth curve calculated in this study, while the asymptotic length calculated from Britton (2007) was larger. The greater growth coefficient resulted in mean lengths at age from this study being greater in the first three years, after which an abrupt decline in the mean grow rate resulted in lower lengths at age when compared to those from Britton (2007).

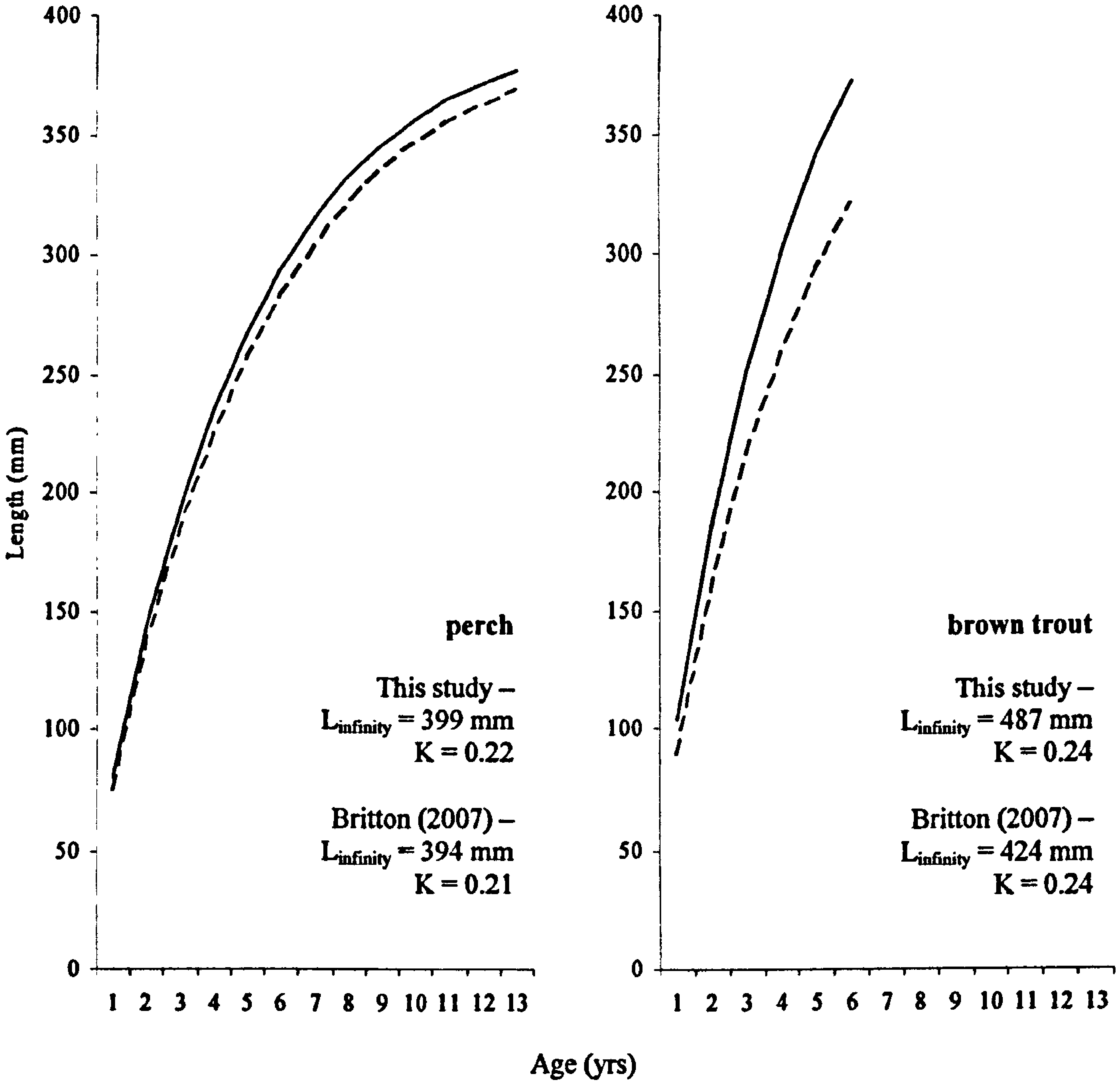
Comparison of the mean growth curves for bleak from this study and Britton (2007), revealed no significant difference ($P>0.05$, Table 3.10, Figure 3.17). The asymptotic length was seen to be greater for the mean growth curve calculated from this study, while the growth coefficient was greater in the mean growth curve calculated from Britton (2007). The greater asymptote and lower growth coefficient calculated in this study resulted in mean lengths at age being initially smaller prior to age four, but slightly larger after age four when compared to the mean lengths at age calculated from Britton (2007).



Figures 3.16-17 – Mean growth curves of gudgeon and bleak from this study ——— and Britton (2007) - - - - - - - .

Comparison of mean growth curves for perch from this study and Britton (2007), revealed no significant difference ($P>0.05$, Table 3.10, Figure 3.18). Both the asymptotic length and growth coefficients calculated from this study were slightly greater than those calculated from Britton (2007). The greater asymptote and growth coefficient resulted in mean lengths at age calculated in this study being slightly higher at all ages than those described by Britton (2007).

Comparison of mean growth curves for brown trout from this study and Britton (2007) revealed a significant difference ($P<0.01$, Table 3.10, Figure 3.19). The asymptotic length calculated in this study was greater than that described by Britton (2007), while the growth coefficients were the same in both examples. The greater asymptote and similar growth coefficient resulted in mean lengths at age for this study to be greater at all ages.



Figures 3.18-19 – Mean growth curves of perch and brown trout from this study ——— and Britton (2007) - - - - - - - .

3.4 – DISCUSSION

3.4.1 – Comparison of mean growth curves

Changes in the mean growth curves have occurred between those produced by Hickley and Dexter (1979), Hickley and Sutton (1984) and those calculated both in this study and Britton (2007), confirming the need to update these mean growth estimates for all available species on a regular basis. Reduced mean lengths at age 1 was found in both roach and dace and may be related to a number of factors.

There is an underlying trend for improvement in water quality in rivers throughout England and Wales in recent years. For example the Environment Agency (2001 2005a; 2005b) has reported improvements through their General Quality Assessment

(GQA) scheme, not only in chemical terms but also in biological terms. Since 1990 the biological quality of more than a quarter of the rivers of England and Wales has improved with three quarters of the rivers now classified as 'good quality' (Environment Agency 2007). Cowx and Broughton (1986) described the River Trent to be poor, post the Industrial Revolution, but it has improved after much effort. Water quality changes consequently led to changes in fish species composition, which was reflected in the relative importance of the major angling species in catches (Cowx and Broughton 1986). Since 1969/70 a steady decline in roach and dace in angler catches was observed, which coincided with a corresponding increase in chub, perch and bream populations. The decline in roach populations was attributed to a concomitant decline in the river's nutrient status. Decreasing turbidity and increasing water quality led to a recovery of previously suppressed species (Cowx and Broughton 1986). Improving water quality makes fewer nutrients available for phytoplankton growth, which impacts zooplankton populations by limiting phytoplankton populations. Increased competition from previously suppressed species for available space and food resources could cause a reduction in the growth rates of the River Trent roach populations. If these same changes are assumed to have occurred throughout the rivers of England and Wales due to the improvements in water quality, the increased competition may account, at least in part, for the reduced early growth rates of roach observed in this study.

Competition for food resources was also thought to be one of the reasons behind the reduction in the dace populations within the River Trent, although more directly from increasing chub populations (Cowx and Broughton 1986). Dace and chub are known to occupy similar niches, which combined with low habitat heterogeneity and increasing competition for food resources would have seen the chub populations become the more dominant species. If this pattern is assumed to have occurred throughout the rivers of England and Wales, the initial increase in lengths at age for chub and decreased growth rates of dace, may be related to the increasing dominance of the chub populations increasing the competition for resources. Increased water quality and improved competitive status through increased population densities providing conditions ideal for chub to increase their growth potential (Cowx and Broughton 1986).

Hickley and Dexter (1979) stated 'that as more growth studies are published, the mean lengths at age on which the mean growth curves are based should be altered, but doing this would defeat the object of having a mean'. The number of observations available to Hickley and Dexter during the inception of their mean growth curves was, however, low (roach 14; dace 11 and chub eight). Dytham (2005) stated that the number of observations taken in a sample can be of importance and 'more is always better than few'. Considerably larger numbers of observations were available in this study. It could therefore be argued the mean growth curves produced in this study offer greater robustness around the mean lengths at age values produced. Indeed it may be possible that the low number of populations used by Hickley and Dexter in the compilation of their mean growth curves was not representative of the entire range of lengths at age at that time, which may have resulted in a bias toward the differences observed. The robustness of the mean values compiled in this study, in conjunction with changes in the environment and subsequent changes in the observed mean growth rates since their inception must therefore merit the need for updated mean growth curve data, which should be re-evaluated, perhaps every 10 years. 10 years being a length of time that it was felt would be sufficient to allow any changes in the growth rate to manifest to an extent that they would be detectable.

3.4.2 – Standardised growth as a comparative tool

Comparative growth tools are basic indices used to assess population mean growth parameters, and remain valuable to fishery managers because of their ease of interpretation and their role in supporting identification of populations that are not performing well in terms of growth (Britton 2007). For example, when poor growth is identified in a population, it may be possible to relate it to causal factors that may be addressed. Harvey and Cowx (1998) found the roach and dace populations in the Leven Canal (Yorkshire) had poor growth rates in their early life histories. This initial poor growth was related to poor food quality in the early years of life and the productivity of the canal. This was coupled with reduced predation pressure on the population because of earlier cull of pike; this cull appears to have resulted in an over abundance of roach, and possible increased intra-specific competition for limited resources (Harvey and Cowx 1998).

The use of standard growth curves and associated indices allows comparison of growth parameters, to determine whether any part of the growth history deviates in relation to the mean. For instance, growth in larval fishes is strongly influenced by the availability of appropriate food items (Welker *et al.* 1994). Many larval fishes rely on small zooplankter as prey due to limited gape width (Bremigan and Stein 1994), and can be susceptible to fluctuations in prey availability (Graeb *et al.* 2004). Poor early growth, when identified, may therefore be due to the lack of, or the size of the zooplankters available to the juvenile fish, which may be related to such factors as productivity or pollution. Good initial growth however, may be due to high zooplankter availability, through increased primary productivity, although other factors such as temperature and flow dynamics will also, in conjunction with food availability, be of importance. The adult stages of slow growing populations are therefore expected to achieve greater lengths and weights, due to the inverse relationship between the growth rate and asymptotic length. Achieving greater lengths could be advantageous to the fish community, due to the relationship between fish length and fecundity. If it is assumed that increased fecundity is related to increasing length and greater length associated with greater age, and therefore the number of spawning events, the reproductive potential of the fishery may be improved. Improved reproductive potential may ultimately lead to increased recruitment, although increased numbers of fish would also lead to increased competition for resources leading to a possible decrease in the growth rate in the future. This would be of importance to many anglers as larger, heavier fish are highly prized and therefore of greater importance.

A number of what were considered as artificially high mean lengths at age 1 were found in this study. It was felt that for bleak, gudgeon and to a lesser degree chub, the mean length at age 1 was too high. One reason for this is a form of mis-interpretation during the ageing process. A missing first year annulus on fish scales has been reported for a number of species such as herring (*Clupea harengus harengus* L.) (Hodgson 1934), sprats (*Sprattus sprattus sprattus* L.) (Iles and Johnson 1962) and charr (*Salvelinus willughbii* Gunther) (Frost 1978). Frost (1978) postulated that this was due to the juvenile fish not reaching a sufficient length to lay down scales before the first winter of life. The first annulus laid down on the scale is therefore formed at the end of the second year of life. The missing first year of life is therefore not considered in the back-calculation of length at age, leading to an artificially high length at age estimate. In a number of cases the interpretation of the first annulus laid down was difficult, as it was either very small, weakly formed or missing. Nunn (2005) showed a number of species have the potential to spawn more than once a year, which acts as an 'insurance policy' against discharge-induced 0+ mortality. Late spawning of species, such as chub therefore increases the possibility of very small fish to persist through the winter period as they have not had sufficient time to attain larger lengths. Nunn *et al.* (2007c) showed chub of 16 mm on the Yorkshire Ouse and 18 mm on the River Trent persisted through their first winter, which is around the length of 15.9 mm given by Economou *et al.* (1991) as the length at which squamation of scales begins in chub. It is easily possible to misidentify the first annulus in these species and allocate a larger mean length at age than that which should be given, which would in turn increase the reported mean length at age (Bolland *et al.* 2007), however, due to the stringent quality control measures that accompanied each survey in this study, has helped to alleviate this problem.

3.4.3 – Relationship between Von Bertalanffy growth parameters ($L_{Infinity}$ and K)

Among those whom study ageing, one long accepted maxim is that the bigger you are the longer you live (Tangley 2007). A number of authors have described an inverse relationship between asymptotic length and the growth coefficient for many fish species (Zirkov *et al.* 1999; Pilling *et al.* 2002; Kozlowski *et al.* 2004; Heibo and Magnhagen 2005; Britton 2007) as was found in this study. However, a degree of plasticity exists in these relationships as specific values for the growth coefficient coincide with variable values for asymptotic length and vice-versa. Populations that displayed a fast growth rate for their species, and as such considered as fast growing, can display low asymptotic lengths which suggests a trade off between the growth rate and their ultimate length (Britton 2007).

Growth plasticity has been demonstrated for a number of species and a variety of reasons put forward to explain the variation. Cowx (1989) showed increased growth rates relating to habitat preferences. Growth within preferred areas, where such factors as temperature and flow conditions were best, was shown to be high, whereas growth outside of the preferred habitat was shown to be slower. Wootton (1990) described growth as an output based upon food consumption, with both the quality and quantity of the food being relevant to the growth performance. Food quality differs in both the energy and nutrient content and in the size of the food particle, with good quality food providing sufficient energy for good growth. Competition for available resources has an effect upon the growth rate. Growth rates have been described as negatively density dependant (Davey 2006), where high densities increase the competition for available resources resulting in a reduced growth rate.

One theory for the trade off between growth rate and asymptotic length is the effect of growth rate upon the size at first maturity. As the growth rate of fish changes, a reproductive adjustment through changes in age and size at maturity is normally observed (Jonsson *et al.* 1984). Juvenile growth rates are important in determining the age at first maturity, as early maturing individuals grow faster and are thus larger than immature specimens at any specific age. Early maturing individuals are, however, smaller at maturity than those that grow slowly and mature later (Hesthagen *et al.* 2004). A larger size at maturity is benefited by an increased fecundity, assuming a log linear relationship between length and fecundity (Berrigan and Charnov 1994). Tsikliras *et al.* (2007) postulated that fast growth rates are at the expense of the number of oocytes produced, but the potential for future reproduction is increased due to the increased length of the fish in the following year and therefore an increased population fecundity. Therefore decreased fecundity due to increased energy allocation to growth implies an increased reproductive potential of the stock in the subsequent years as larger individuals are more fecund and produce better quality oocytes (Birkeland and Dayton 2005).

Longitudinal variation in the life histories of fish has been demonstrated along the course of a river (Cowx 1989; Przbylski 1995). Zonation patterns show the preferences each fish species has toward specific habitat qualities, where considerable variation is seen between the growth rates between preferred and less than preferred habitats (Cowx 1988). Given the relationship between growth rate and the preference for specific habitat requirements leading to specific fecundity measures, it may be that increased fecundity beyond the second reproductive cycle may be an adaptive process allowing for a maximisation of the reproductive effort of fast growing fish which leads to high abundances within their preferred areas. Whereas in slower growing populations where somatic growth is lower and sexual maturity is achieved at a longer length, the fish select for a higher quality of oocytes (Hancock 1979) at the cost of lowered fecundity (Vøllestad and L'Abée-Lund 1990). This may benefit the offspring as better quality oocytes benefit from an increased energy input from the parent and therefore larger, older females produce eggs and larvae that are more likely to survive (Palumbi 2004) due to the increased energy input to oocytes. Life-history theory predicts that females should increase their investment in offspring quality if young fish encounter adverse environmental conditions (Bernardo 1996; Mousseau and Fox 1998). In several species of fishes, larger offspring do better under adverse environmental conditions than small young, whereas under favourable conditions the latter survive equally well or even better (Mousseau and Fox 1998; Einum and Fleming 1999). The production of larger, more energy-rich eggs is traded off against brood size or against future reproductive potential (Roff 1992).

CHAPTER FOUR

GROWTH PERFORMANCE OF FISH AT THE CATCHMENT AND NATIONAL LEVELS

4.1 – INTRODUCTION

The study of factors structuring ecological communities has focused on whether or not those communities contain discrete and non-random assemblages (Connor and Simberloff 1979), and whether those species, and therefore the communities, are regulated by biotic and abiotic factors (Andrewartha and Birch 1954). Riverine fish communities have been described as highly structured, following non-random patterns along a longitudinal profile (Jackson *et al.* 2001, Ibarra *et al.* 2005). The River Continuum Concept is a theory used to describe the physical, chemical and biological changes that occur along a longitudinal gradient from the headwaters to the lower reaches of the river system (Vannote *et al.* 1980). Numerous studies of fish in streams and rivers found variation in fish species composition along longitudinal gradients. Adaptations to habitat conditions are associated with upstream through downstream variation in water depth, current velocity and substratum (Vila-Gispert *et al.* 2002), and the significance of primary productivity of lotic phytoplankton and macrophytes, which increase within streams and rivers, as they increase in size and decrease in flow velocity (Wetzel 1983).

Intraspecific variation in the growth of freshwater fish on large spatial scales has often been related to latitudinal clines. Growth rates are expected to decrease with increasing latitude for many fish species, because of the direct effect of temperature on growth (Blank and Lamouroux 2007). Testing life history traits in a number of European fish species, populations at high latitudes often displayed reduced growth rates, had an increased life span, greater asymptotic lengths and allocated more energy to reproduction than populations of the same species at lower latitudes (Blank and Lamouroux 2007).

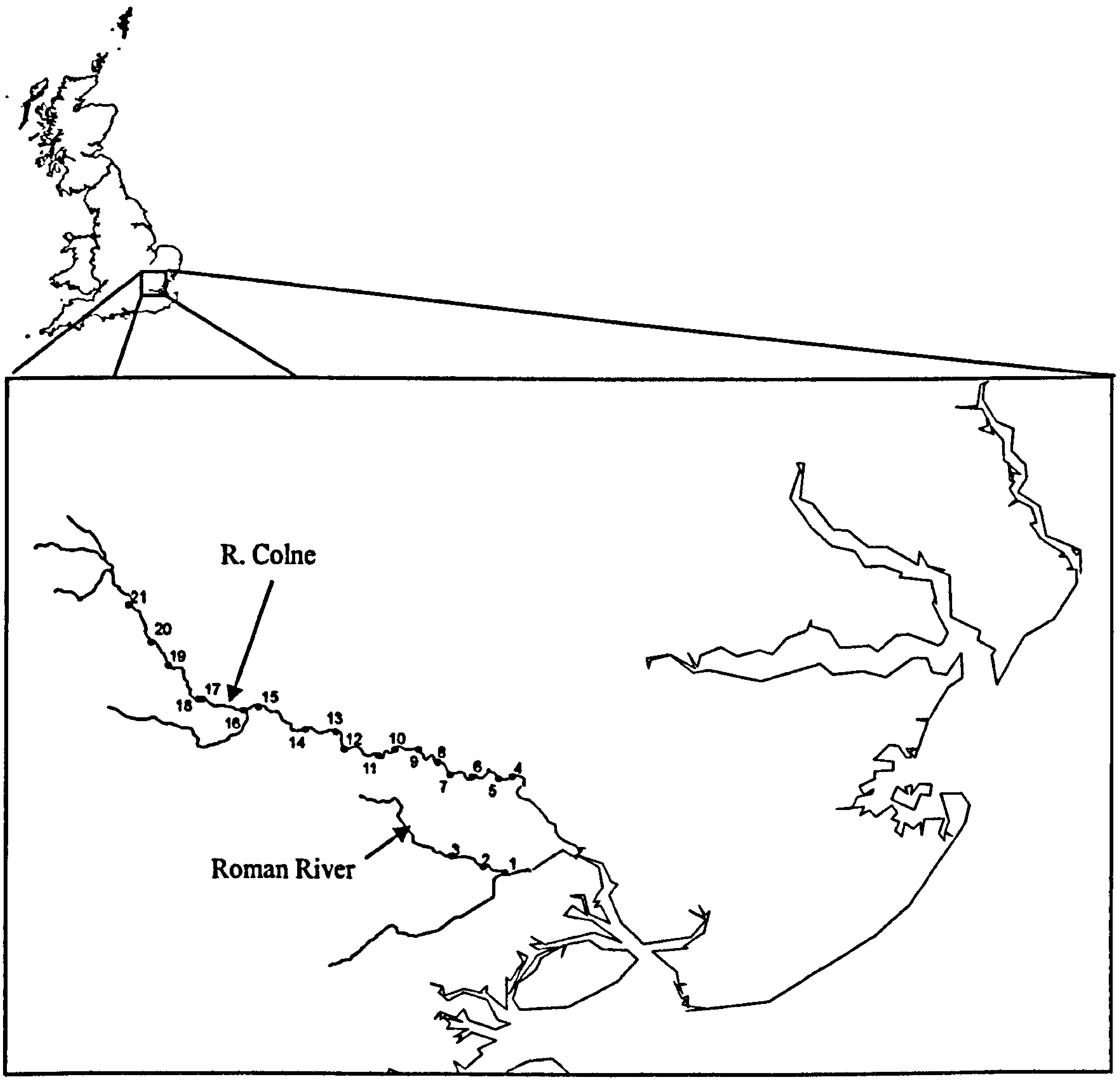
Longitudinal zonation concepts describe the downstream changes in chemico-physical and biological properties of rivers, which change gradually along its course from headwaters to mouth. One conspicuous result of these shifting environmental parameters is that most fish will find suitable living conditions within specific stretches of the river (Cowx 1988; Aarts and Nienhuis 2003). The aim of this chapter was, using growth data derived from fish ageing studies and site specific data, (1) to determine patterns within the physical habitat from which longitudinal characteristics of the rivers in question can be used, in conjunction with biotic variables; (2) using abiotic data from a number of catchments, use the characteristics to determine any affect of differing abiotic variables on a number of biotic growth characteristics; (3) from abiotic variables collected from rivers throughout England and Wales, determine whether growth characteristics differ along an entire UK gradient, i.e. does the influence of latitudinal position influence observed growth characteristics.

4.2 – METHODS AND MATERIALS

4.2.1 – Factors affecting growth characteristics at the catchment level

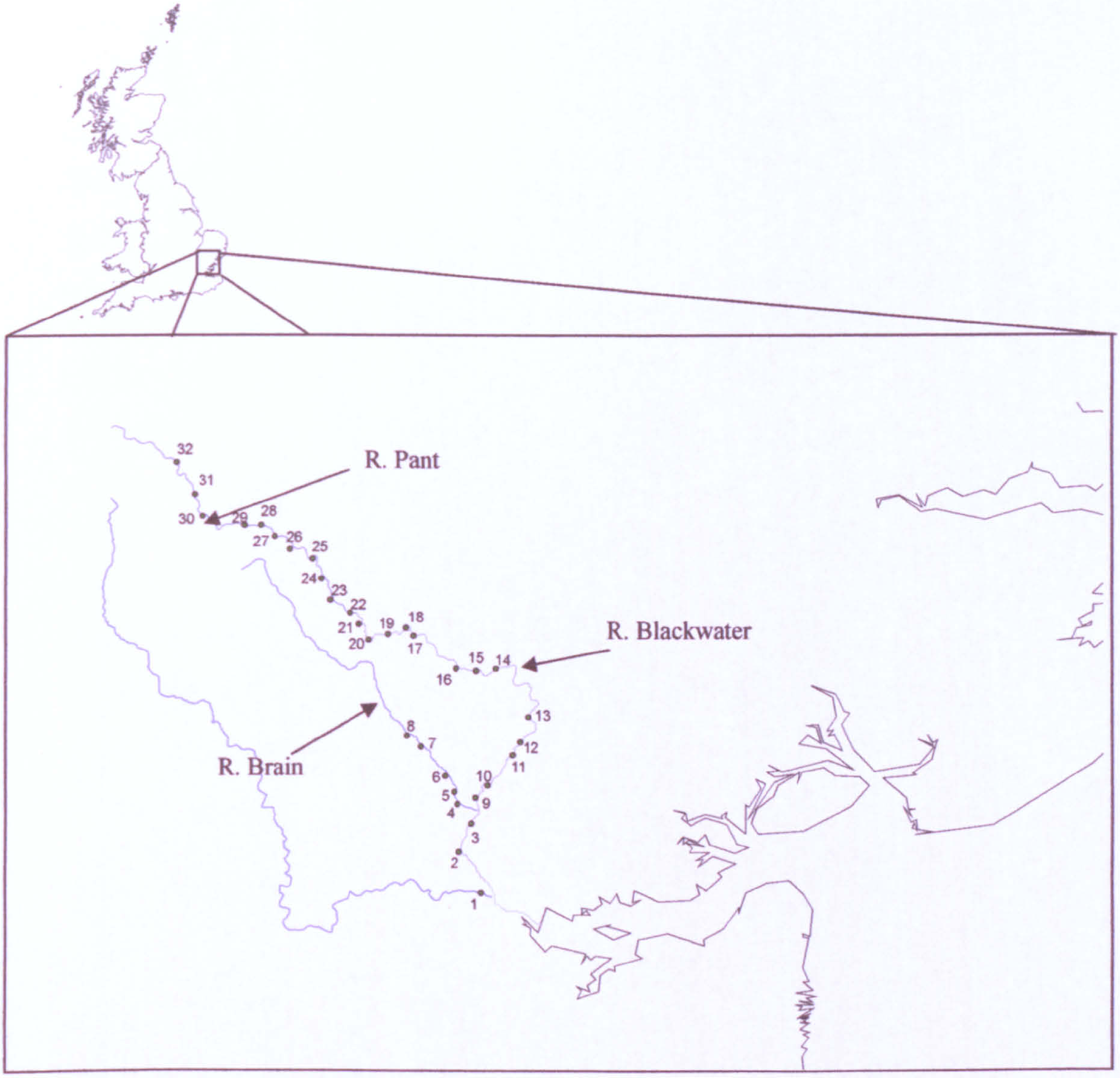
To test for relationships between growth characteristics and abiotic variables at the catchment level, multiple regression analysis was used. The Colne, Blackwater and Yorkshire Ouse catchments (Figures 4.1 - 4.3) were chosen for study as these catchments contained large numbers of sites where site specific growth characteristics and abiotic data were available. From each catchment a number of growth characteristics were chosen from data derived from scale reading. Growth characteristics included the asymptotic length ($L_{infinity}$), the rate at which the fish grows toward the asymptote, the growth coefficient (K), a measure of longevity (the oldest recorded age of the species in question at each specific site, max age), percentage standard growth and mean length attained at age one.

Abiotic environmental variables were derived from Environment Agency data, and included the size of the catchment upstream of each site (km^2), the altitude of each site (m above datum), wetted width (m) and distance from source (km). No direct data for river discharge rates were available for each site, so a measure of river bed gradient ($^0/_{00}$, derived from ARC GIS) was used to give an approximation of flow dynamics, where greater gradients indicate increased velocity. As with discharge, no water temperature parameters from each site were available, so mean air temperature from June to September during the study period was used to approximate mean water temperature during the growing season. Sett (1940) from records of air and water temperatures, demonstrated the daily rate of water temperature was a linear function and that this relation can be used to predict water temperatures. Relationships between each of the abiotic variables and growth parameters were examined separately using linear regression, while relationships between each growth parameter and all identified abiotic variables were identified using multiple regression analysis performed in SPSS (ver14).



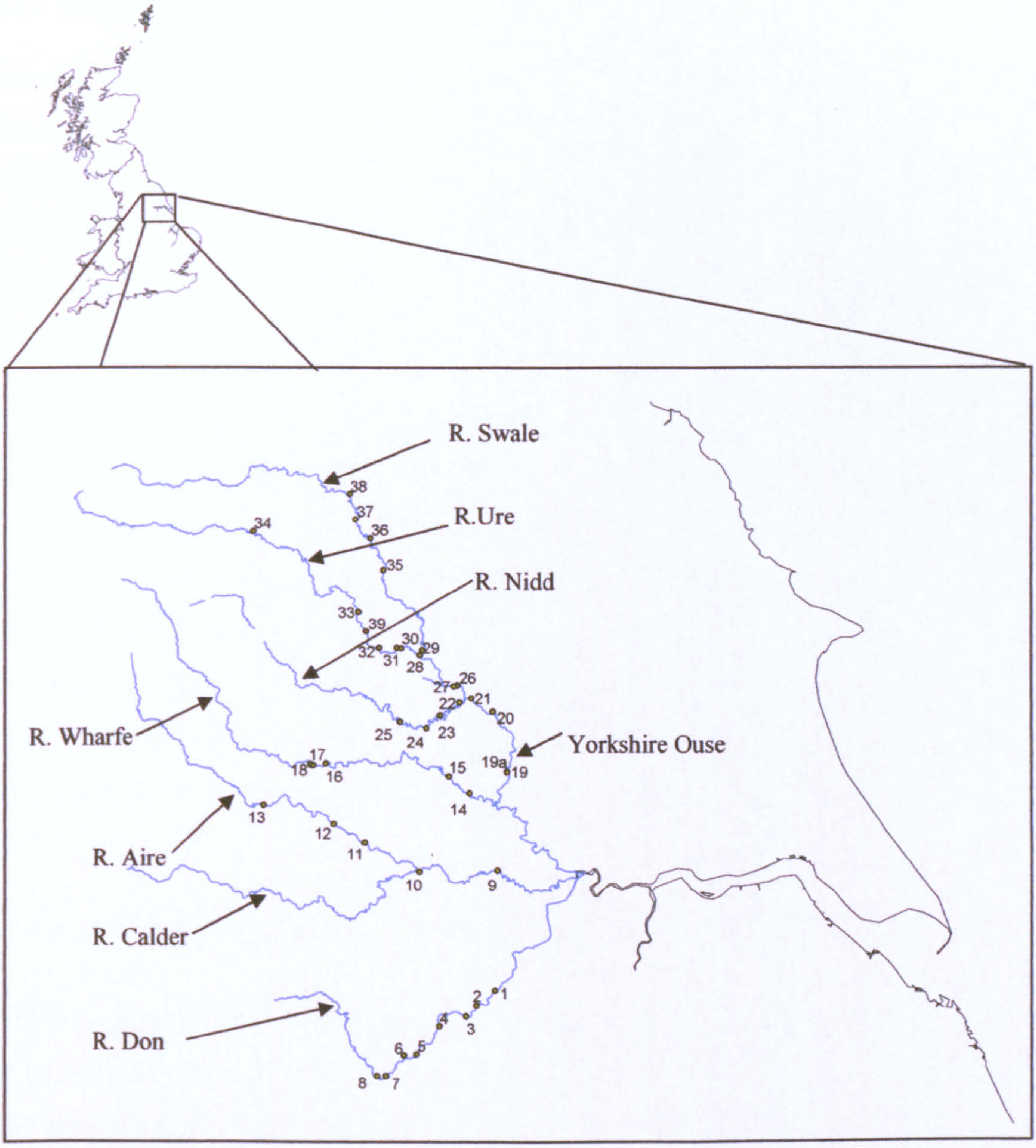
1	Park Farm (r)	2	Bounstead FGS (r)	3	Olivers Farm (r)
4	Cricket Ground (r)	5	North Bridge (r)	6	Spring Lane (rd)
7	u/s A12 Bridge (rc)	8	New Bridge (c)	9	Cooks Mill (rd)
10	Fiddlers Mill (d)	11	Fordstreet (rdc)	12	Broom House (dc)
13	Wakes Colne Viaduct (rdc)	14	Swanscombe Farm (c)	15	Earls Colne FGS (rdc)
16	Elms Hall (rd)	17	Blue Bridge (dc)	18	Halstead (rdc)
19	Brook Street Farm (rdc)	20	Alderford Mill (r)	21	Nunnery Bridge (r)

Figure 4.1 – Distribution of sites along the River Colne catchment (Essex), codes after each site name referring to the species at each site where biotic and abiotic data were gained, r = roach, d = dace and c = chub.



1	Langford (c)	**2**	Smallands Hall (d)	**3**	Blue Mills (c)
4	Witham Park (rdc)	**5**	Guithavon FGS (rdc)	**6**	Bramble Road (rdc)
7	Faulbourne Ford (dc)	**8**	White Notley STW (dc)	**9**	d/s Braxted Hall (rc)
10	u/s Braxted Hall (rc)	**11**	Ashmans Farm (c)	**12**	Greys Mill (c)
13	Kelvedon Coalyard (rd)	**14**	Coggeshall (rc)	**15**	West Mill (dc)
16	Bradwell Hall (rc)	**17**	Stisted FGS (rdc)	**18**	Covenbrook Hall (r)
19	Lyons Hall (rc)	**20**	Hobbs Meadow (r)	**21**	Dorewards Hall (r)
22	Courtaulds Mill (r)	**23**	Bovington Hall (rdc)	**24**	Goldsticks Farm (rdc)
25	Iron Bridge (rdc)	**26**	Wethersfield Mill (rc)	**27**	Ashwell Hall (rdc)
28	Petches Bridge (dc)	**29**	Robjohns Farm (dc)	**30**	Little Farm (dc)
31	Gambers Hall (dc)	**32**	d/s Great Sampford (c)		

Figure 4.2 – Distribution of sites along the River Blackwater catchment, Essex, codes after each site name referring to the species at each site where biotic and abiotic data were gained, r = roach, d = dace and c = chub.



1	Crimpsall (rdc)	**2**	Sprotborough Weir (rc)	**3**	Connisborough (r)
4	Kilnhurst bridge (rc)	**5**	Rotherham Weir (rd)	**6**	Blackburn Meadows (rd)
7	Attercliffe (r)	**8**	Kelham island (d)	**9**	Chapel Haddersley (r)
10	Castleford (r)	**11**	Thwaite Mills (rdc)	**12**	Kirkstall (dc)
13	Hirstwood weir (rc)	**14**	Ulleskelf (rd)	**15**	Tadcaster (dc)
16	Castley (dc)	**17**	Pool Mill (dc)	**18**	Knotford (c)
19	Acaster Malbis (r)	**19a**	Naburn (r)	**20**	Nether Poppleton (r)
21	Benningborough (r)	**22**	Nun Monkton (rc)	**23**	Kirkhammerton (rdc)
24	Cowthorpe (dc)	**25**	Ribstone Park (c)	**26**	Linton weir (r)
27	u/s Linton weir (r)	**28**	Dunsforth (r)	**29**	Myton Grange (r)
30	Boroughbridge (rdc)	**31**	Langthorpe (r)	**32**	Westwick Weir (rdc)
33	Ripon Golf Club (c)	**34**	Middleham (c)	**35**	Holme on Swale (c)
36	Maunby (c)	**37**	Morton on Swale (c)	**38**	Langton (dc)
39	Hewick Bridge (rdc)				

Figure 4.3 – Site distribution along Yorkshires River Ouse, codes after each site name referring to the species at each site where biotic and abiotic data were gained, r = roach, d = dace and c = chub.

4.2.2 – Catchment wide growth characteristics

Hierarchical cluster analysis was used to examine any relationships between growth characteristics of roach, dace and chub and abiotic variables at each site from which each species was recorded within the Blackwater, Colne and Yorkshire Ouse catchments. Growth variables for roach, dace and chub were obtained from scale reading (Section 4.2.1). Abiotic data were extracted from Environment Agency data and were the same as those used for the regression analysis (Section 4.2.1).

Hierarchical cluster analysis, using within groups linkage, was used to cluster growth characteristics and abiotic data separately. Sites were grouped into clusters that shared an association, such that sites were linked with increasing dissimilarity (Statsoft 2005). After an initial output was gained, and dendrograms compiled, a decision was made as to the number of clusters evident in the data, this was achieved by identifying within the dendrogram areas where the cluster structure remained stable over a long distance. The analysis was then re-run to assign each site to a cluster group, and mean values for each of the growth characteristics and abiotic variable clusters identified, gained.

4.2.3 – Variation in growth of roach, dace and chub at the national level

Multiple regression analysis was used to determine whether environmental variables interact to determine the observed growth characteristics in roach, dace and chub in rivers throughout England. Growth characteristics as defined in Section 4.2.1 were extracted for roach, dace and chub from all rivers where individual site data were available from scale reading. With the exception of the inclusion of latitudinal position, the same abiotic variables as those identified in Section 4.2.1 were used. Multiple regression analysis was performed on each of the growth characteristics (dependant) variables against all abiotic (independent) variables individually.

4.2.4 – Canonical correspondence analysis of nation wide growth characteristics and abiotic data

Canonical correspondence analysis (CCA), a multivariate direct gradient analysis technique whereby a set of species data is related directly to a set of environmental variables was used to identify an environmental basis for ordination using growth variables for roach, dace and chub. This is achieved by detecting patterns of variation within the growth characteristics that can be explained by environmental variables (Ter Braak 1986). To achieve this, all rivers where site specific data were available were identified and a number of growth characteristics for roach, dace and chub derived from scale reading extracted. The growth characteristics used were the asymptotic length ($L_{infinity}$), growth coefficient (K), max age, and the lengths of each species at ages one, two, three, four and five (these ages being chosen as they represented the period when growth is at it's fastest and best represents the growth of the fish). Environmental variables were selected from Environment Agency derived data, and included latitudinal and longitudinal co-ordinates for each site, a measure of river bed slope ($^{0}/_{00}$), altitude (m above datum), distance from source (km), mean summer air temperature (^{0}C), wetted width (m) and the size of the catchment above each site (km^{2}). Before any analysis was attempted data were first transformed to down-weight high abundances; growth characteristics were square root transformed and environmental data log transformed, as recommended by Ter Braak (1986). Data were then imported into CANOCO for Windows (ver 4.52). Canonical correspondence analyses were performed on each species separately.

4.3 – RESULTS

4.3.1 – Variation of abiotic characteristics at the catchment level – linear regression analysis of catchment wide abiotic factors

Linear regression of abiotic variables from the Yorkshire Ouse Catchment, revealed a number of both significant and non-significant trends (Table 4.1). As distance from source increased there was a concurrent increase in both catchment area above each site and wetted width. Decreases in altitude (Figure 4.4) and river bed gradient were found with increasing distance from source. Similar trends were observed with catchment area above each site. Decreasing altitude and river bed gradient were found with increasing catchment area above each site. Wetted width increased with a decreasing river bed gradient, while an increasing river bed gradient was found with increasing altitude. Mean air temperature was 9°C across all sites in this catchment making regressions of mean air temperature redundant.

Table 4.1 - Relationships (r^2) between abiotic variables of the Yorkshire Ouse catchment.

	Distance from source	Catchment area above site	Altitude	Mean air temperature	River bed gradient	Wetted width
Distance from source		0.700	0.270	-	0.102	0.002
Catchment area above site			0.482	-	0.308	0.371
Altitude				-	0.153	0.088
Mean air temperature					-	-
River bed gradient						0.018
Wetted width						

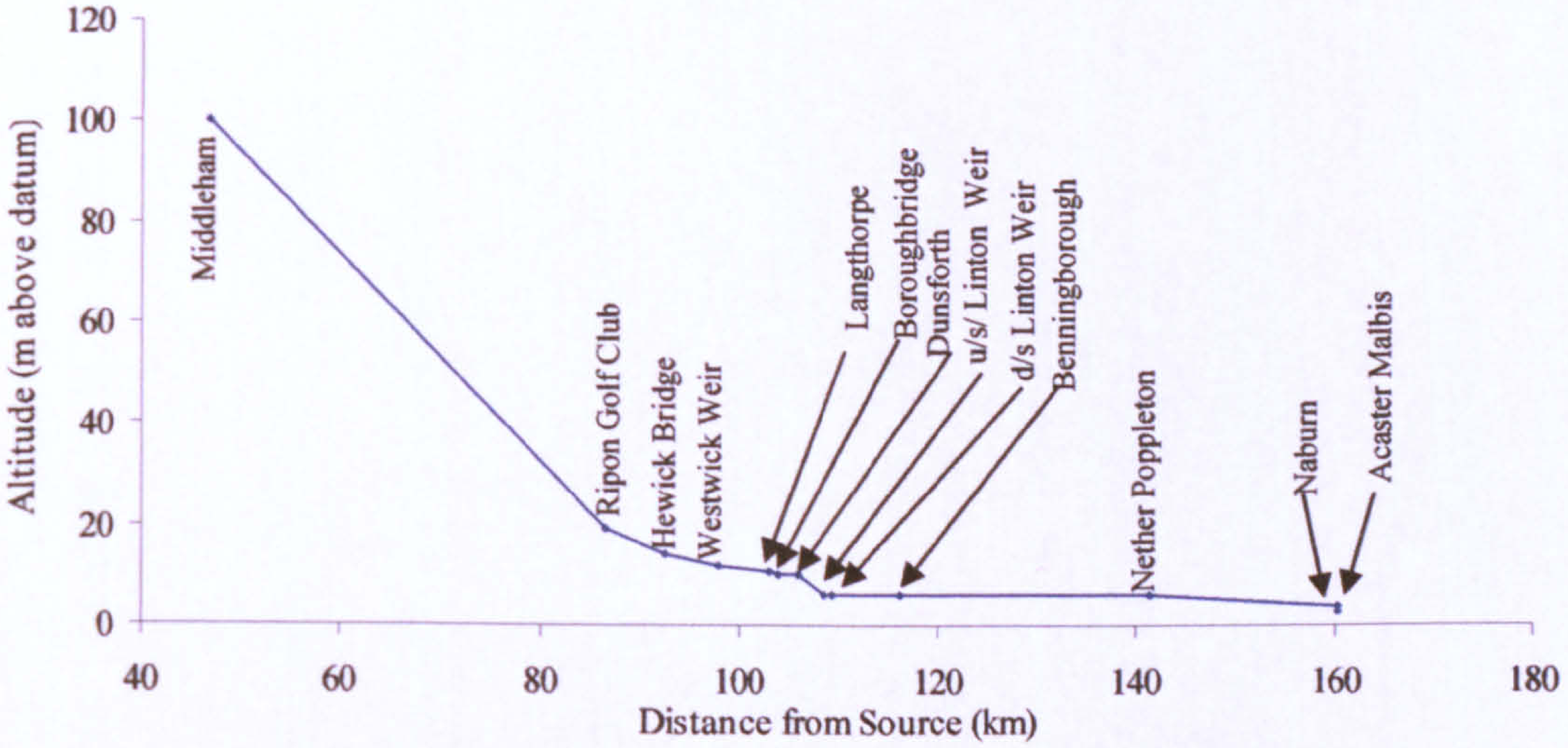


Figure 4.4 – Longitudinal profile of the Yorkshire Ouse catchments main river corridor showing sites situated along the River Ure and Yorkshire Ouse, showing distance from source for each site and the altitude at which the site occurs.

Similar, although in most cases stronger relationships were found between the abiotic variables from the Colne (Essex) catchment (Table 4.2). As distance from source increased a concurrent increase in catchment area above each site and wetted width was found. Decreases were found in altitude (Figure 4.5) and river bed gradient with increasing distance from source. Decreasing altitudes and river bed gradients were also found with increasing catchment area above each site. Decreased wetted widths were found with increasing altitude. Wetted width decreased with increased river bed gradient, while river bed gradient increased with increasing altitude. Mean air temperature was 10°C across all sites in this catchment making regressions of mean air temperature redundant.

Table 4.2 - Relationships (r^2) between abiotic variables of the River Colne (Essex) catchment.

	Distance from source	Catchment area above site	Altitude	Mean air temperature	River bed gradient	Wetted width
Distance from source		0.967	0.988	-	0.810	0.49
Catchment area above site			0.963	-	0.807	0.431
Altitude				-	0.811	0.423
Mean air temperature					-	-
River bed gradient						0.343
Wetted width						

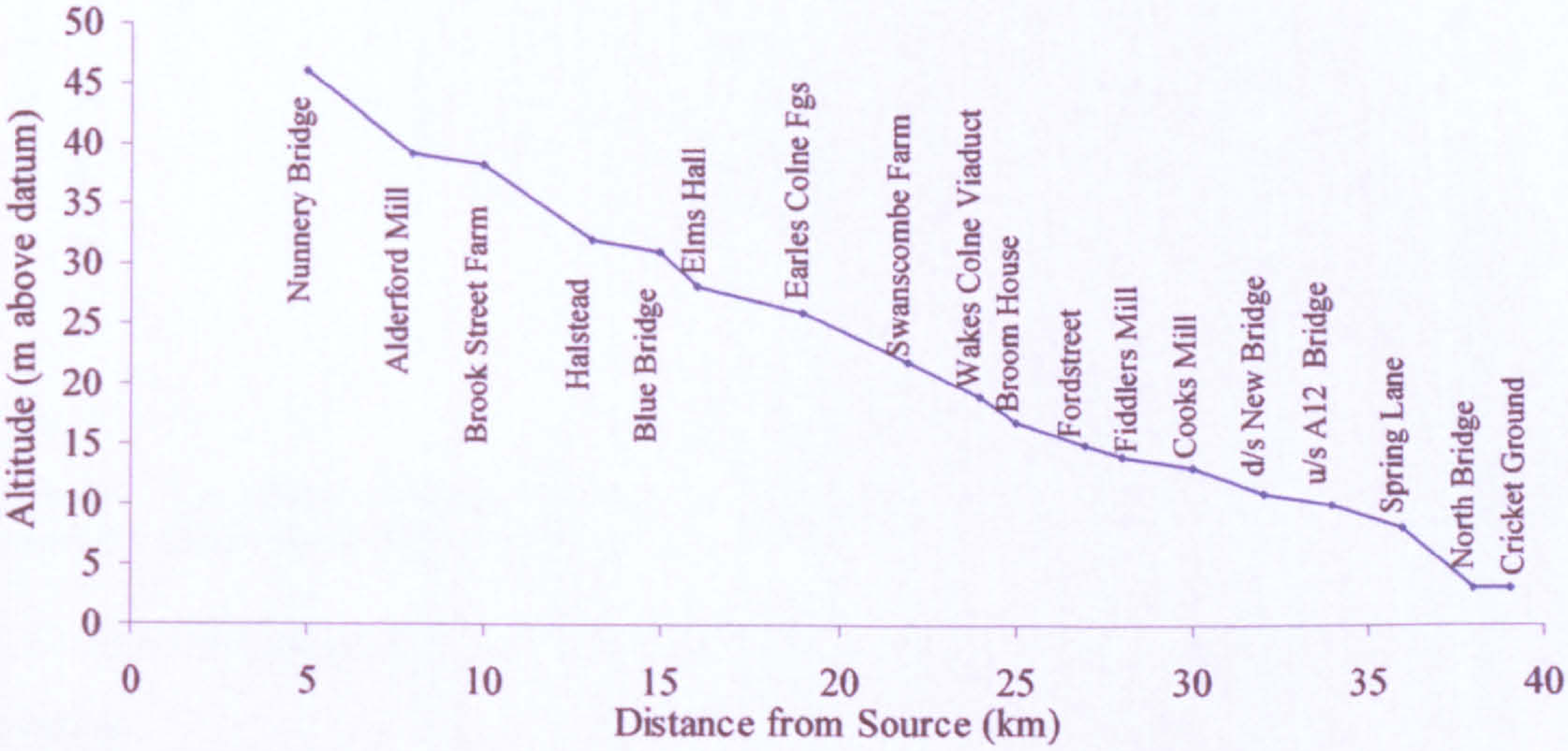


Figure 4.5 – Longitudinal profile of the River Colne (Essex) showing distance from source for each site and the altitude at which the site occurs.

Similar relationships were found in the Blackwater catchment (Table 4.3). With increasing distance from source, concurrent increases in catchment area above each site and wetted width were found, while altitude decreased (Figure 4.6). Decreasing altitude was found with increasing catchment area above each site, while wetted width increased. Wetted width increased with decreasing altitude. Relationships for river bed gradient were found to be weak in all cases as increases in river bed gradient were found between some sites indicating inaccuracies in the data derived for abiotic characteristics in this catchment. Mean air temperature was 10°C across all sites in this catchment making regressions of mean air temperature redundant.

Table 4.3 - Relationships (r^2) between abiotic variables for the Blackwater catchment.

	Distance from source	Catchment area above site	Altitude	Mean air temperature	River bed gradient	Wetted width
Distance from source		0.658	0.917	-	0.186	0.675
Catchment area above site			0.682	-	0.004	0.693
Altitude				-	0.004	0.827
Mean air temperature					-	-
River bed gradient						0.001
Wetted width						

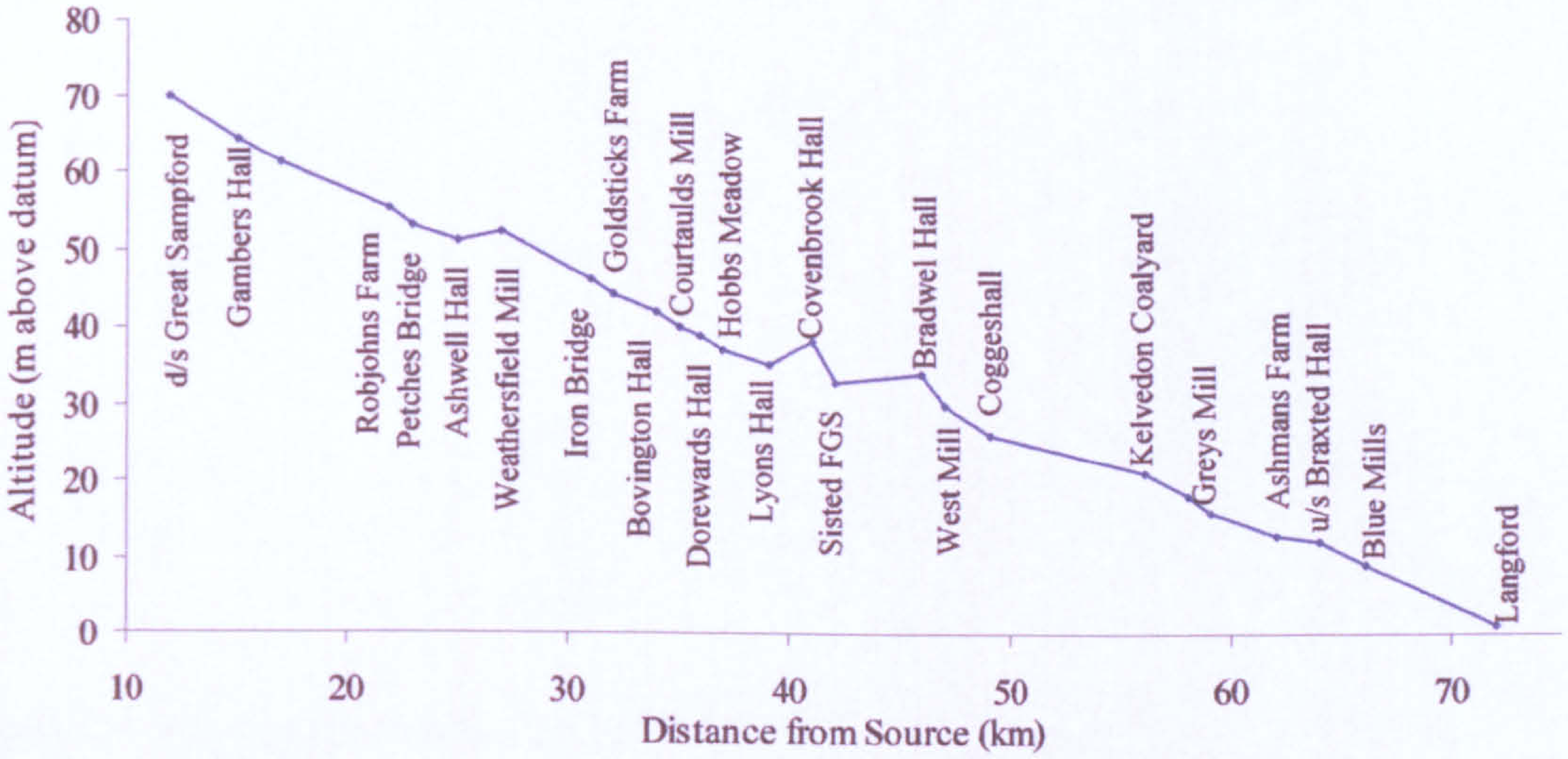


Figure 4.6 – Longitudinal profile of the River Blackwater showing distance from source for each site and the altitude at which the site occurs.

4.3.2 – Relationships between catchment wide growth characteristics and abiotic variables

Blackwater catchment roach

Growth data from 20 populations of roach from the Blackwater catchment were available for study (Figure 4.7). Multiple regressions revealed mainly weak relationships existed between each growth characteristic and all abiotic variables for roach from the Blackwater catchment (Table 4.4). The strongest relationship was between the abiotic variables and percentage standard growth, where the t value, derived from β coefficient, revealed wetted width had the greatest influence (t=2.0643). $L_{\text{-infinity}}$ was shown to be influenced by altitude (t=1.5656). The growth coefficient was influenced most by an inverse relationship with altitude (t=-1.3092).

The growth of roach in the Blackwater catchment was therefore found to be faster in the downstream area of the catchment where wetted widths were greatest.

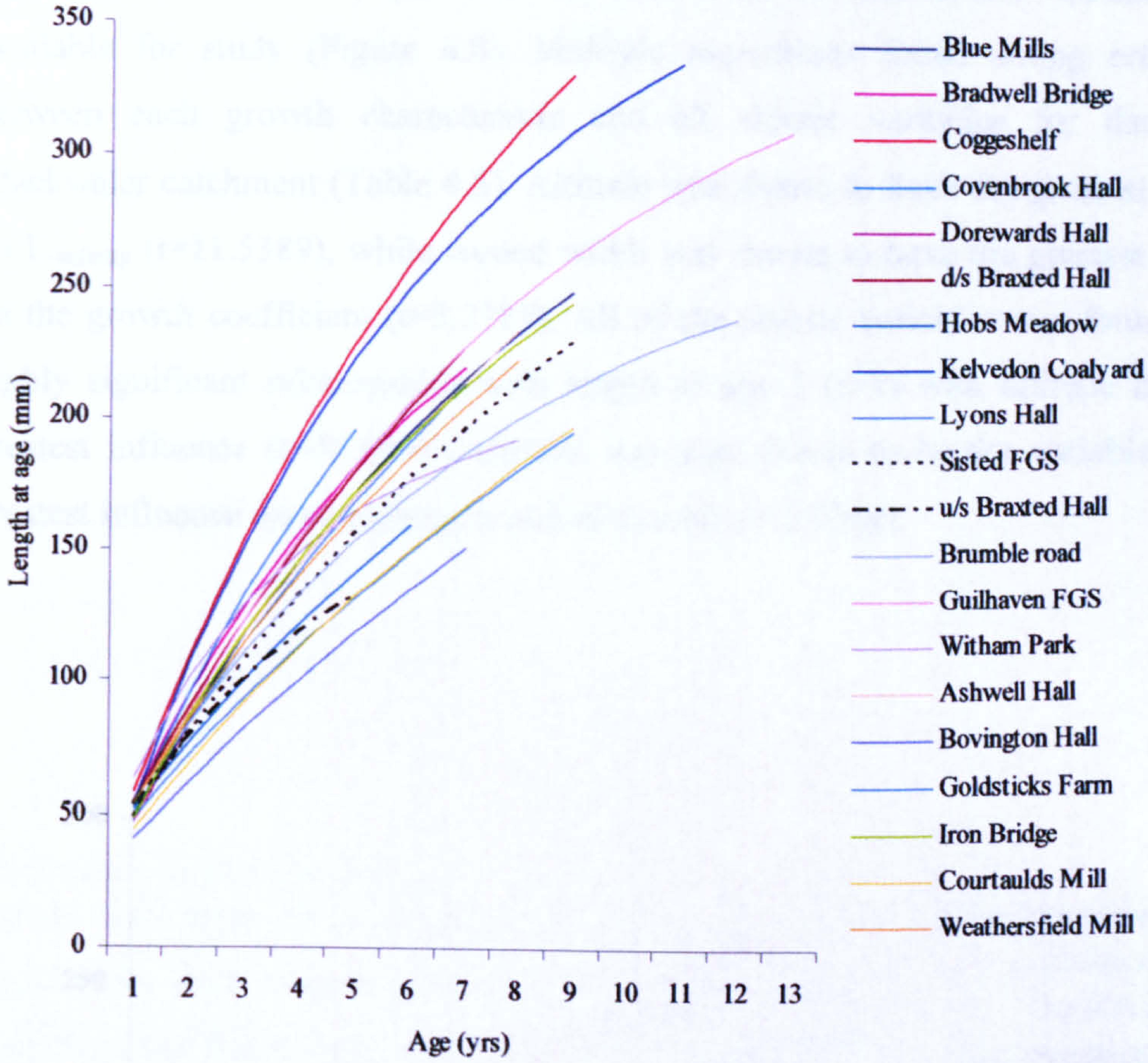


Figure 4.7 - Growth curves of roach from the Blackwater catchment.

Table 4.4 – Relationships (R^2) between the growth characteristics and abiotic variables of roach from the Blackwater catchment from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.4135	31858.37	45192.42	0.211
K	0.3485	0.019	0.035	0.333
max age	0.2185	11.654	41.679	0.767
L1	0.2024	90.631	357.258	0.695
% std growth	0.5148	2314.579	2181.421	0.112

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment	t	-0.6843	-0.0256	-0.8613	0.1155	-0.9873
	P					
Altitude	t	1.5656	-1.3092	0.9469	-0.4521	0.1209
	P					
Gradient	t	1.1206	-0.6129	0.9560	-0.0487	0.5088
	P					
Distance from source	t	1.1666	-0.3409	1.2569	-0.0515	0.8419
	P					
wetted width	t	-0.5849	0.0623	-0.3511	-0.9571	2.0643
	P					

*** = P<0.05   ** = P<0.01**

Blackwater catchment dace

Growth data from 18 populations of dace from the Blackwater catchment were available for study (Figure 4.8). Multiple regressions found strong relationships between each growth characteristic and all abiotic variables for dace in the Blackwater catchment (Table 4.5). Altitude was shown to have the greatest influence on $L_{\text{-infinity}}$ (t=11.5389), while wetted width was shown to have the greatest influence on the growth coefficient (t=5.2285). All of the abiotic variables was found to have highly significant relationships with length at age 1 (t>2) with altitude having the greatest influence (t=48.6093). altitude was also shown to be the variable with the greatest influence on percentage standard growth (t=2.7245).

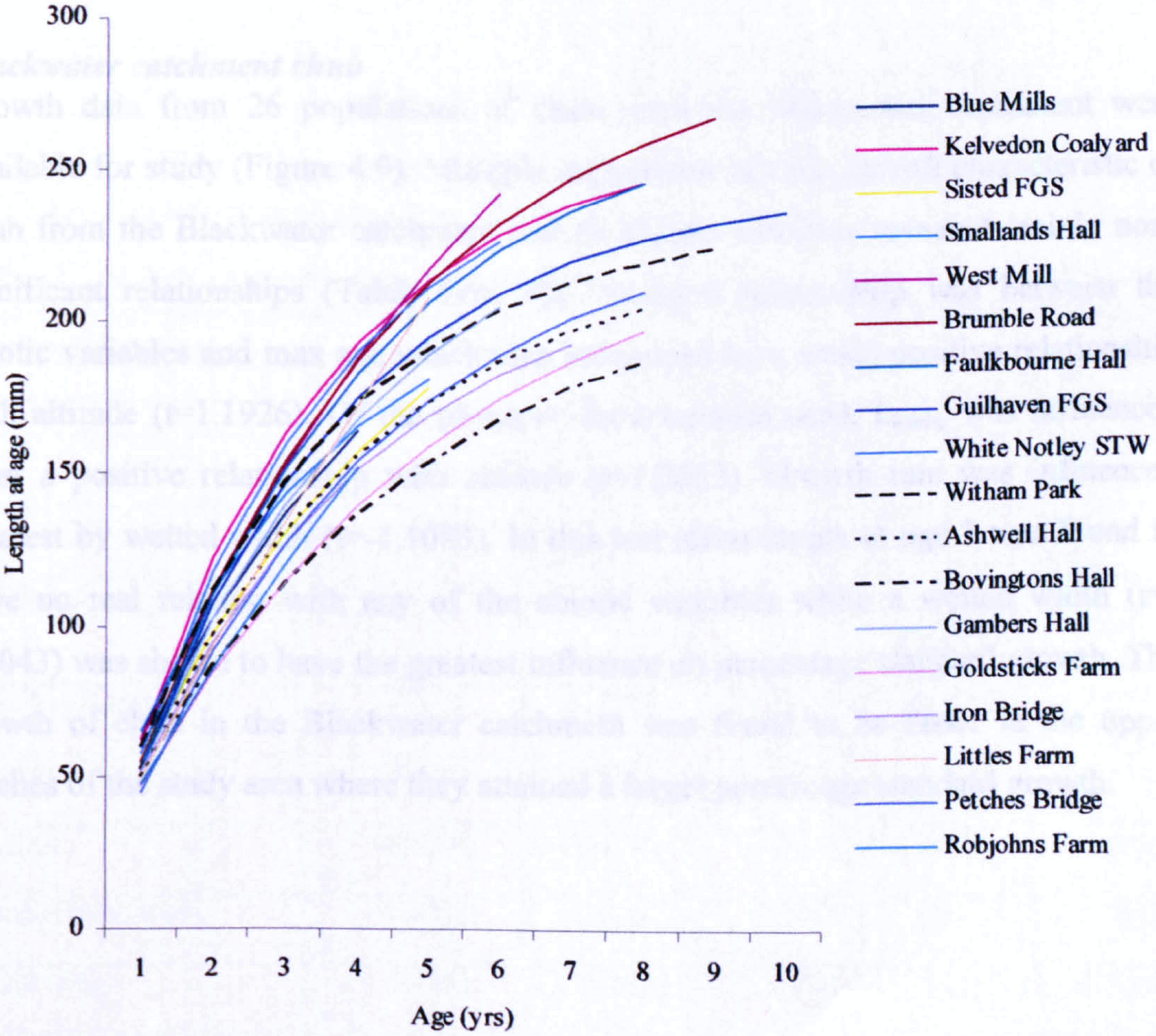


Figure 4.8 - Growth curves of dace from the Blackwater catchment.

Table 4.5 – Relationships (R^2) between the growth characteristics and abiotic variables of dace from the Blackwater catchment from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.9937	19394.03	123.742	0.016
K	0.9838	0.016	0.001	0.040
max age	0.6825	6.825	3.175	0.615
L1	0.9996	192.815	0.075	0.001
% std growth	0.8399	833.050	158.825	0.354

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment	t	2.4235	1.1225	1.2699	-15.5096	-0.6200
	P				**	
Altitude	t	11.5389	-0.7849	-1.4521	48.6093	2.7245
	P	**			**	
Gradient	t	2.4935	1.8267	-1.2964	30.8013	1.8425
	P				**	
Distance from source	t	8.3524	-1.5254	-1.7920	46.6258	2.5758
	P	*			**	
Wetted width	t	-5.3954	5.2285	0.2491	2.6305	-0.5394
	P	*	*			

* = $P<0.05$ ** = $P<0.01$

Blackwater catchment chub

Growth data from 26 populations of chub from the Blackwater catchment were available for study (Figure 4.9). Multiple regressions of each growth characteristic of chub from the Blackwater catchment and all abiotic variables revealed mainly non-significant relationships (Table 4.6). The strongest relationship was between the abiotic variables and max age which was influenced by a weak, positive relationship with altitude (t=1.1926). Of the physical characteristics used, $L_{infinity}$ was influenced most a positive relationship with altitude (t=1.2855). Growth rate was influenced greatest by wetted width (t=-1.1083). In this test mean length at age 1 was found to have no real relation with any of the abiotic variables while a wetted width (t=-1.8043) was shown to have the greatest influence on percentage standard growth. The growth of chub in the Blackwater catchment was found to be faster in the upper reaches of the study area where they attained a larger percentage standard growth.

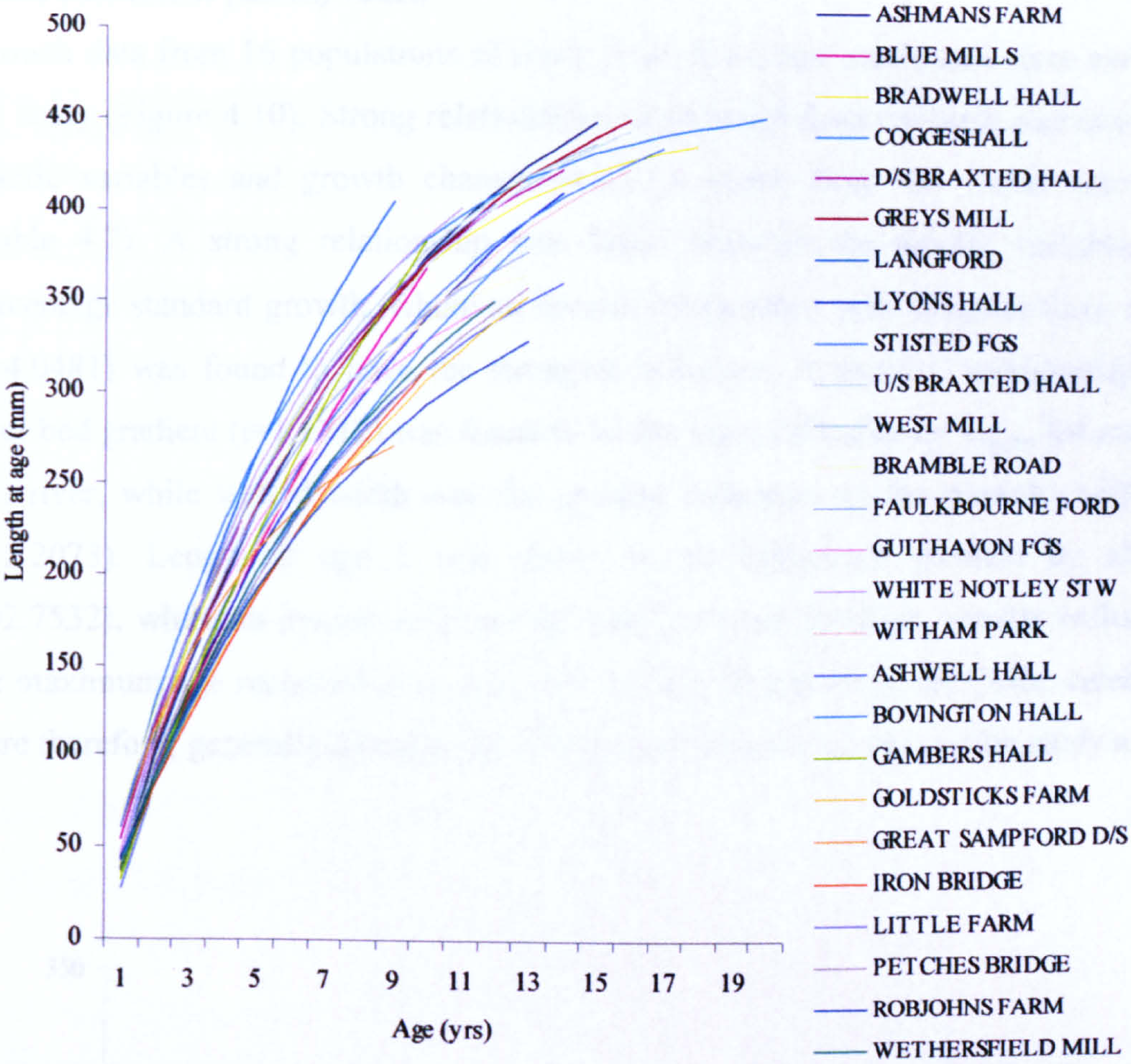


Figure 4.9 - Growth curves of chub from the Blackwater catchment.

Table 4.6 – Relationships (R^2) between the growth characteristics and abiotic variables of chub from the Blackwater catchment from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.4444	70628.85	88288.09	0.035
K	0.1668	0.006	0.031	0.589
max age	0.6864	84.395	38.558	0.002
L1	0.0298	56.742	1848.834	0.987
% std growth	0.3357	606.097	1199.344	0.138

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment	t	-0.0092	0.3713	-1.3094	-0.2231	0.9038
	P					
Altitude	t	1.2855	-1.0301	1.1926	0.0026	-0.6363
	P					
Gradient	t	-0.4220	0.4645	-0.0610	-0.1191	0.0056
	P					
Distance from source	t	1.1242	-0.6906	0.0865	0.0277	-0.7963
	P					
Wetted width	t	0.9866	-1.1083	0.1709	-0.3445	-1.8043
	P					

* = P<0.05 ** = P<0.01

Colne catchment (Essex) roach

Growth data from 16 populations of roach from the Colne catchment were available for study (Figure 4.10). Strong relationships were found from multiple regressions of abiotic variables and growth characteristics for roach from the Colne catchment (Table 4.7). A strong relationship was found between the abiotic variables and percentage standard growth, where an inverse relationship with distance from source (t=4.0481) was found to have the strongest influence. A positive relationship with river bed gradient (t=1.1712) was found to be the main influence on $L_{infinity}$ for roach in this river, while wetted width was the greatest influence on the growth coefficient (t=2.2073). Length at age 1 was shown to be influenced greatest by altitude (t=2.7532), while an inverse relationship with river bed gradient, weakly influenced the maximum age recorded at each site (t=1.1349). Roach from the Colne catchment were therefore, generally found to grow faster in the lower reaches of the study area.

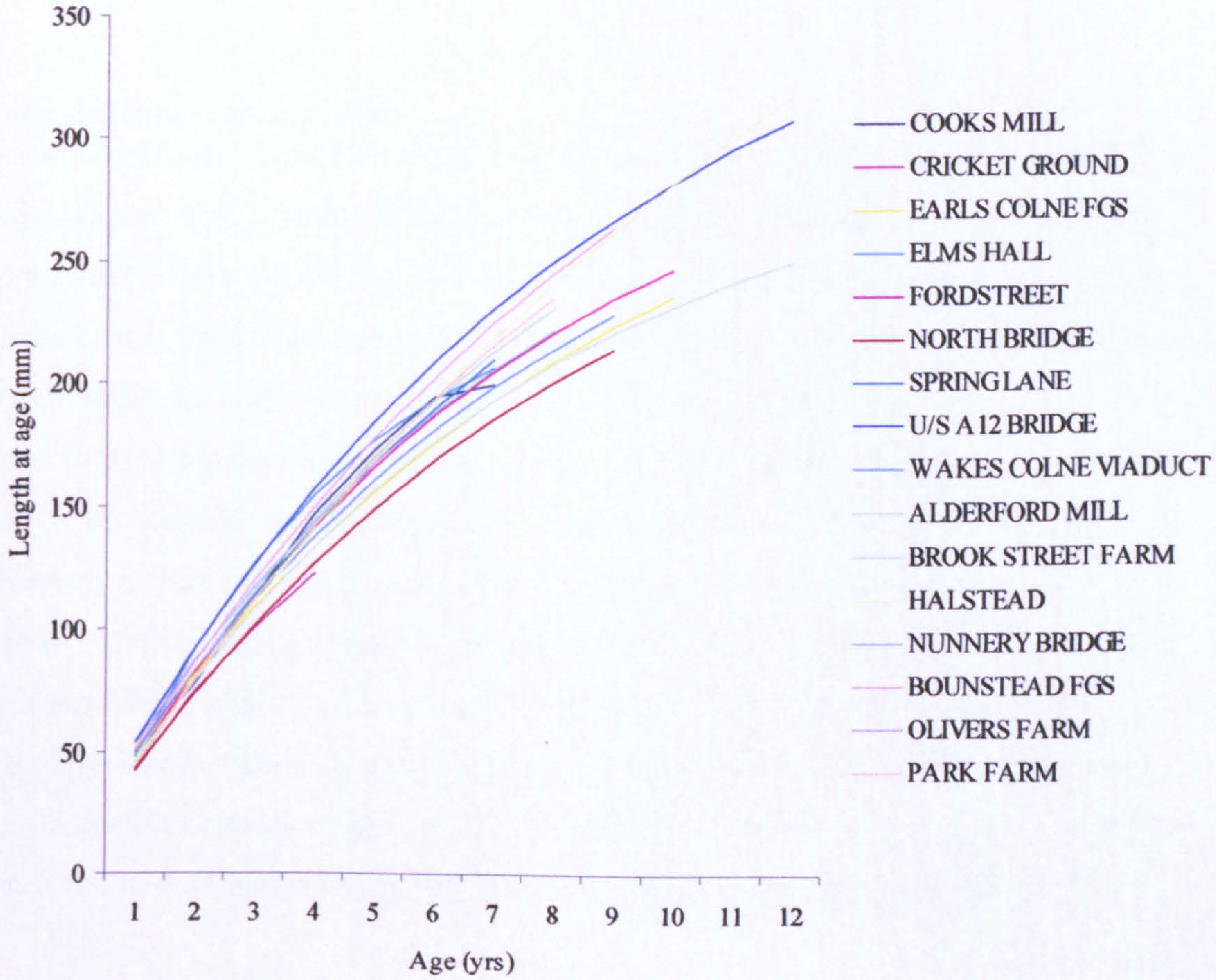


Figure 4.10 - Growth curves of roach from the River Colne catchment.

Table 4.7 – Relationships (R^2) between the growth characteristics and abiotic variables of roach from the R. Colne, Essex from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.6113	14243	9058	0.316
K	0.5867	0.007	0.005	0.267
max age	0.3722	21.19	35.73	0.637
L1	0.6068	89	58	0.172
% std growth	0.7754	486.73	140.96	0.031

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment above site	t	0.7376	0.8494	0.5441	0.4697	-2.6563
	P					*
Altitude	t	1.1017	-0.0743	-1.1183	2.7532	3.4724
	P				*	*
Gradient	t	1.1712	-1.1171	1.1349	-0.2136	-2.2054
	P					
Distance from source	t	0.3616	-0.7603	-1.0485	1.5330	4.0481
	P					**
Wetted width	t	-0.9387	2.2073	0.4337	-1.3523	-2.8716
	P					*

*** = $P<0.05$ ** = $P<0.01$**

Colne catchment (Essex) dace

Growth data from 11 populations of dace from the Colne catchment were available for study (Figure 4.11). Both strong and weak, although non-significant, relationships were found from multiple regressions of abiotic variables and growth characteristics for dace from the Colne catchment (Essex) (Table 4.8). A positive relationship with wetted width (t=1.6690) and an inverse relationship with altitude (t=-1.5112) were found to have the greatest influence on $L_{infinity}$. The growth coefficient was influenced mainly by altitude (t=1.8069), showing growth rates to increase in an upstream direction, within the study area. Non-significant relationships between max age at each site and percentage standard growth and the abiotic variables in this test suggest variables other than those used in this test; have a greater influence on longevity in dace from the R. Colne. A non-significant, inverse relationship existed between size of catchment and mean length at age 1 (t=-1.0191). Growth of dace in the R Colne was found to be faster in the upper reaches leading to larger mean lengths at age 1.

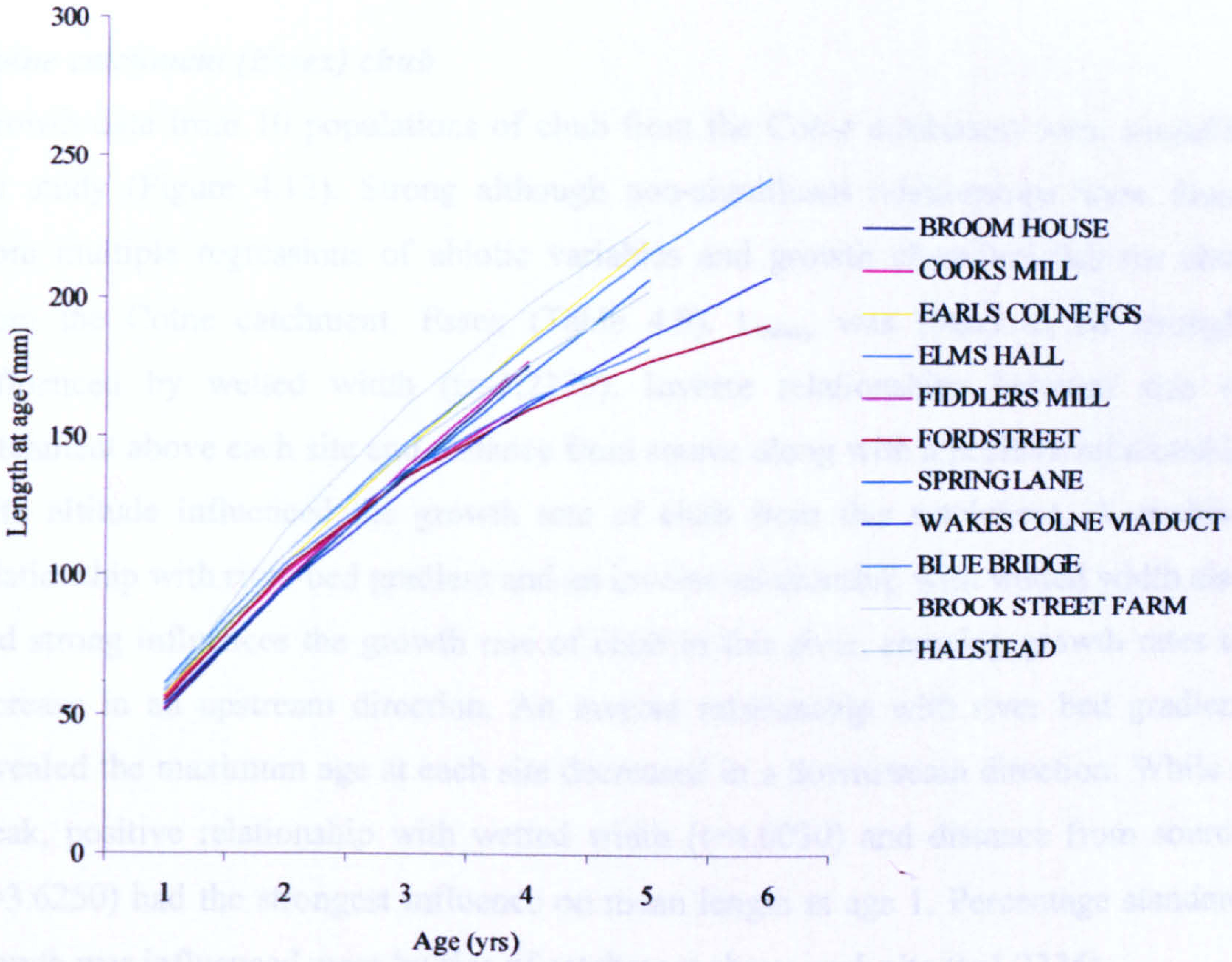


Figure 4.11 - Growth curves of dace from the River Colne catchment.

Table 4.8 – Relationships (R^2) between the growth characteristics and abiotic variables of dace from the R. Colne, Essex from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.7829	175661	48719	0.279
K	0.7964	0.042	0.011	0.257
max age	0.2036	1.22	4.78	0.920
L1	0.7069	70	29	0.178
% std growth	0.6802	270.85	127.33	0.214

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment above site	t	0.3415	-0.8797	0.2548	-1.0191	0.0924
	P					
Altitude	t	-1.5112	1.8069	-0.4010	-0.6232	0.2100
	P					
Gradient	t	0.4982	-1.1751	0.6741	0.4300	0.6929
	P					
Distance from source	t	-1.2687	1.7290	-0.4641	-0.1194	-0.0709
	P					
wetted width	t	1.6690	-0.8284	-0.4647	0.3323	0.2590
	P					

*** = P<0.05 ** = P<0.01**

Colne catchment (Essex) chub

Growth data from 10 populations of chub from the Colne catchment were available for study (Figure 4.12). Strong although non-significant relationships were found from multiple regressions of abiotic variables and growth characteristics for chub from the Colne catchment, Essex (Table 4.9). $L_{infinity}$ was found to be strongly influenced by wetted width (t=-1.2379). Inverse relationships between size of catchment above each site and distance from source along with a positive relationship with altitude influenced the growth rate of chub from this catchment. A positive relationship with river bed gradient and an inverse relationship with wetted width also had strong influences the growth rate of chub in this river, showing growth rates to increase in an upstream direction. An inverse relationship with river bed gradient revealed the maximum age at each site decreased in a downstream direction. While a weak, positive relationship with wetted width (t=4.0030) and distance from source (t=3.6250) had the strongest influence on mean length at age 1. Percentage standard growth was influenced most by size of catchment above each site (t=1.2336).

Table 4.9 – Relationships (R^2) between the growth characteristics and abiotic variables of chub from the R. Colne, Essex from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.8394	16191	3099	0.355
K	0.7608	0.002	0.001	0.495
max age	0.7464	7.04	2.39	0.751
L1	0.9492	414	22	0.122
% std growth	0.7780	46.68	13.32	0.466

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment	t	-0.2532	0.0084	0.4142	0.3449	1.2336
	P					
Altitude	t	-0.8903	0.1833	0.3679	2.7304	1.1563
	P					
Gradient	t	1.0057	-0.1657	-0.5238	-1.8149	-0.1682
	P					
Distance from source	t	-0.7090	-0.0280	0.4697	4.0030	1.0021
	P					
wetted width	t	-1.2379	0.4170	-0.3982	3.6250	1.0326
	P					

* = $P<0.05$ ** = $P<0.01$

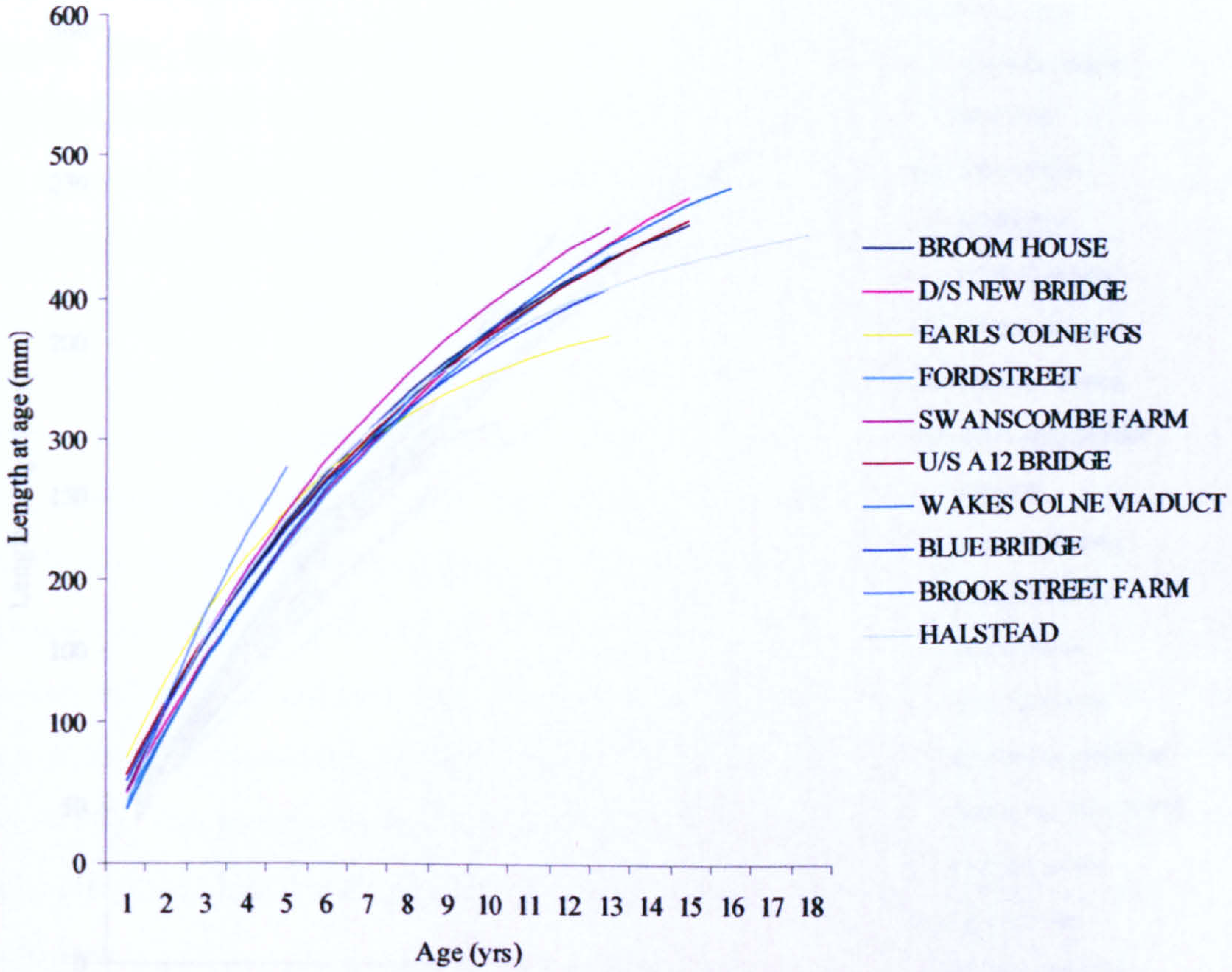


Figure 4.12 - Growth curves of chub from the River Colne catchment.

Yorkshire Ouse roach

Growth data from 21 populations of roach from the Yorkshire Ouse were available for study (Figure 4.13). Both strong and weak, although non-significant relationships were found from multiple regressions of abiotic variables and growth characteristics for roach from the Yorkshire Ouse catchment (Table 4.10). The abiotic variables used were found to have the strongest influence on percentage standard growth, where gradient had the strongest influence (t=-0.9236). A positive relationship with distance from source (t=0.9631) and catchment size above each site (t=-0.9085) was found to have the greatest influence on mean length at age 1. A non-significant relationship with wetted width was seen to influence $L_{infinity}$ (t=-0.7864), while a weak positive relationship with and wetted width influenced the growth coefficient (t=0.5088). The growth of roach in the Yorkshire Ouse catchment, grew faster and achieved greater mean lengths at age 1 in the lower reaches of the study area.

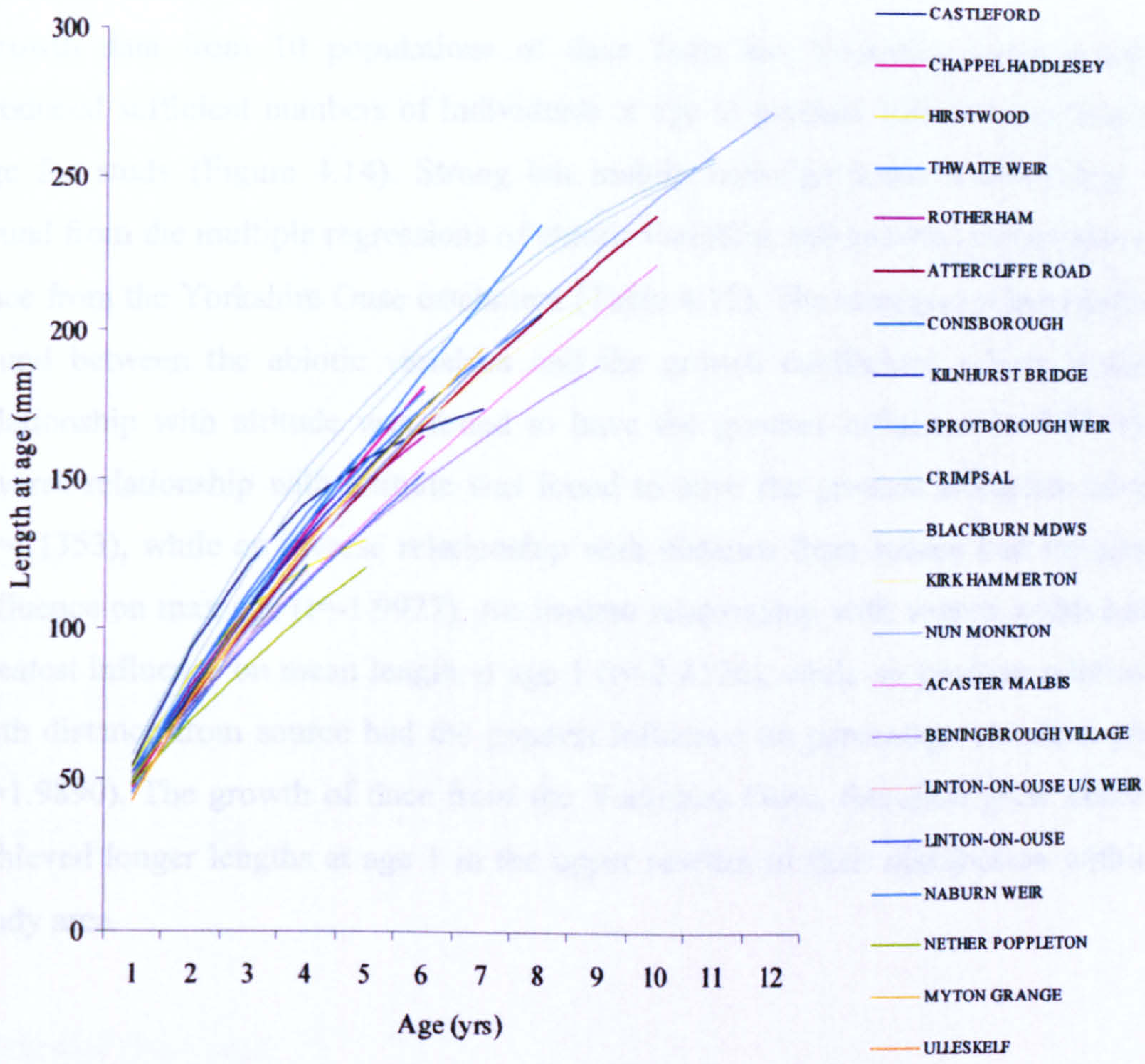


Figure 4.13 - Growth curves of roach from the Yorkshire Ouse catchment.

Table 4.10 – Relationships (R^2) between the growth characteristics and abiotic variables of roach from the Yorkshire Ouse from multiple from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.3201	71667.48	152240.6	0.786
K	0.3255	0.010	0.020	0.717
max age	0.4616	49.113	57.288	0.269
L1	0.5698	102.349	77.258	0.122
% std growth	0.6584	42.400	22.000	0.348

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment above site	t	0.3888	-0.0402	-1.5238	-0.9085	0.0300
	P					
Altitude	t	0.0555	0.4576	2.1282	-0.5914	0.1138
	P					
Gradient	t	0.1607	0.1083	0.4290	0.3516	-0.9236
	P					
Distance from source	t	0.2413	0.1499	-2.1039	0.9631	-0.0821
	P					
wetted width	t	-0.7864	0.5088	1.8375	0.5489	-0.4486
	P					

*** = P<0.05   ** = P<0.01**

Yorkshire Ouse dace

Growth data from 10 populations of dace from the Yorkshire Ouse catchment produced sufficient numbers of individuals at age to produce robust mean lengths at age for study (Figure 4.14). Strong but mainly non-significant relationships were found from the multiple regressions of abiotic variables and growth characteristics for dace from the Yorkshire Ouse catchment (Table 4.11). The strongest relationship was found between the abiotic variables and the growth coefficient, where a positive relationship with altitude was found to have the greatest influence (t=7.7431). An inverse relationship with altitude was found to have the greatest influence on $L_{infinity}$ (t=4.1353), while an inverse relationship with distance from source had the greatest influence on max age (t=-1.9927). An inverse relationship with wetted width had the greatest influence on mean length at age 1 (t=-2.8126), while an positive relationship with distance from source had the greatest influence on percentage standard growth (t=1.9890). The growth of dace from the Yorkshire Ouse, therefore grew faster and achieved longer lengths at age 1 in the upper reaches of their distribution within the study area.

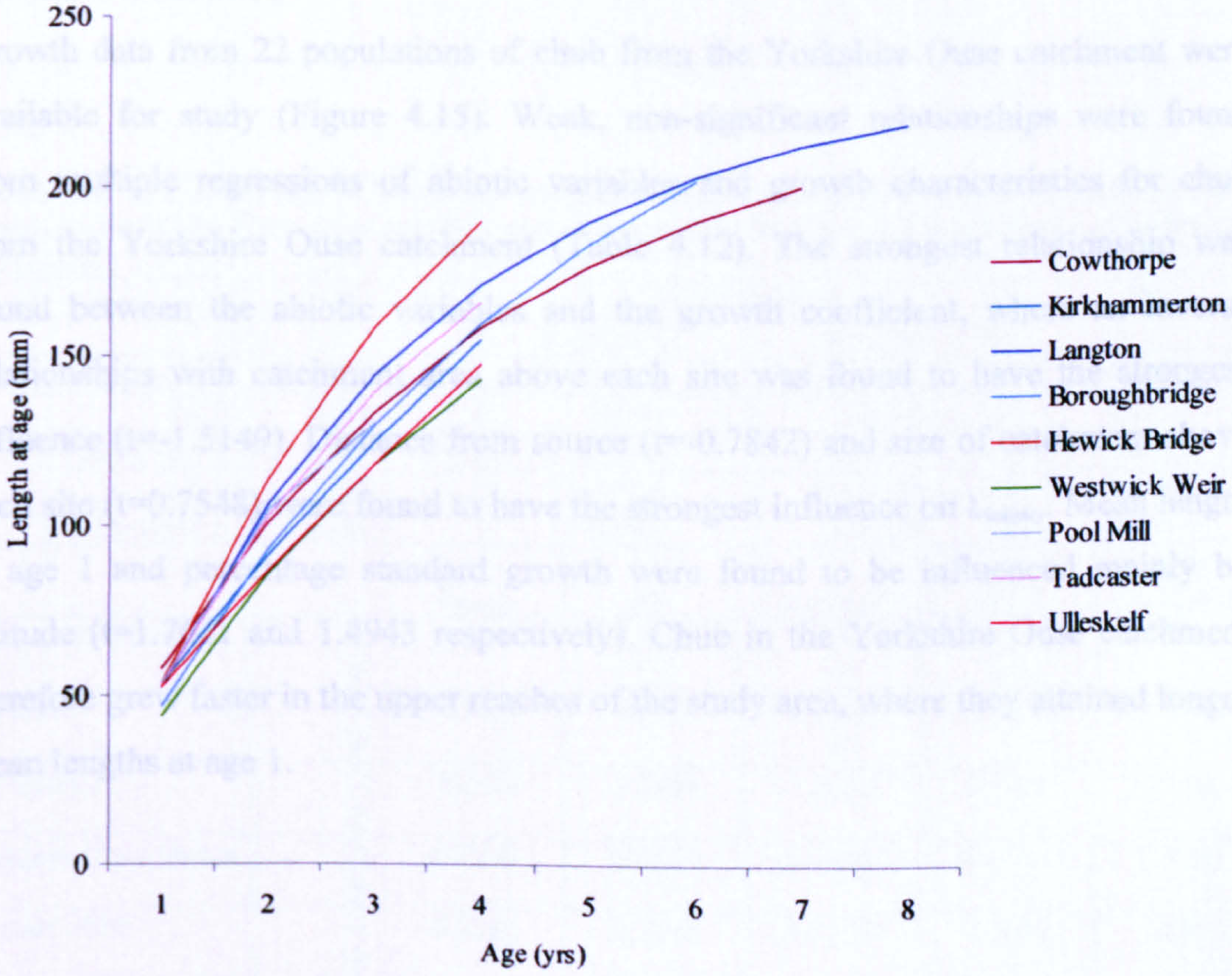


Figure 4.14 - Growth curves of dace from the Yorkshire Ouse catchment.

Table 4.11 – Relationships (R^2) between the growth characteristics and abiotic variables of dace from the Yorkshire Ouse from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.9666	23192.79	801.6542	0.081
K	0.9945	0.213	0.001	0.014
max age	0.5018	11.842	11.758	0.599
L1	0.7305	94.924	35.028	0.237
% std growth	0.6956	559.580	244.920	0.289

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment above site	t	-1.3270	2.8894	0.0890	2.2850	-0.8467
	P					
Altitude	t	-4.1353	7.7431	1.0436	0.2315	-1.1725
	P		**			
Gradient	t	-2.8731	-2.0347	0.4466	-0.5270	-0.7372
	P					
Distance from source	t	-0.3610	2.5950	-1.9927	0.5395	1.9890
	P					
wetted width	t	-1.9944	-1.4880	0.5324	-2.8126	-0.7094
	P				*	

*** = $P<0.05$ ** = $P<0.01$**

Yorkshire Ouse chub

Growth data from 22 populations of chub from the Yorkshire Ouse catchment were available for study (Figure 4.15). Weak, non-significant relationships were found from multiple regressions of abiotic variables and growth characteristics for chub from the Yorkshire Ouse catchment (Table 4.12). The strongest relationship was found between the abiotic variables and the growth coefficient, where an inverse relationships with catchment area above each site was found to have the strongest influence (t=-1.5149). Distance from source (t=-0.7842) and size of catchment above each site (t=0.7548) were found to have the strongest influence on $L_{infinity}$. Mean length at age 1 and percentage standard growth were found to be influenced mainly by altitude (t=1.7641 and 1.4943 respectively). Chub in the Yorkshire Ouse catchment therefore grew faster in the upper reaches of the study area, where they attained longer mean lengths at age 1.

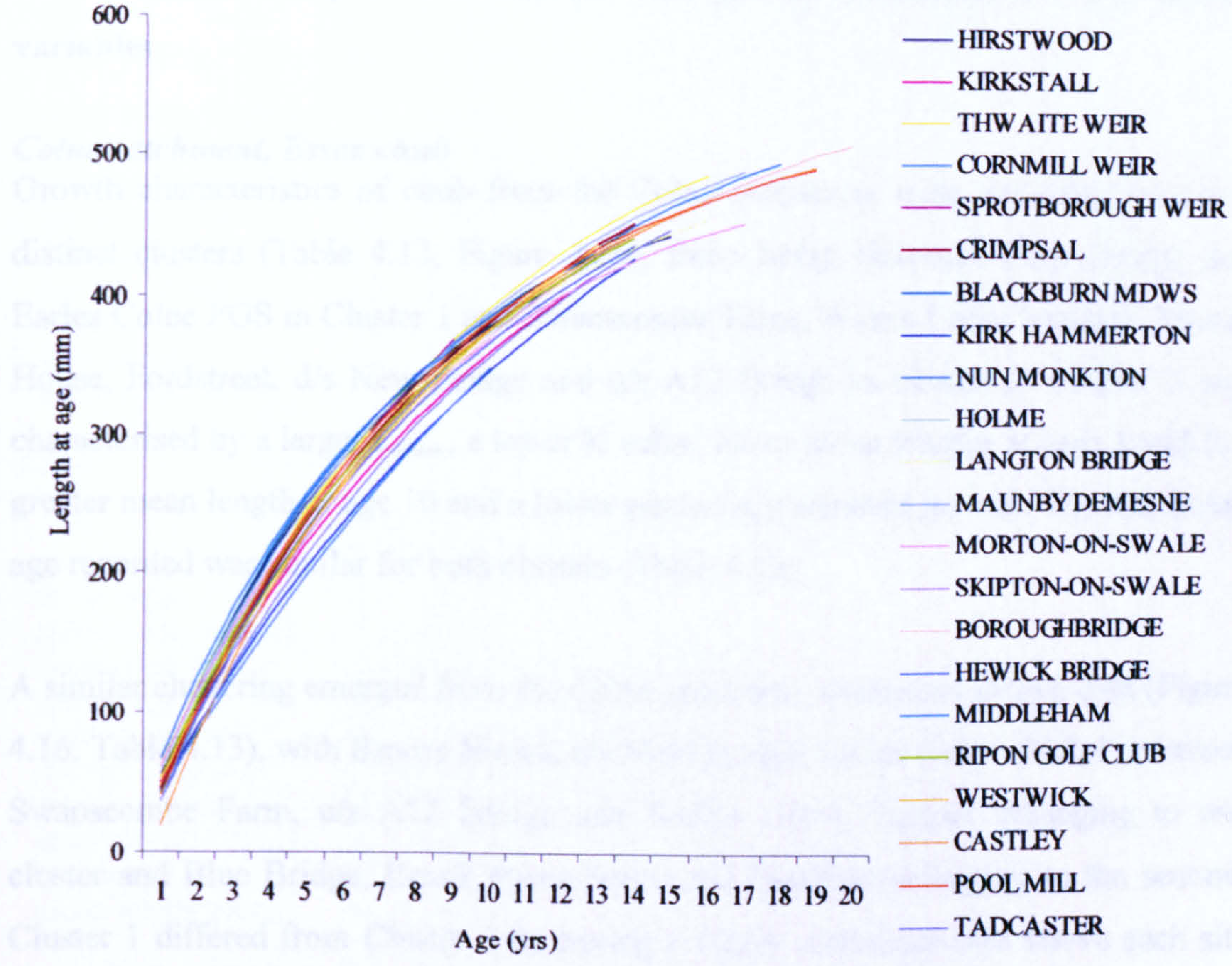


Figure 4.15 - Growth curves of dace from the Yorkshire Ouse catchment.

Table 4.12 – Relationships (R^2) between the growth characteristics and abiotic variables of chub from the Yorkshire Ouse from multiple regression and significance (t(β coefficient)) of individual variables.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.3593	26139.35	46602.49	0.232
K	0.4965	0.004	0.005	0.061
max age	0.4403	82.14	104.427	0.091
L1	0.3454	578.354	1096.128	0.259
% std growth	0.4699	300.182	338.618	0.083

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Size of catchment	t	0.7548	-1.5149	2.9797	0.1508	-0.7515
	P			**		
Altitude	t	-0.5935	0.5978	3.0080	1.7641	1.4943
	P			**		
Gradient	t	0.8178	-1.0033	-1.2052	0.5856	0.1102
	P					
Distance from source	t	-0.7842	0.6129	-0.7852	-0.9515	0.1104
	P					
wetted width	t	-0.5266	0.7714	0.1193	0.7806	1.4808
	P					

* = P<0.05 ** = P<0.01

4.3.3 – Cluster analysis of catchment wide growth characteristics and abiotic variables

Colne catchment, Essex chub

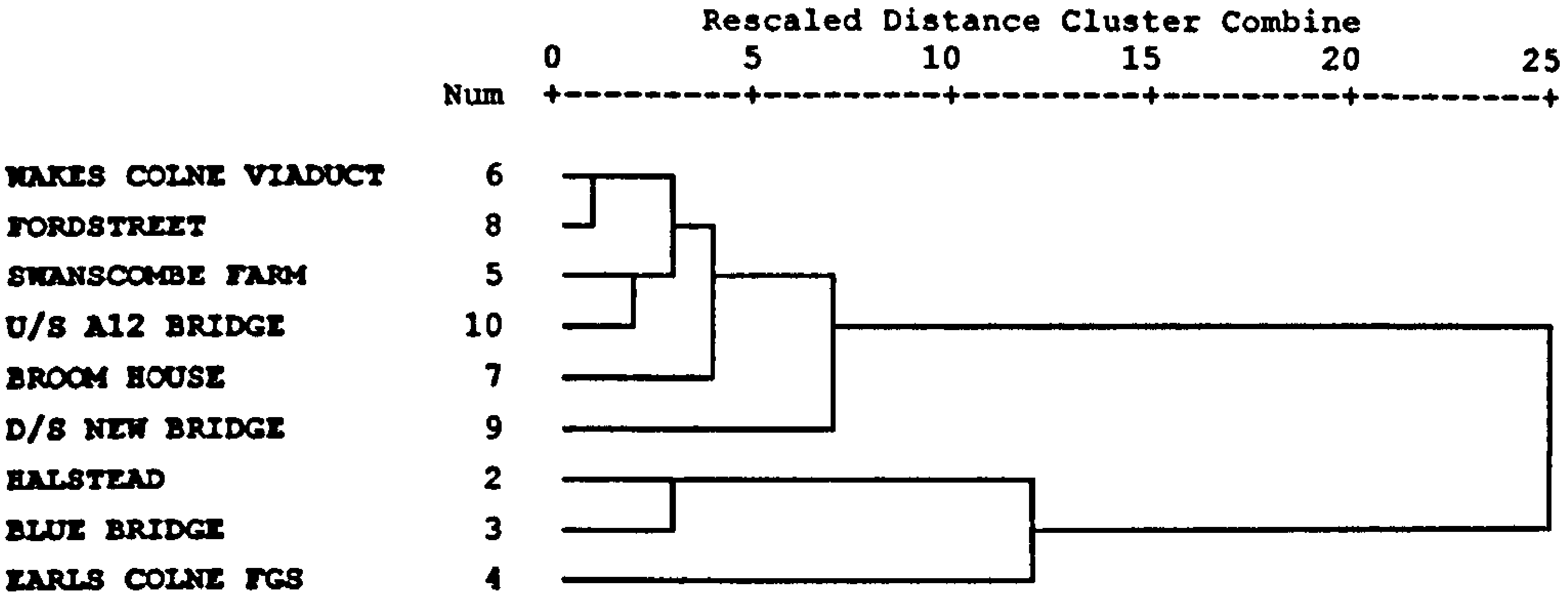
Growth characteristics of chub from the Colne catchment were separated into two distinct clusters (Table 4.13, Figure 4.16), these being Halstead, Blue Bridge and Earles Colne FGS in Cluster 1 and Swanscombe Farm, Wakes Colne Viaduct, Broom House, Fordstreet, d/s New Bridge and u/s A12 Bridge in Cluster 2. Cluster 2 was characterised by a larger $L_{infinity}$, a lower K value, lower mean lengths at ages 1 and 5, a greater mean length at age 10 and a lower percentage standard growth. The maximum age recorded was similar for both clusters (Table 4.13).

A similar clustering emerged from the Colne catchment chub sites abiotic data (Figure 4.16, Table 4.13), with Broom House, d/s New Bridge, Earles Colne FGS, Fordstreet, Swanscombe Farm, u/s A12 Bridge and Wakes Colne Viaduct belonging to one cluster and Blue Bridge, Brook Street Farm, and Halstead belonging to the second. Cluster 1 differed from Cluster 2 by having a larger catchment area above each site (Table 4.13, Figure 4.16), a lower altitude, a reduced river bed gradient, an increased distance from source and a larger wetted width. Mean air temperature was identical for both clusters at 10°C. Cluster 2 defined the upper reaches of the sampled area and Cluster 1 the lower.

Table 4.13 – Cluster membership of the chub sites on the Colne catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

Site	Cluster Membership growth characteristics	abiotic	Mean	growth cluster 1	variables cluster 2	Mean	abiotic cluster 1	variables cluster 2
Halstead	1	2	$L_{infinity}$	461mm	580mm	Size of catchment (km)	198	99
Blue Bridge	1	2	K	0.16	0.11	Altitude (m)	17.14	33.67
Brook Street Farm	1	2	Max Age	14.7	14.5	Gradient $(^{0}/_{00})$	1.03	1.36
Earles Colne FGS	1	1	L 1	58mm	49mm	Distance from source (km)	26.14	12.67
Swanscombe Farm	2	1	L 5	243mm	235mm	Wetted Width (m)	8.07	5.02
Wakes Colne Viaduct	2	1	L 10	359mm	378mm			
Broom House	2	1	% std growth	108	100			
Fordstreet	2	1						
d/s New Bridge	2	1						
u/s A12 Bridge	2	1						

Biotic



Abiotic

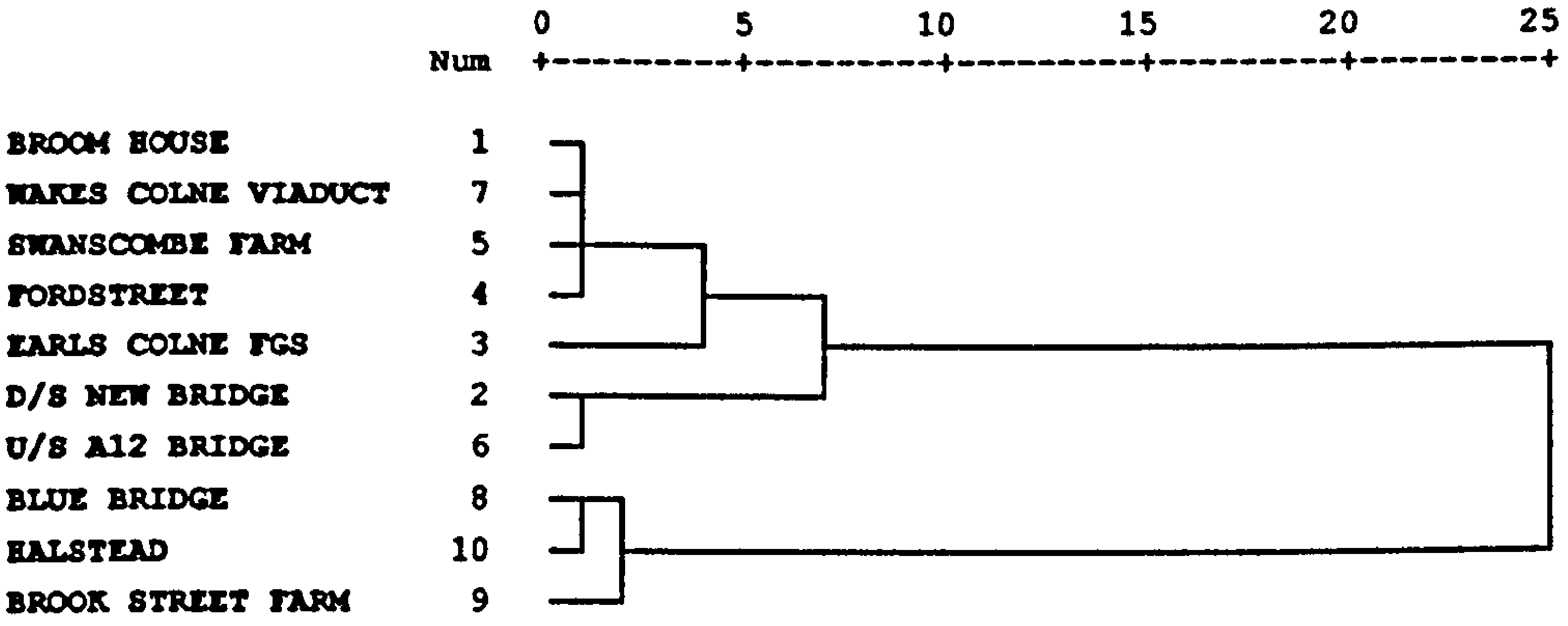


Figure 4.16 – Dendrogram using Average Linkage (Within Group) cluster analysis of Colne catchment chub sites growth characteristics and abiotic variables.

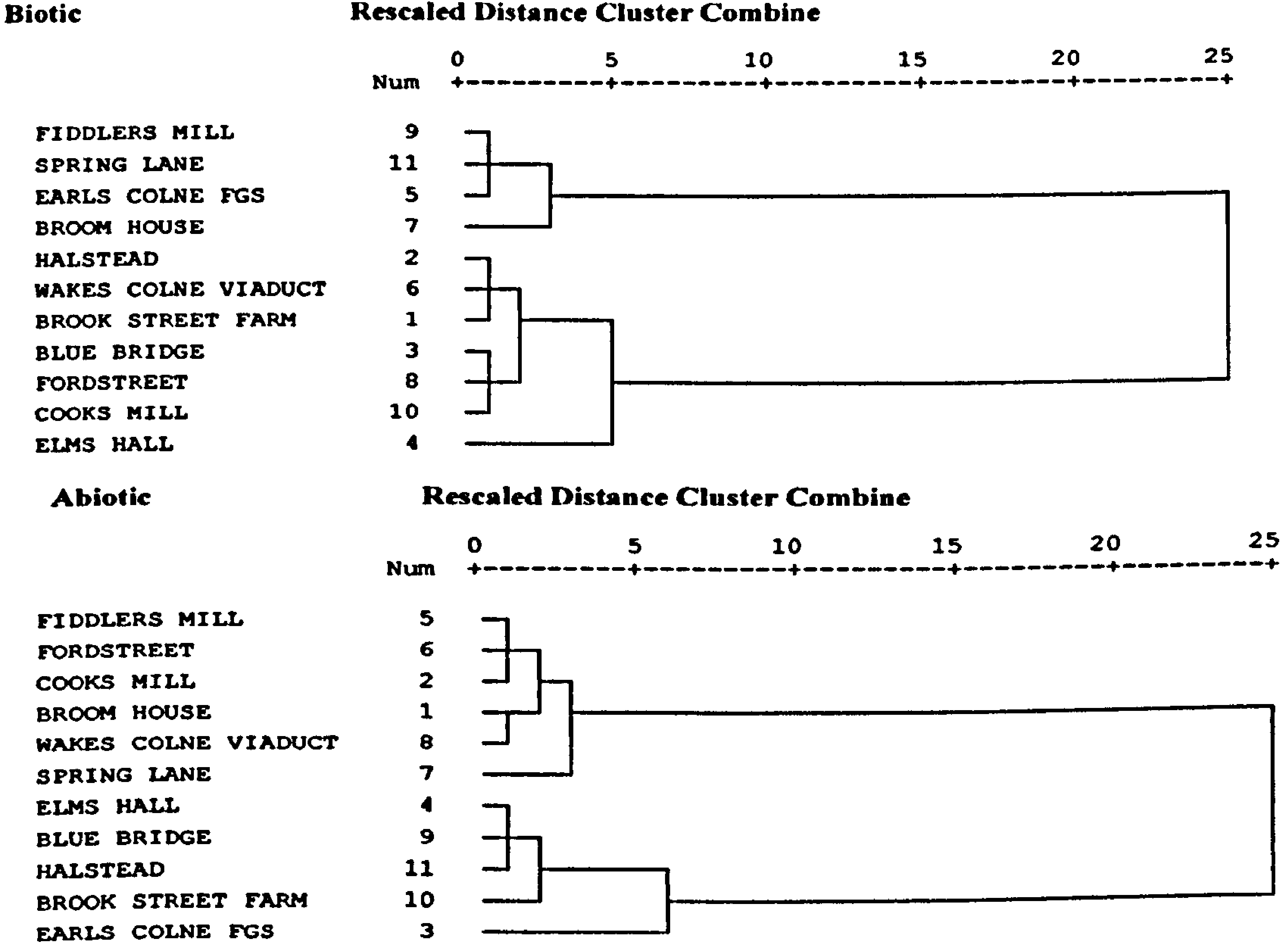
Colne catchment, Essex dace

Two clusters were separated from the growth characteristics of dace from the Colne catchment (Table 4.14, Figure 4.17). One cluster was defined by dace characterised by a lower mean $L\infty$, a greater growth coefficient (K) a greater maximum age, greater lengths at ages 1 and 3 and a larger percentage standard growth. The remaining cluster group was defined by a larger $L_{infinity}$, a lower growth coefficient, a lower longevity and smaller mean lengths at ages 1 and 3 and a lower percentage standard growth.

The abiotic variables from the dace sites of the Colne catchment were separated into two distinct clusters, but were not completely consistent with the clustering of the growth characteristics (Table 4.14). Cluster 1 was characterised by a larger catchment size above the site. Cluster 2 had a higher mean altitude with a steeper river bed gradient. Mean distance from source and wetted width were both greater in Cluster 1 than Cluster 2, defining Cluster 1 as the lower reaches and Cluster 2 the upper reaches of the sampled area.

Table 4.14 – Cluster membership of the dace sites on the Colne catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

Site	Cluster Membership Growth characteristics	abiotic	Mean growth variables	cluster 1	cluster 2	Mean abiotic variables	cluster 1	cluster 2
Brook Street Farm	1	2	$L_{infinity}$	303mm	622mm	Size of catchment (km)	112.8	209.17
Wakes Colne Viaduct	1	1	K	0.23	0.08	Altitude (m)	31	14.33
Fordstreet	1	1	Max Age	4.86	4.5	Gradient (‰)	1.38	1.03
Cooks Mill	1	1	L 1	57mm	54mm	Distance from source (km)	14.60	28.33
Halstead	1	2	L 3	142mm	140mm	Wetted Width (m)	6.54	7.92
Blue Bridge	1	2	% std growth	110	109			
Elms Hall	1	2						
Fiddlers Mill	2	1						
Spring Lane	2	1						
Earles Colne	2	2						
Broom House	2	2						


Biotic Rescaled Distance Cluster Combine

Abiotic Rescaled Distance Cluster Combine

Figure 4.17 - Dendrogram using Average Linkage (Within Group) cluster analysis to show clustering of Colne catchment dace sites growth characteristics and abiotic variables.

Colne catchment, Essex roach

Three clusters were separated from the growth characteristics of roach populations from the Colne catchment (Table 4.15; Figure 4.18). Cluster 2, consisting of just the Halstead site, was defined as having the greatest $L_{infinity}$ and Cluster 1 the lowest. Cluster 1 recorded the greatest growth coefficient and Cluster 2 the lowest. Maximum age was greater in Cluster 2 while maximum ages were similar in Clusters 1 and 3 (u/s A12 Bridge and Spring Lane). Similar values for mean length at age 1 were recorded in all three clusters. The greatest mean length at age 3 and the largest percentage standard growth was recorded in Cluster 3, an intermediate was found in Cluster 1 and the lowest values for mean length at age 3 and percentage standard growth were found in Cluster 2.

Two clusters were separated from the abiotic data within the Colne catchment roach sites (Table 4.15, Figure 4.18). Cluster 1 had a greater mean distance from source, the largest catchment area and greatest mean wetted width. Cluster 2, the Earls Colne FSG site, recorded the highest altitude and a greatest river bed gradient. Cluster 2 therefore characterised the upper reaches of the study area, while Cluster 1 characterised the lower reaches of the study area.

Table 4.15 – Cluster membership of the roach sites on the Colne catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

	Cluster Membership		Mean	growth	variables	Mean	abiotic	variables
	Growth characteristics	abiotic		cluster 1	cluster 2		cluster 1	cluster 2
Nunnery Bridge	1	3	$L_{infinity}$	312mm	572mm	Size of catchment (km)	226	89.2
Alderford Mill	1	3	K	0.15	0.066	Altitude (m)	10.14	36.6
Brook Street Farm	1	3	Max Age	8	12	Gradient ($^0/_{00}$)	1.26	1.40
Elms Hall	1	3	L 1	47mm	46mm	Distance from source (km)	32.57	10.40
Earls Colne FGS	1	2	L 3	112mm	111mm	Wetted Width (m)	10.057	6.28
Wakes Colne Viaduct	1	1	% std growth	116	113			
Fordstreet	1	1		cluster 3				
Cooks Mill	1	1	$L_{infinity}$	415mm				
North Bridge	1	1	K	0.11				
Cricket Ground	1	1	Max Age	9				
Halstead	2	3	L 1	49mm				
u/s A12 Bridge	3	1	L 3	118mm				
Spring Lane	3	1	% std growth	122				

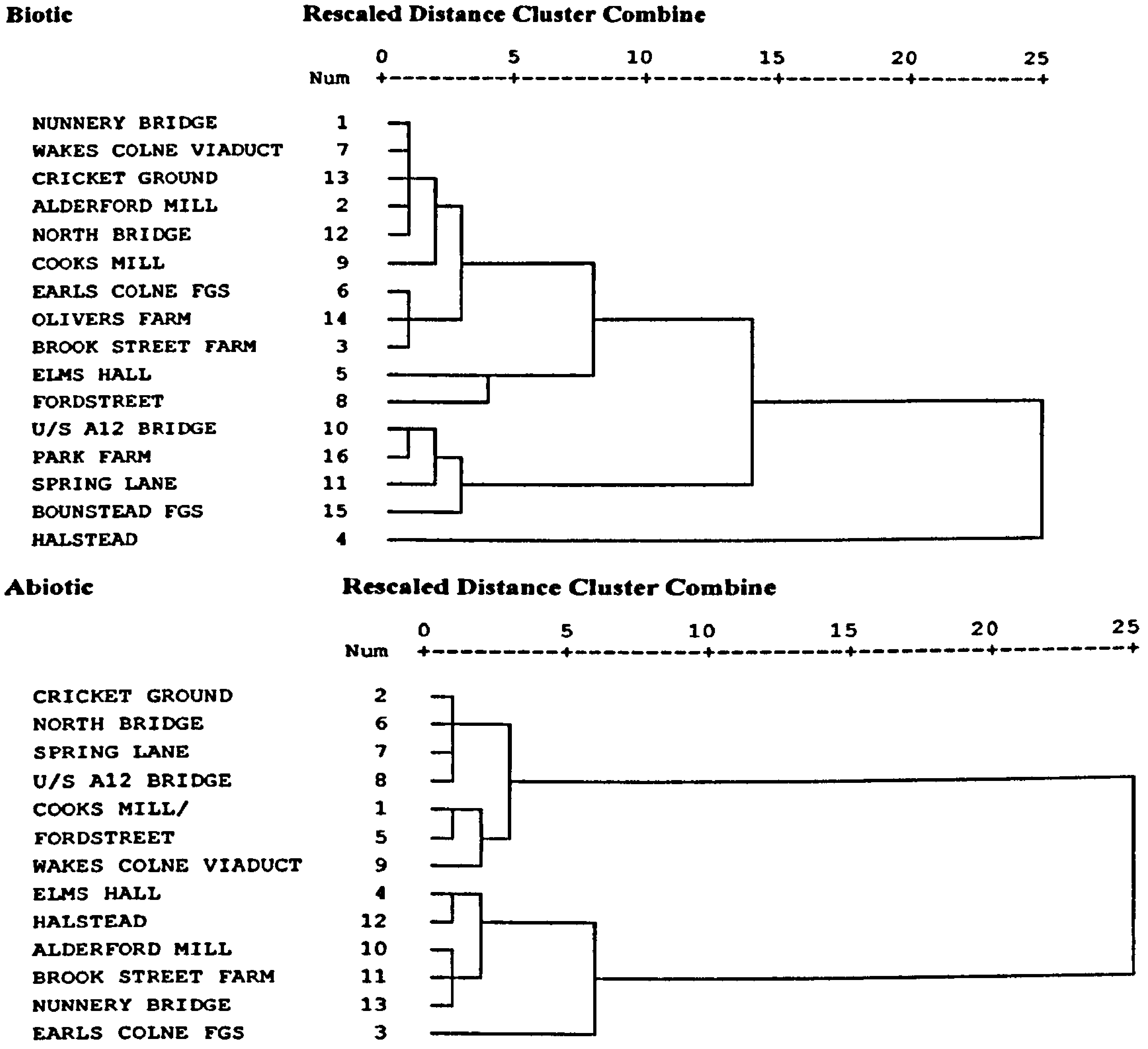


Figure 4.18 - Dendrogram using Average Linkage (Within Group) cluster analysis on Colne catchment roach sites growth characteristics and abiotic variables.

Blackwater catchment chub

Four clusters were separated from the growth characteristics of the Blackwater catchment chub populations (Table 4.16, Figure 4.19). Cluster 2 had the highest $L_{infinity}$, and Cluster 4 the lowest. Clusters 1 and 4 recorded the highest growth coefficients and Cluster 2 the lowest. Maximum age was greatest in Cluster 1 and lowest in Cluster 2. Mean lengths at age's 1 and 5 and percentage standard growth were greatest in Cluster 1. Cluster 2 had the smallest length at age 1 and Cluster 3 the smallest length at age 5. Cluster 2 had the largest length at age 10 and Cluster 3 the smallest. Cluster 3 also recorded the lowest percentage standard growth

Three clusters were separated from the abiotic data from the Blackwater catchment chub sites (Table 4.16, Figure 4.19). Cluster 3 had the largest mean catchment area, the greatest mean distance from source and the lowest altitude, however, Cluster 3 also had the greatest river bed gradient. Cluster 1 had the largest mean wetted width and Cluster 2 the highest altitude. Cluster 3 therefore represented the lower reaches Cluster 1 the middle reaches and Cluster 2 the upper reaches of the sampled area.

Table 4.16 – Cluster membership of the chub sites on the Blackwater catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

	Cluster Membership	
	growth characteristics	abiotic
Ashmans Farm	1	1
Bradwell Hall	1	2
Coggeshall	1	2
d/s Braxted Hall	1	1
Greys Mill	1	1
Sisted FGS	1	2
u/s Braxted Hall	1	1
West Mill	1	2
White Notley STW	1	2
Witham Park	1	2
Litle Farm	1	2
Blue Mills	2	1
Gambers Hall	2	2
Lyons Hall	3	2
Bovington Hall	3	2
Iron Bridge	3	2
Robjohns Farm	3	2
Bramble Road	4	2
Faulkbourne Ford	4	2
Guithavon FGS	4	2
Ashwell Hall	4	2
Goldsticks Farm	4	2
Petches Bridge	4	2
Langford	4	3
Wethersfield Mill	4	2

	growth	variables		
	Cluster 1	Cluster 2	cluster3	cluster4
$L_{infinity}$	491 mm	710 mm	550 mm	431 mm
K	0.15	0.08	0.09	0.15
Max Age	15.5	10	12.5	12.9
L 1	47 mm	36 mm	41 mm	42 mm
L5	242 mm	216 mm	196 mm	213 mm
L10	369 mm	375 mm	318 mm	323 mm
% std growth	99	90	84	91

	abiotic	variables	
	Cluster 1	Cluster 2	cluster3
Size of catchment (km^2)	258.20	95.10	643.00
Altitude (m)	13.60	39.75	1.00
Gradient ($^0/_{00}$)	1..22	1.43	1..53
Distance from source (km)	61.80	27.65	72.00
Wetted Width(m)	9.42	5.24	8.90

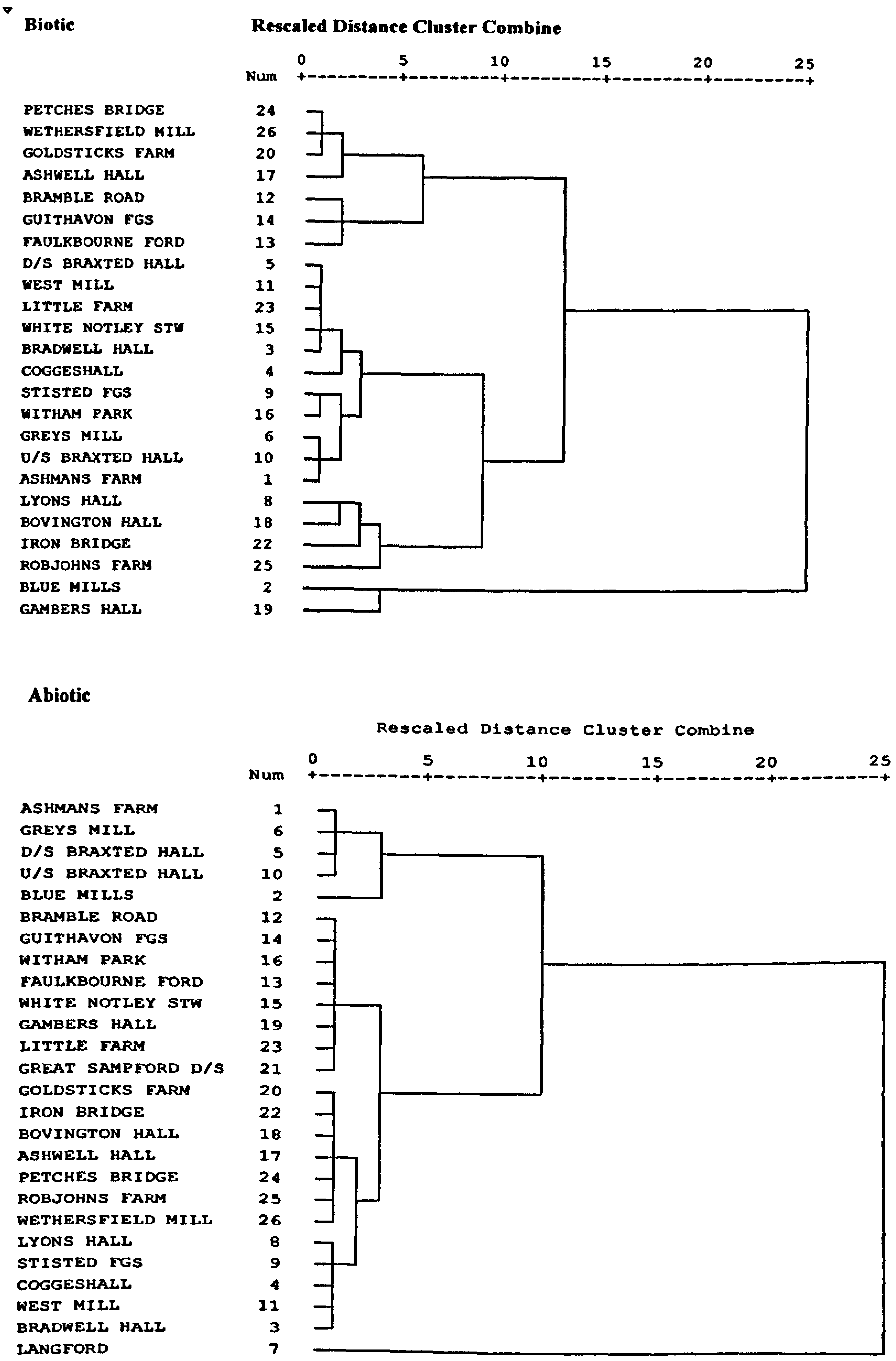


Figure 4.19 - Dendrogram using Average Linkage (Within Group) cluster analysis on Blackwater catchment chub sites growth characteristics and abiotic variables.

Blackwater catchment dace

Three clusters were separated from the growth characteristics of the Blackwater catchment dace populations (Table 4.17, Figure 4.20). Cluster 2 recorded the highest $L_{infinity}$ and Cluster 1 the lowest. Cluster 1 had the greatest K value and Cluster 2 the lowest. The largest percentage growth, oldest maximum age and greatest lengths achieved at ages 1 and 3 were recorded in Cluster 1. Cluster 3 had the lowest maximum age, percentage standard growth and lengths at age 1 and 3.

Three clusters were again separated from the abiotic data of the Blackwater catchment dace populations (Table 4.17, Figure 4.20). Cluster 2 had the largest catchment size above each site, the greatest distance from source, the greatest wetted width and the lowest altitude. Cluster 3 had the smallest mean catchment size was at the highest altitude and was closest to source. Cluster 1 had abiotic values intermediate of Clusters 2 and 3. Cluster 3, therefore represented the upper reaches, Cluster 1 the middle reaches and Cluster 2 the lower reaches of the study area.

Table 4.17 – Cluster membership of the dace sites in the Blackwater catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

	Cluster Membership growth characteristics	abiotic
Kelvedon coalyard	1	1
Smallands Hall	1	2
Sisted FGS	1	1
West Mill	1	1
Bramble Road	1	3
Faulkbourne Ford	1	3
Guithavon FGS	1	3
White Notley STW	1	3
Witham Park	1	3
Ashwell Hall	1	3
Bovington Hall	1	3
Gambers Hall	1	3
Goldsticks Farm	1	3
Iron Bridge	1	3
Petches Bridge	1	3
Little Farm	2	3
Robjohns Farm	3	3

Mean growth variables	cluster1	cluster 2
$L_{infinity}$	256mm	711mm
K	0.29	0.07
Max Age	7.4	5
L 1	55mm	50mm
L 3	140mm	134mm
% std growth	120	109

	cluster3
$L_{infinity}$	504mm
K	0.08
Max Age	4
L 1	48mm
L 3	121mm
% std growth	92

Mean abiotic variables	cluster1	cluster 2
Size of catchment (km^2)	162.33	335
Altitude (m)	28.00	7.00
Gradient (‰)	0.93	1.53
Distance from source (km)	48.33	68.00
Wetted Width (m)	7.50	9.90

	cluster3
Size of catchment (km^2)	77.46
Altitude (m)	39.62
Gradient (‰)	1.62
Distance from source (km)	22.38
Wetted Width (m)	4.63

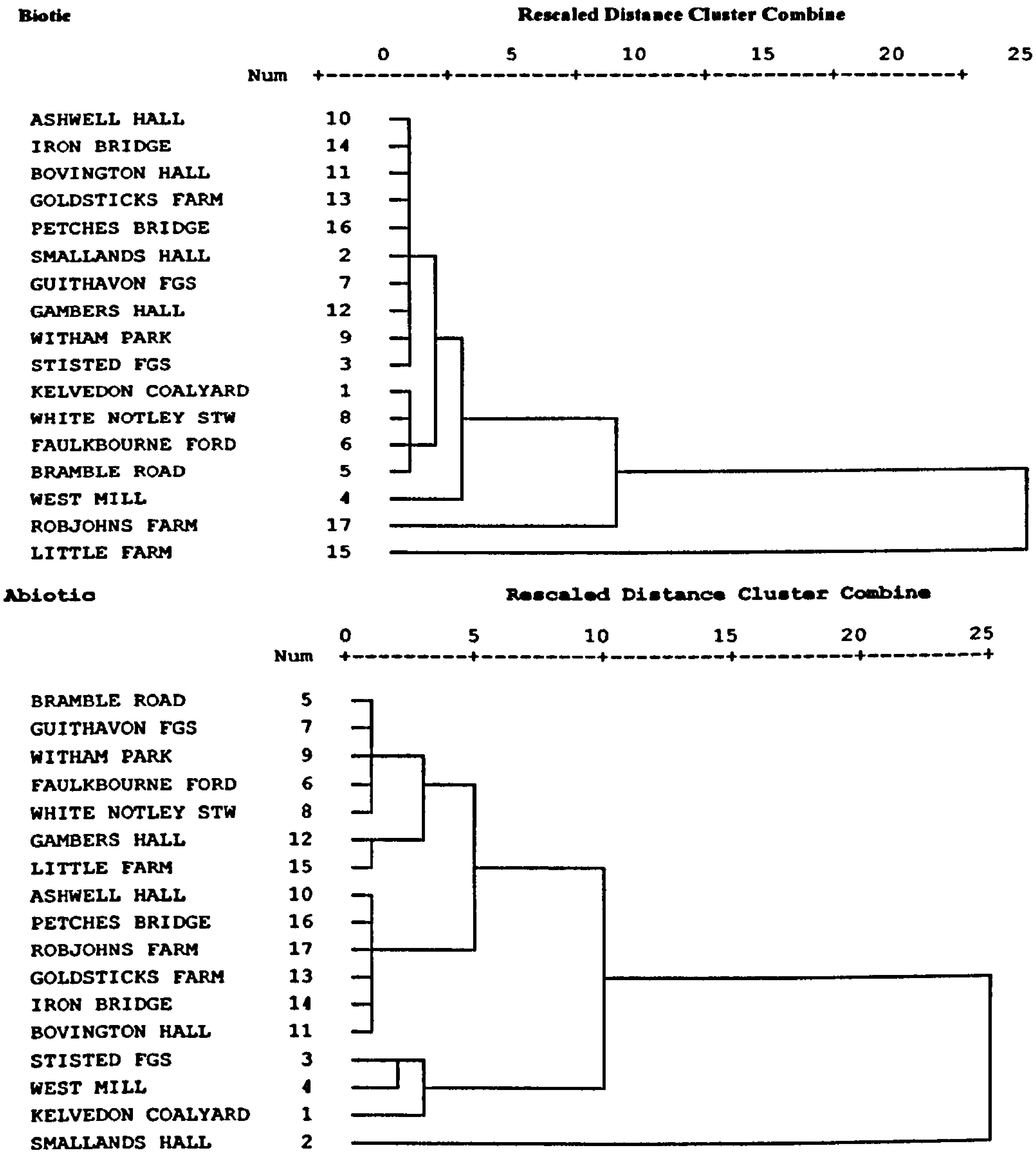


Figure 4.20 - Dendrogram using Average Linkage (Within Group) cluster analysis on Blackwater catchment dace sites growth characteristics and abiotic variables.

Blackwater catchment roach

Two clusters were separated from the growth characteristics of roach from the Blackwater catchment (Table 4.18, Figure 4.21). Cluster 2 recorded the largest $L_{infinity}$, lowest K value and the greatest maximum age. Cluster 1 had slightly larger lengths at ages 1 and 3 and a larger percentage standard growth than Cluster 2.

Three clusters were separated from the abiotic data of the Blackwater catchment roach sites (Table 4.18; Figure 4.21). Cluster 2 was furthest from source with the largest mean catchment area above each site and had the largest wetted width. Cluster 3 was closest to source with the smallest mean catchment area above each site, while Cluster

1 recorded the highest altitude. Cluster 3 therefore represented the upper reaches of the samples area, while Cluster 2 represented the lower reaches.

Table 4.18 – Cluster membership of the roach sites on the Blackwater catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

	Cluster Membership growth characteristics	abiotic	Mean	growth cluster1	variables cluster 2	Mean	abiotic cluster1	variables cluster 2
Bradwell Hall	1	1	$L_{infinity}$	257mm	403mm	Size of catchment (km²)	129.29	257.00
Dorewards Hall	1	1	K	0.19	0.1	Altitude (m)	38.43	12.50
u/s Braxted Hall	1	2	Max Age	7	8.36	Gradient ($^{0}/_{00}$)	1.09	1.14
Bramble Road	1	3	L 1	54mm	51mm	Distance from source (km)	37.79	63.00
Witham Park	1	3	L 3	117mm	116mm	Wetted Width (m)	8.09	9.25
Coggeshall	2	1	% std growth	127	120		cluster3	
Covenbrook Hall	2	1				Size of catchment (km²)	61.33	
d/s Braxted Hall	2	2				Altitude (m)	16.33	
Hobbs Meadow	2	1				Gradient ($^{0}/_{00}$)	2.00	
Kelvedon Coalyard	2	1				Distance from source (km)	20.00	
Lyons Hall	2	1				Wetted Width (m)	4.53	
Sisted FGS	2	1						
Guithavon FGS	2	3						
Ashwell Hall	2	1						
Bovington Hall	2	1						
Courtaulds Mill	2	1						
Goldsticks Farm	2	1						
Iron Bridge	2	1						
Wethersfield Mill	2	1						

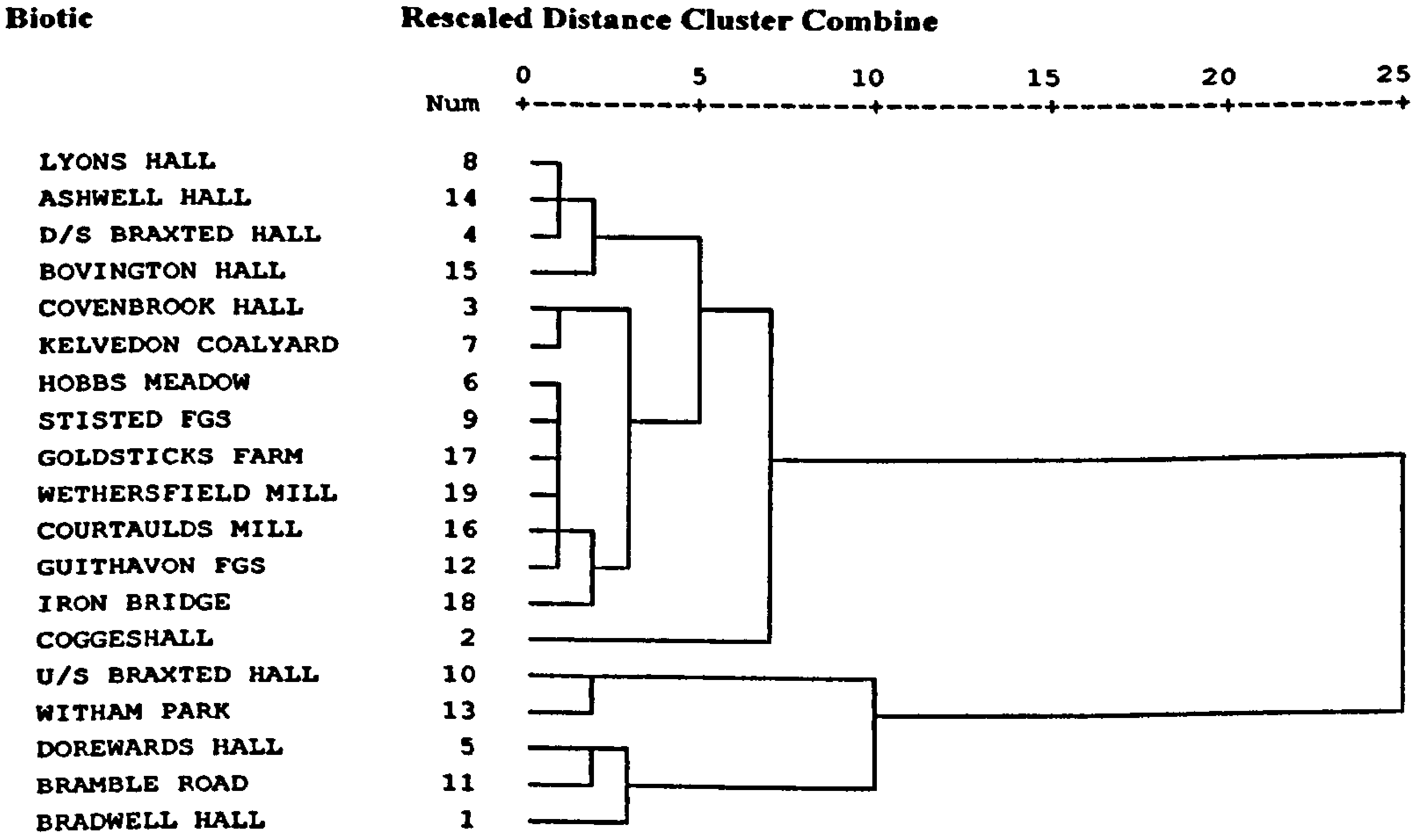


Figure 4.21 - Dendrogram using Average Linkage (Within Group) cluster analysis on Blackwater catchment roach sites growth characteristics and abiotic variables.

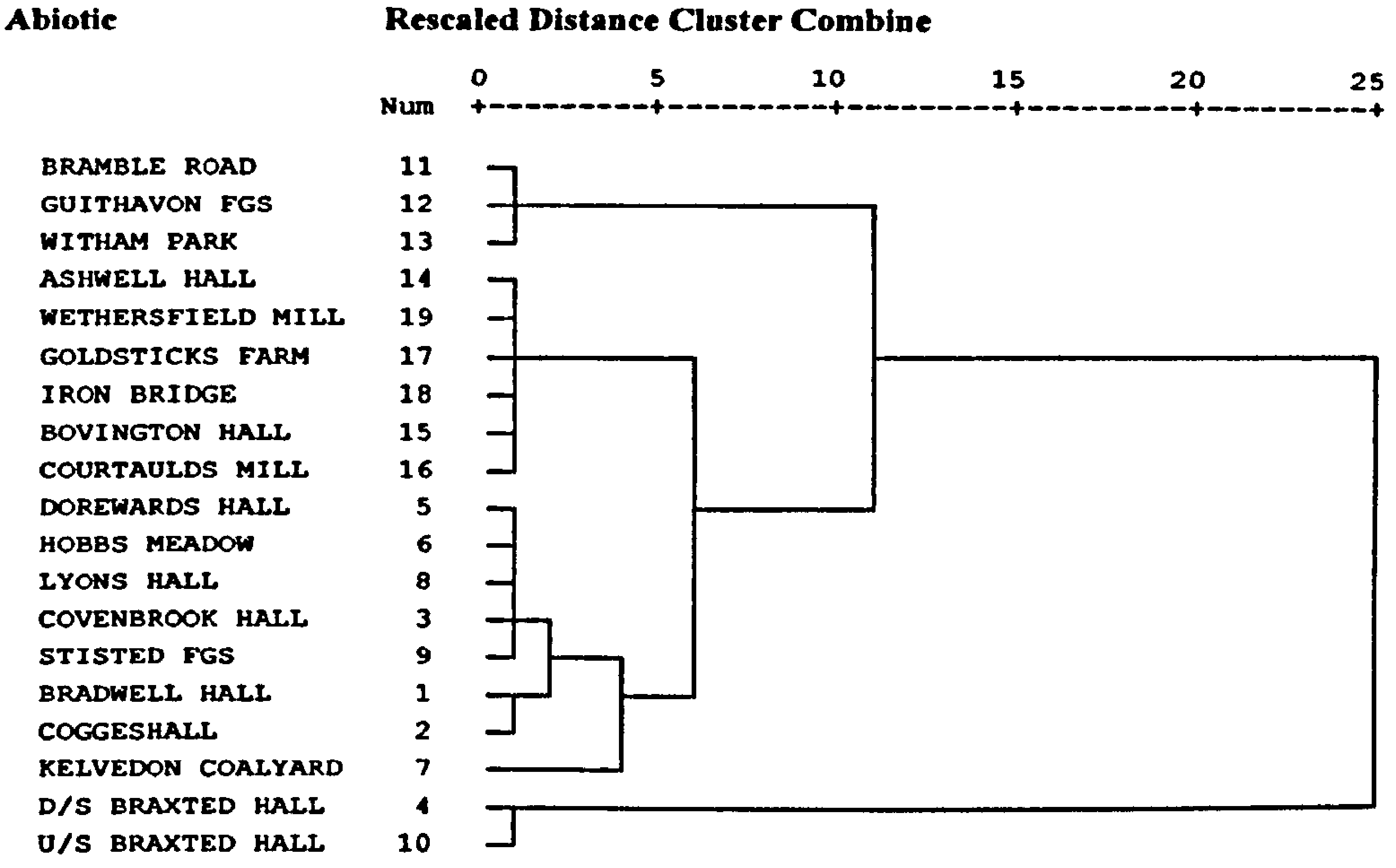


Figure 4.21 (continued) - Dendrogram using Average Linkage (Within Group) cluster analysis on Blackwater catchment roach sites growth characteristics and abiotic variables.

Yorkshire Ouse chub

Four clusters were separated from the growth characteristics from the chub sites of the Yorkshire Ouse catchment (Table 4.19, Figure 4.22). Cluster 4, consisted of one site (Nun Monkton, R. Nidd), which had the greatest L_{infinity} and the lowest K value. Cluster 2 had the lowest L_{infinity} and the greatest K value. Maximum age, mean lengths at age's 1, 5 and 10 as well as percentage standard growth were all highest in Cluster 2. Conversely, Cluster 4 recorded the lowest lengths at ages 1 and 5 and the lowest percentage standard growth. The smallest length at age 10 was found in Cluster three.

Two clusters were separated from the abiotic date from the Yorkshire Ouse chub sites (Table 4.19, Figure 4.22). Cluster 1 was furthest from source, had the largest catchment area above each site and the greatest wetted width. Conversely, Cluster 1 showed the highest mean altitude and the greatest mean river bed gradient. Cluster 2 therefore represented the upper reaches of the sampled area while Cluster 1 represented the lower.

Table 4.19 – Cluster membership of the chub sites on the Yorkshire Ouse catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

	Cluster Membership growth characteristics	abiotic	Mean	growth	variables	Mean	abiotic	variables
				cluster 1	cluster 2		Cluster 1	cluster 2
Crimpsall	1	1	$L_{infinity}$	569mm	510mm	Size of catchment (km²)	966.60	467.90
Kirkstal	1	2	K	0.11	0.14	Altitude (m)	14.00	34.30
Thwaite Weir	1	1	Max Age	15.64	16	Gradient $(^0/_{00})$	1.50	2.50
Castley	1	2	L 1	47mm	55mm	Distance from source (km)	88.90	61.90
Pool Mill	1	2	L 5	232mm	248mm	Wetted Width (m)	23.90	22.10
Tadcaster	1	1	L10	373mm	378mm			
Cowthorpe	1	2	% std growth	98	103			
Holme	1	1		cluster 3	cluster 4			
Maunby demesne	1	1	$L_{infinity}$	645mm	767mm			
Boroughbridge	1	1	K	0.08	0.06			
Hewick Bridge	1	1	Max Age	14	10			
Middleham	1	2	L 1	43mm	40mm			
Ripon Golf Club	1	2	L 5	204mm	198mm			
Westwick	1	1	L10	346mm	348mm			
Hirstwood	2	2	%std growth	90	85			
Knotford	2	2						
Langton Grange	2	2						
Morton on Swale	2	2						
Kirk Hammerton	3	2						
Nun Monkton	4	2						

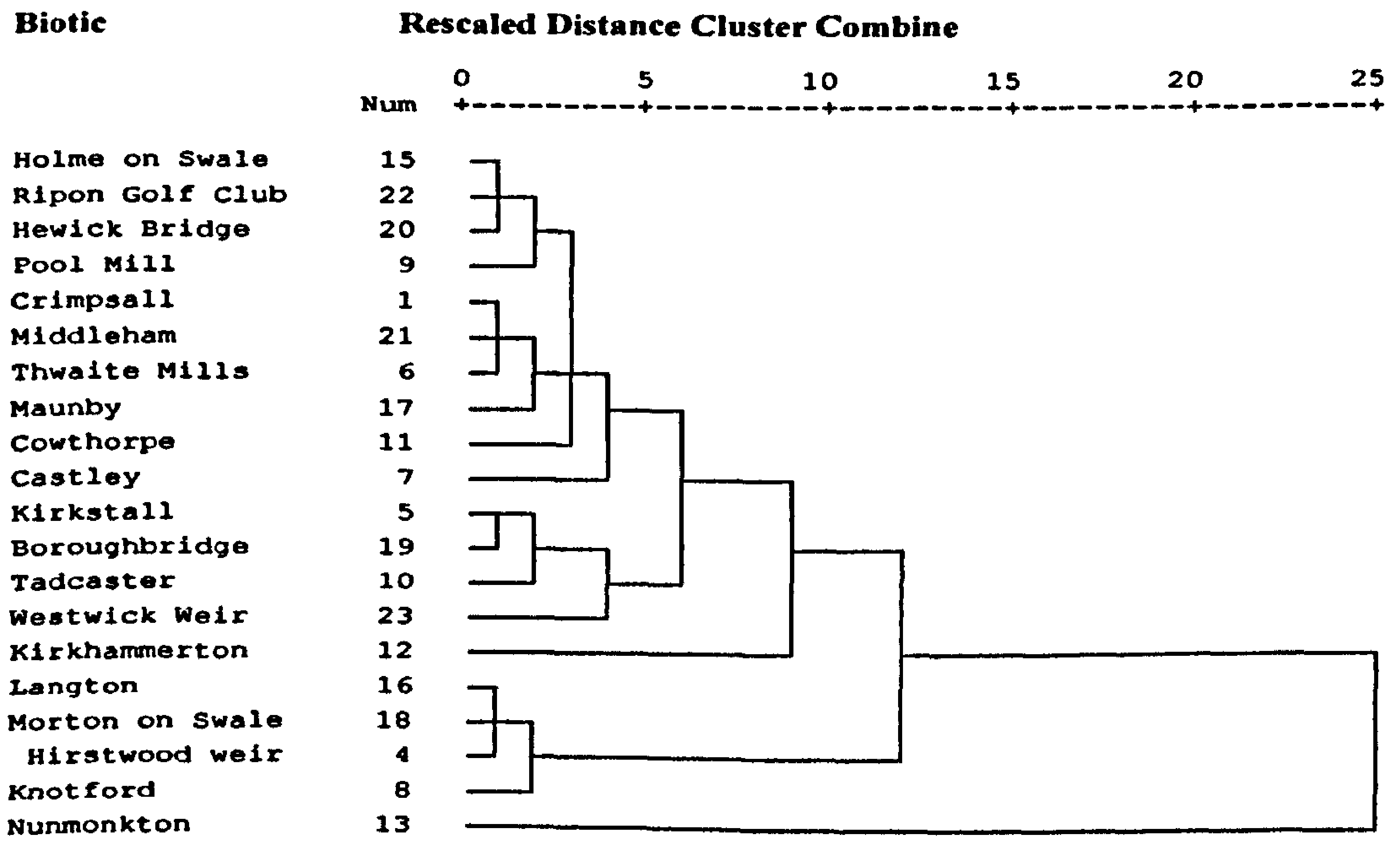


Figure 4.22 - Dendrogram using Average Linkage (Within Group) cluster analysis on Yorkshire Ouse catchment chub sites growth characteristics and abiotic variables.

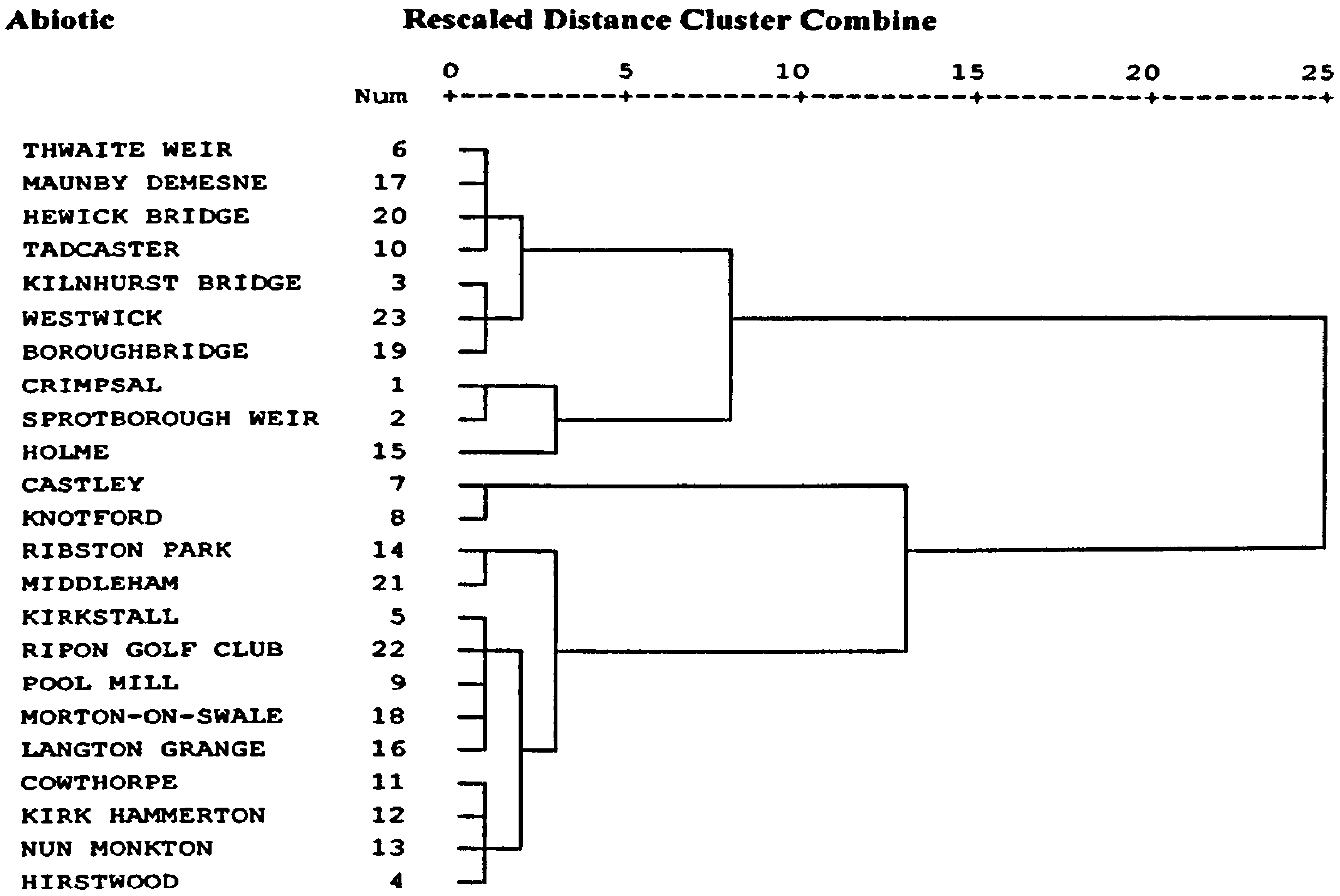


Figure 4.22 (continued) - Dendrogram using Average Linkage (Within Group) cluster analysis on Yorkshire Ouse catchment chub sites growth characteristics and abiotic variables.

Yorkshire Ouse dace

Three clusters were separated from the growth characteristics from the dace sites of the Yorkshire Ouse catchment (Figure 4.20, Table 4.23). Two of these clusters consisted of just one site each, Cluster 2 (Castley) and Cluster 3 (Ulleskelf), while the growth characteristics of dace from the remaining sites were similar. Cluster 1 was found to be the fastest growing but had the smallest asymptotic length. Cluster 1 also had the greatest longevity and the greatest lengths at ages 1 and 3. Cluster 3 was found to have the greatest percentage standard growth while Cluster 2 had the lowest percentage standard growth.

Three clusters were separated from the abiotic data of the dace sites on the Yorkshire Ouse (Figure 4.23, Table 4.20). Cluster 3 had the largest catchment area above each site, was the furthest from source with the greatest wetted width. Cluster 1 was closest to source, had the least mean catchment size above each site, was at the highest altitude and had the greatest river bed gradient. Cluster 1 therefore represented the upper regions of the sampled area, while Cluster 3 represented the lower region.

Table 4.20 – Cluster membership of the dace sites on the Yorkshire Ouse catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

	Cluster Membership growth characteristics	abiotic	Mean	growth	variables	Mean	abiotic	variables
				cluster 1	cluster 2		cluster 1	cluster 2
Blackburn Meadows	1	1	L_{infinity}	247 mm	483 mm	Size of catchment (km^2)	7.00	528.20
Kelham island	1	2	K	0.35	0.08	Altitude (m)	59.50	29.20
Crimpsall	1	3	Max Age	5.2	4	Gradient (‰)	9.00	1.30
Thwaite Mill	1	3	L 1	57 mm	52 mm	Distance from source (km)	4.20	69.30
			L 3	141 mm	136 mm	Wetted Width (m)	24.00	19.50
Tadcaster	1	3	% std growth	109	97			
Cowthorpe	1	2		cluster 3			cluster 3	
Langton	1	2	L_{infinity}	729 mm		Size of catchment (km^2)	920.50	
Boroughbridge	1	3	K	0.08		Altitude (m)	12.80	
Hewick Bridge	1	3	Max Age	4		Gradient (‰)	1.50	
Westwick Weir	1	3	L 1	54 mm		Distance from source (km)	93.40	
			L 3	127 mm		Wetted Width (m)	25.10	
Rotherham Wei	1	3	% std growth	122				
Kirkhammerto	1	2						
Kirkstall	1	2						
Pool Mill	1	2						
Castley	2	1						
Ulleskelf	2	3						

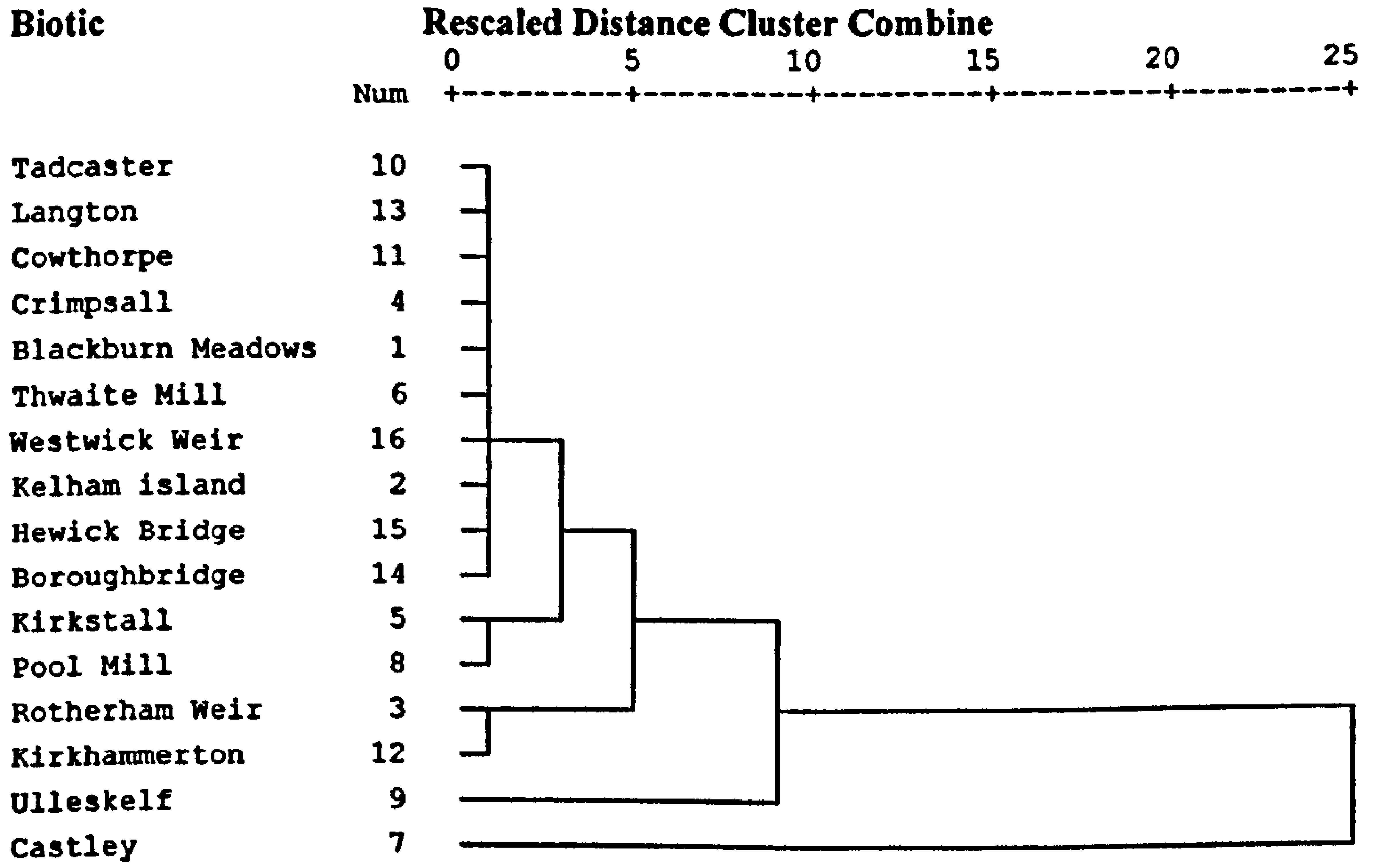


Figure 4.23 - Dendrogram using Average Linkage (Within Group) cluster analysis on Yorkshire Ouse catchment dace sites growth characteristics and abiotic variables.

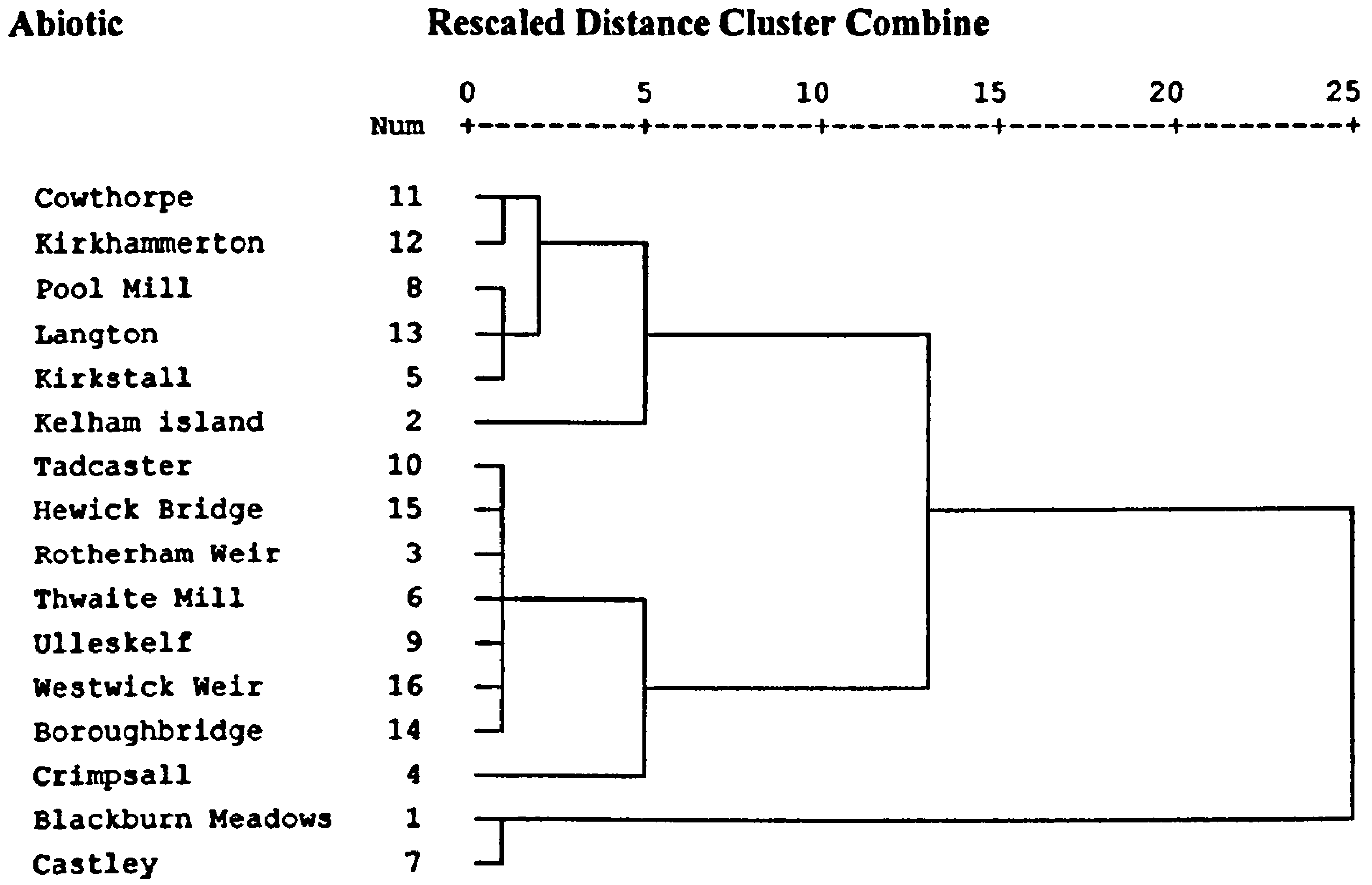


Figure 4.23 (continued) - Dendrogram using Average Linkage (Within Group) cluster analysis on Yorkshire Ouse catchment dace sites growth characteristics and abiotic variables.

Three clusters were separated from the growth characteristics of roach from the Yorkshire Ouse (Figure 4.24, Table 4.21). Cluster 3 had the largest $L_{infinity}$, while Cluster 2 had the lowest. The growth coefficient was lowest in Cluster 3 and greatest in Cluster 2. Cluster 1 had the smallest length at age 1 but longevity within this cluster was found to be greatest. The largest mean length at age 1 along with the largest percentage standard growth was found in Cluster 3 while Cluster 2 recorded the largest mean length at age 3. The lowest percentage standard growth was found in Cluster 2.

Two clusters were separated from the abiotic data from the roach sites of the Yorkshire Ouse catchment (Table 4.21 Figure 4.24). Cluster 1 defined the upper reaches of the catchment and was characterised by a smaller catchment area above each site while being situated at greater altitudes with greater river bed gradients. Cluster 2 defined the lower reaches of the study area and was characterised by greater distances from source and catchment area above each site with wider wetted widths and lower river bed gradients.

Table 4.21 – Cluster membership of roach sites from the Yorkshires Ouse catchment showing growth characteristics, abiotic variables and mean values for descriptor variables.

Case	Cluster Membership growth characteristics	abiotic
Acaster Malbis	1	1
Linton weir	1	1
Attercliffe	1	2
Connisborough	1	3
Chapel Haddersley	1	4
Ulleskelf	1	3
Nun Monkton	1	2
Myton Grange	1	3
Boroughbridge	1	3
Langthorpe	1	3
Westwick weir	1	3
Benningborough	2	1
Nether Poppleton	2	1
Blackburn Meadows	2	3
Crimpsall	2	3
Kilnhurst bridge	2	3
Rotherham	2	2
Sprotborough	2	3
Castleford	2	4
Hirstwood weir	2	2
Thwaite mill	2	3
Kirkhammerton	2	2
Dunsforth	2	4
Hewick Bridge	2	3
Naburn	3	1
u/s Linton w	3	1

Mean growth variables	cluster 1	cluster 2
$L_{infinity}$	524mm	275mm
K	0.06	0.17
Max Age	8	7.8
L 1	47mm	50mm
L 3	99mm	108mm
% std growth	107	110

	cluster 3
$L_{infinity}$	865mm
K	0.03
Max Age	6
L 1	50mm
L 3	102mm
% std growth	115

Mean abiotic variables	cluster 1	cluster 2
Size of catchment (km^2)	1064.55	3402.17
Altitude (m)	14.05	5.67
Gradient ($^0/_{00}$)	0.90	0.00
Distance from source (km)	86.97	155.13
Wetted Width (m)	27.38	39.17

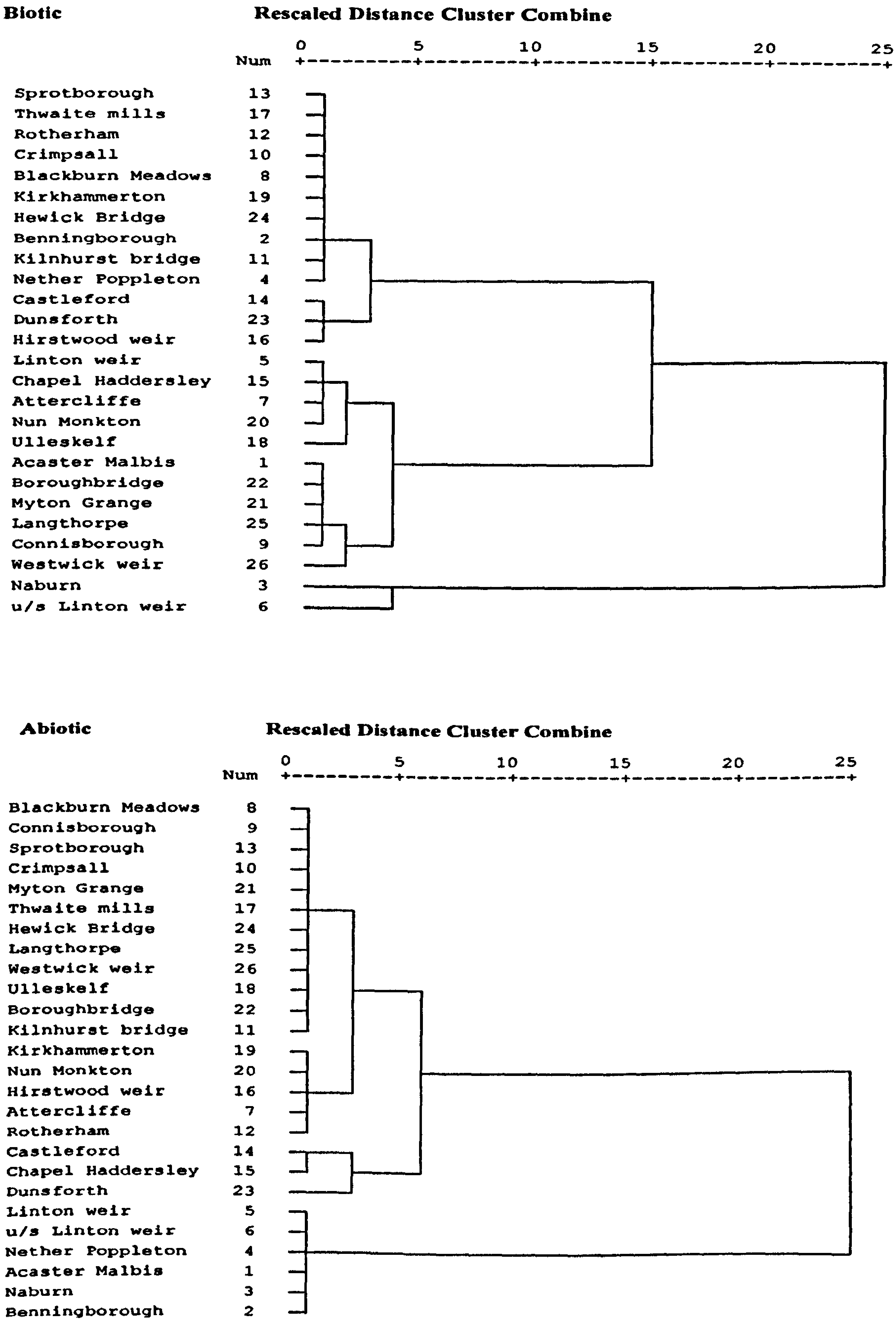


Figure 4.24 - Dendrogram using Average Linkage (Within Group) cluster analysis on Yorkshire Ouse catchment roach sites growth characteristics and abiotic variables.

4.3.4 – Growth at the national level – multiple regression of growth characteristics and abiotic variables

Weak relationships were found from multiple regressions between the growth characteristics of roach and abiotic variables from rivers throughout England and Wales (Table 4.22). The t value, derived from β coefficient revealed a positive relationship with river bed gradient and an inverse relationship with distance from source had the greatest influence on $L_{infinity}$. The growth coefficient was found to be influenced most by positive relationships with distance from source and catchment area above each site. Longevity of roach in this catchment was influenced mainly by an inverse relationship with wetted width. Mean length at age 1 was influenced most by an inverse relationship with latitudinal position, while inverse relationships with both latitude and altitude coupled with a positive relationship with mean air temperature had the greatest influence on percentage standard growth. The growth of roach is therefore faster within the lower reaches of the rivers at lower latitudes.

Table 4.22 – Relationships (R^2) and significance of relationships (t) between the growth characteristics and abiotic variables of roach from rivers throughout England and Wales from multiple regressions.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.1164	401682.196	3050493	0.020
K	0.1348	0.1172	0.752005	0.007
max age	0.0565	51.725966	863.2455	0.348
L1	0.0653	270.89518	3877.762	0.247
% std growth	0.1557	3603.685	19546.99	0.002

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Latitude	t	0.7855	0.2694	0.4112	-2.6390	-2.8211
	P		**		**	**
Altitude	t	-0.3085	-1.0324	0.3198	-0.2652	-2.0061
	P					*
Distance from source	t	2.5515	-3.4531	0.7409	-0.0527	-1.7894
	P	*				
River Bed Gradient	t	3.1155	-1.4759	-0.3637	-0.4976	1.5533
	P	**				
Mean Air Temperature	t	1.9599	-1.4524	0.7558	-2.4659	-2.4297
	P				*	*
Wetted width	t	-0.3737	-0.2536	-1.7589	0.6253	0.2325
	P					
Catchment Area Above Site	t	-1.7322	3.5051	-0.1103	-0.6222	1.8441
	P		**			

* = $P<0.05$ ** = $P<0.01$

Weak, although mainly significant, relationships were found from multiple regressions of the growth characteristics and abiotic variables of dace from rivers throughout England and Wales (Table 4.23). The t value, derived from β coefficient revealed asymptotic length was influenced most by an inverse relationship with increasing latitude and a positive relationship with wetted width. The growth coefficient was influenced most by positive relationships with latitude, catchment area above each site and an inverse relationship with mean air temperature. Longevity in dace was influenced most by a positive relationship with mean air temperature and an inverse relationship with distance from source. Positive relationships with both catchment area above each site and distance from source were found to have the greatest influence on mean length at age 1, while a positive relationship with catchment area above each site and an inverse relationship with mean air temperature had the strongest influence on percentage standard growth. Altitude was removed from this model by SPSS ver14 as it contributed little to the model.

Table 4.23 – Relationships (R^2) and significance of relationships (t) between the biotic and abiotic variables of dace from rivers throughout England and Wales from multiple regressions.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.1111	267382.4	2139116	0.094
K	0.1922	0.291	1.222	0.003
max age	0.2404	114.470	361.695	<0.01
L1	0.1621	1197.402	6187.694	0.012
% std growth	0.1806	3233.733	14674.41	0.006

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Latitude	t	-1.7249	1.4299	0.4223	0.3970	-0.2014
	P					
Altitude	t					
	P					
Distance from source	t	0.6245	-1.2099	-2.1099	-2.4966	-1.6376
	P			*	*	
River Bed Gradient	t	0.2624	-0.9508	0.9809	-0.2555	-0.4240
	P					
Mean Air Temperature	t	0.2171	-1.4104	2.1211	-1.1205	-1.9711
	P			*		
Wetted width	t	1.7510	-1.0859	-0.4155	1.4740	1.9479
	P					
Catchment Area Above Site	t	-0.8895	1.6662	1.0736	3.0386	2.1878
	P				**	*

* = $P<0.05$ ** = $P<0.01$

Weak, although mainly significant, relationships were found from multiple regressions of abiotic variables and the growth characteristics of chub from rivers throughout England and Wales (Table 4.24). the t value, derived from β coefficient revealed an inverse relationship with mean air temperature coupled with positive relationships with latitude and catchment area above each site had the greatest influence on $L_{infinity}$. A positive relationship with catchment area above each site along with an inverse relationship with mean air temperature was found to have the greatest influence on the growth coefficient. Positive relationships with distance from source and catchment area above each site and an inverse relationship with altitude were found to influence longevity. A positive relationship with mean air temperature was found to have the greatest influence on mean length at age 1. Positive relationships with mean air temperature coupled with an inverse relation with latitude were found to have the strongest influence on percentage standard growth.

Table 4.24 – Relationships (R^2) and significance of relationships (t) between the biotic and abiotic variables of chub from rivers throughout England and Wales from multiple regressions.

	R^2	Sum of Squares		P
		Regression	Residual	
$L_{infinity}$	0.1040	179086.3	1542086	0.062
K	0.1381	0.019	0.118	0.011
max age	0.1212	150.233	1089.767	0.027
L1	0.2610	3288.192	9312.274	<0.01
% std growth	0.1358	1811.934	11528.71	0.013

		$L_{infinity}$	K	max age	length at age 1	%Std Growth
Latitude	t	1.2588	-0.8968	-1.5541	3.1881	2.3880
	P				**	*
Altitude	t	-0.8262	-0.0394	2.1060	-0.4790	-1.8969
	P			*		
Distance from source	t	1.1088	-1.8798	2.9945	-0.5361	-1.4637
	P			**		
River Bed Gradient	t	-0.5194	1.2321	-0.9705	0.6370	1.0151
	P					
Mean Air Temperature	t	1.6328	-2.2371	-0.9095	4.1998	1.6581
	P		*		**	
Wetted width	t	1.0665	-0.0993	1.7679	-0.1399	2.0495
	P					*
Catchment Area Above Site	t	-1.3302	2.5214	-2.9144	0.3278	1.9769
	P		*	**		*

* = $P<0.05$ ** = $P<0.01$

4.3.5 – Canonical correspondence analysis (CCA) of nation wide biotic and abiotic variables

CCA ordination (Figure 4.25) for roach, showed latitude and wetted width had the strongest relation between the first species axis (0.1224 and 0.1091 respectively) and the first environmental axis (0.6572 and 0.5858 respectively) these values accounted for 2% of the variance in the first axis of the species data, and 52.2% of the variance in the first axis of the species-environment relationship. These values increased with the cumulative addition of the second axis which accounted for 3.3% of the variance observed in the species data and 85.9% of the variance observed in the species-environment relationship. Of the growth characteristics, the growth coefficient was strongly related to an inverse relationship with altitude and river bed gradient. This inverse relationship, although to a lesser degree, also influenced mean lengths at ages 1, 2 and 3. The asymptote was positively related to catchment size while the mean length at age 4 was related to longitude. Mean air temperature was discounted in this test as all values were identical (10°C).

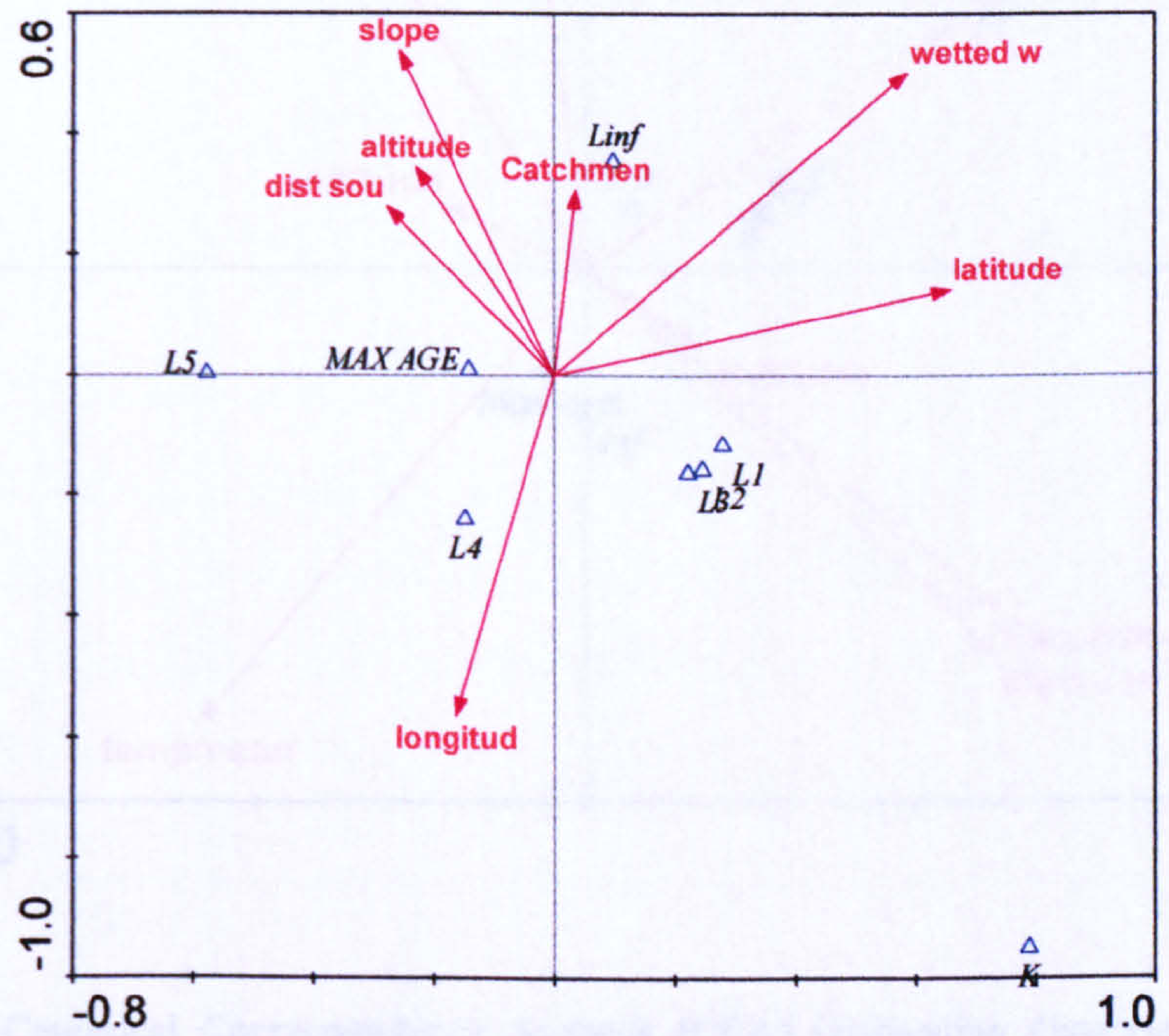


Figure 4.25 –CCA ordination diagram of the growth characteristics of roach (Δ) from sites throughout England and Wales and associated environmental variables (arrows). The growth characteristics of the roach being – Asymptotic length (Linf), the rate at which the asymptotic length is achieved (K), the maximum age achieved within the population (MAX AGE), mean length at age 1 (L1), age 2 (L2), age 3 (L3), age (L4) and age 5 (L5). The abiotic environmental variables being latitude, longitude (longitud), area of catchment above site (Catchmen), distance from source (distsou), altitude, wetted width (wetted w) and river bed gradient (slope).

CCA of dace populations from throughout England and Wales and the abiotic variables were significant ($P<0.05$). CCA ordination for dace (Figure 4.26) showed latitude as having the strongest relationship to both the first species axis (0.3335) and the first environmental axis (0.7443), which accounted for 13.8% of the variance seen in the species data, and 87.7% of the variance seen in the species-environment relationship. An inverse relationship existed between latitude and mean air temperature, whereby an increase in latitude resulted in a reduction in air temperature. Positive relationships existed between catchment size above each of the sites, distance from source and wetted width, which were all inversely related to altitude, river bed gradient and longitude. Of the growth characteristics, the growth coefficient was strongly related to latitude, with weaker relationships existing between mean lengths at ages 1, 2, 3 and 4 with latitude. Longevity of dace from each site was related with mean air temperature, as was L∞, although L∞ was equally influenced by increasing catchment size, distance from source and wetted width.

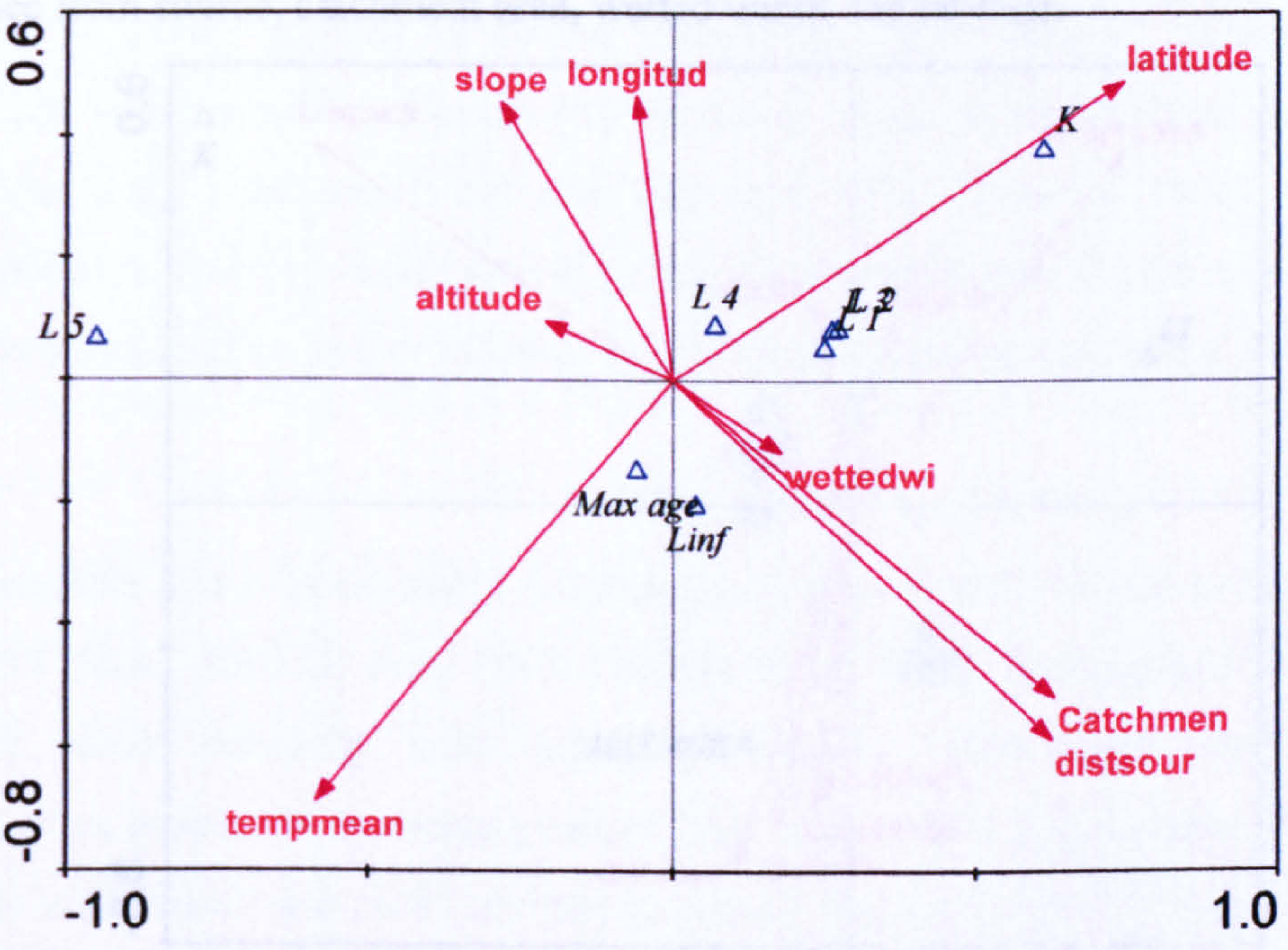


Figure 4.26 – Canonical Correspondence Analysis (CCA) Ordination diagram of the growth characteristics of dace (Δ) from sites throughout England and Wales and the sites associated environmental variables (arrows). The growth characteristics of the roach being – Asymptotic length (Linf), the rate at which the asymptotic length is achieved (K), the maximum length achieved within the population (MAX AGE), length at age 1 (L1), length at age 2 (L2), length at age 3 (L3), length at age (L4), length at age 5 (L5). The abiotic environmental variables from each site being latitude, longitude (longitud), mean air temperature (tempmean), area of catchment above site (Catchmen), distance from source (distsour), altitude, wetted width (wetted wi) and river bed gradient (slope).

The CCA ordination for chub populations from throughout England and Wales (Figure 4.27) revealed longitude had the strongest relationship to the first species axis (-0.3307) and the environmental axis (-0.795), with the first ordination axis accounting for 3.2% of the variance observed in the species variables and 45.3% of the variance observed in the species-environment relationship. Mean air temperature had the strongest relationship to the second species ordination axis (0.0966) and the second environment axis (0.4831), which increased the observed variance accounted for by the first two ordination axis, where the two axes accounted for 5.4% of the species variables and 77% of the variance observed in the species-environment relationship. Of the biotic variables, longitude had a strong influence upon the observed K value and a negative relationship with $L_{infinity}$, and to a lesser extent had a reduced influence upon the lengths achieved at ages 3, 4 and 5. The length at age one was shown to be strongly influenced by higher than average temperatures which were the inverse of longevity which was also influenced by a positive relationship with distance from source, catchment area, wetted width and latitude.

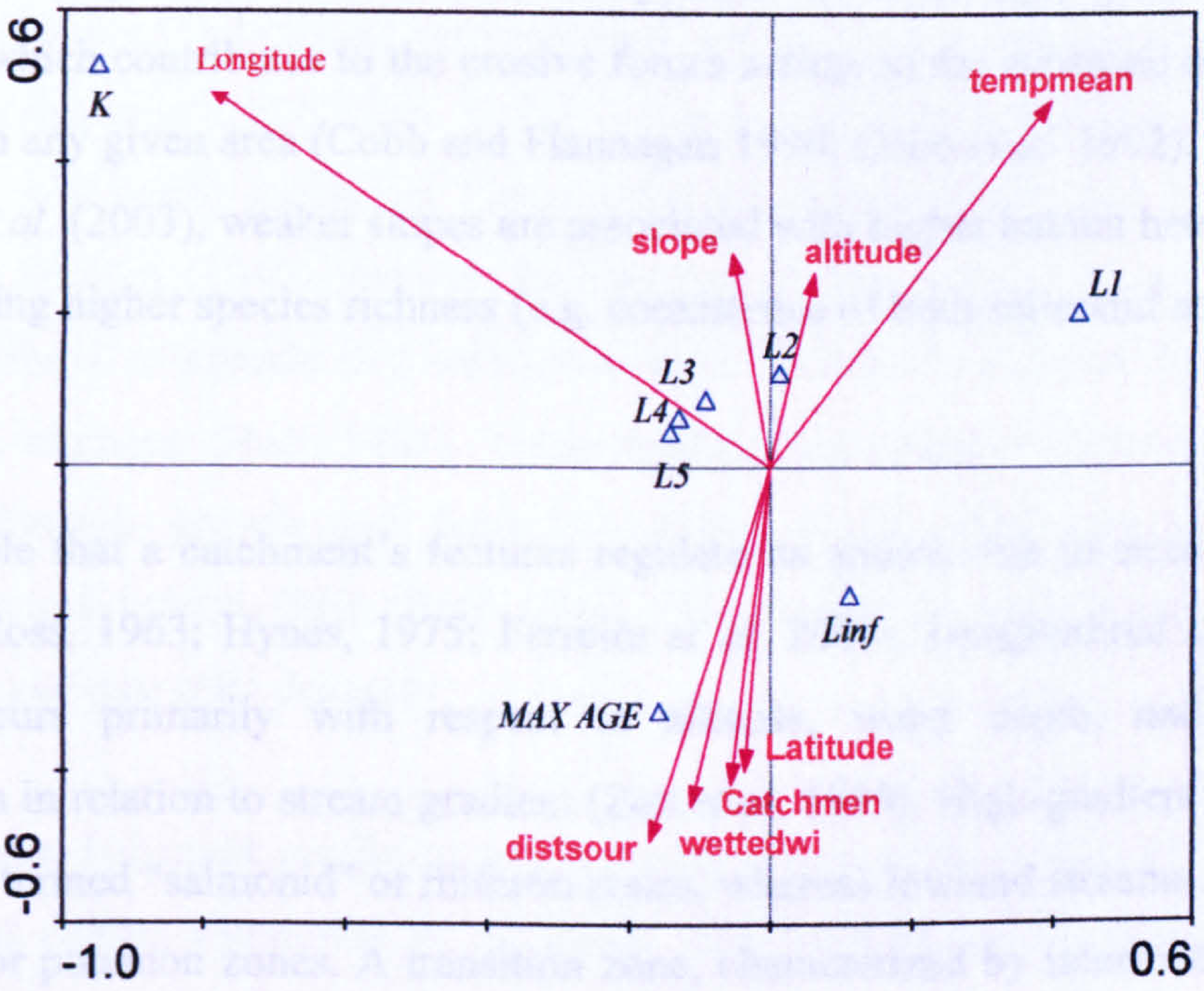


Figure 4.27 – Canonical Correspondence Analysis (CCA) Ordination diagram of the growth characteristics of chub (Δ) from sites throughout England and Wales and the sites associated environmental variables (arrows). The growth characteristics of the roach being – Asymptotic length (Linf), the rate at which the asymptotic length is achieved (K), the maximum length achieved within the population (MAX AGE), length at age 1 (L1), length at age 2 (L2), length at age 3 (L3), length at age (L4), length at age 5 (L5). The abiotic environmental variables from each site being latitude, longitude (longitud), mean air temperature (tempmean), area of catchment above site (Catchmen), distance from source (distsour), altitude, wetted width (wetted wi) and a measure of river bed gradient (slope).

4.4 – DISCUSSION

4.4.1 – Growth at the catchment level – abiotic variation along a longitudinal gradient

The physical character of a river changes markedly from headwater streams to lowland rivers (Poff *et al.* 1997). Hydrology varies markedly among basins and longitudinally along the river course, depending on geomorphological and local climatic conditions (Economou *et al.* 2005), with species ordinated according to river bed gradient from slow to fast flowing water (Pont *et al.* 2005). Upstream reaches are characterized by turbulent flows, steep gradients, coarse substratum, and cold, well-oxygenated water (Leopold *et al.* 1964). Lowland reaches, however, are typically characterized by warmer water temperatures (especially during summer), gentle gradients, finer substratum, increased turbidity and sediment deposition and reduced concentrations of dissolved oxygen (Schlosser 1982; Zelt *et al.* 1999). River bed gradient is a key variable in stream ecosystems, as it strongly influences flow dynamics, which contributes to the erosive forces acting on the substrate and causing bed scour in any given area (Cobb and Flannagan 1990; Cobb *et al.* 1992). According to Reyjol *et al.* (2003), weaker slopes are associated with higher habitat heterogeneity, thus favouring higher species richness (e.g. coexistence of both salmonid and cyprinid fish).

The principle that a catchment's features regulate its aquatic life in streams is well accepted (Ross, 1963; Hynes, 1975; Ferreira *et al.* 2007). Longitudinal zonation of species occurs primarily with respect to altitude, water depth, and substrate composition in relation to stream gradient (Zelt *et al.* 1999). High-gradient headwater streams are termed "salmonid" or rhithron zones, whereas lowland streams are termed "cyprinid" or potamon zones. A transition zone, characterized by intermediate levels of erosion and deposition, moderate gradients, alternating riffle-pool sequences, and sand-gravel substrates separates the two (Zelt *et al.* 1999). Differences in species assemblage composition along the longitudinal gradient reflect differences in environmental characteristics (Hoeinghaus *et al.* 2004). Survey sites located at high elevations in upper regions experience flash floods during wet seasons, have relatively coarse substrates, and tend to have narrow floodplain habitats (Hoeinghaus *et al.* 2004).

Physicochemical conditions in headwaters tend to be more stressful resulting in fewer fish species that are adapted to survival under these conditions (Mathews and Styron 1981). Survey sites in the lower reaches generally have finer substrates, broad floodplains that are seasonally inundated, (Hoeinghaus *et al.* 2004) and have increased habitat diversity (Reyes-Gavilán *et al.* 1996). High altitude, upstream areas being represented by such species as brown trout, minnow *Phoxinus phoxinus* (L.) and bullhead *Cottus gobio* (L.). Moderate altitude species include dace, chub and gudgeon with low altitude species being represented by rudd *Scardinius erythrophthalmus* (L.), roach and bream (Santoul *et al.* 2005).

One of the most important factors determining the distribution of living forms in fluvial systems is the rate of flow. Flow influences a number of physical and chemical factors such as dissolved oxygen concentration and temperature, which act directly on the fish (Welcomme 1983; Edds 1993). Altitude has also shown to be of great importance as a major ecological factor influencing fish growth and composition. Morin and Naiman (1990) showed the number of fish species in streams to be negatively related to altitude as it influences local fish species richness through water temperature changes (Huet 1959). These temperature changes govern population dynamics through growth and fecundity (Gillet *et al.* 1995), by acting as a physicochemical habitat filter (Poff 1997) with respect to species traits such as metabolism and energetic demands.

The longitudinal thermal profile of rivers resembles, to some extent, the latitudinal geographical pattern (Schiemer *et al.* 2004). The literature supports the idea that temperature plays an important role in explaining the relationship between distance from source (i.e. the downstream gradient) and fish assemblages (Bardonnet and Gaudin 1991). Water temperature varies both seasonally and daily in concert with air temperature, generally increasing in a downstream direction as the cooler, high-elevation climate is displaced by the, usually warmer, lowland climate (Zelt *et al.* 1999). The distribution of abiotic variables in this study was generally shown to follow this longitudinal pattern. The greatest river bed gradients generally observed in the upper reaches, indicating increased flow rates occurring in association with high altitudes reduced wetted widths at distances described as being close to the source. Conversely, reduced river bed gradients and increased wetted widths were found at low altitudes where reduced flow rates would occur in the lower reaches.

4.4.2 – Growth at the catchment level – biotic variation in relation to abiotic gradients

Longitudinal gradients of species composition in rivers and streams have long been recognized by aquatic ecologists (Burton and Odum 1945; Sheldon 1968; Horwitz 1978; Matthews 1986; Schlosser, 1982, 1987, 1990; Angermeier and Schlosser 1989; Rahel and Hubert 1991; Pires *et al.* 1999; Godinho *et al.* 2000). In general, compositional changes have been characterized as distinct faunal breaks or zones reflective of species additions (Hoeinghaus *et al.* 2004), as habitat complexity, width and depth increase in a downstream direction (Schlosser 1990; Pires *et al.* 1999). Although zonal boundaries are not sharply defined by the ichthyofauna, certain fish species may be typical of a region (Edds 1993). This variation suggests water depth, current velocity and substratum are key factors that control fish assemblage structure (Cowx and Welcomme, 1998). In undisturbed lotic systems, fish density and biomass increase from the headwaters in a downstream direction (Schlosser 1990; Pires *et al.* 1999).

Growth of fishes has been shown to exhibit phenotypic plasticity because of systematic changes in response to environmental and anthropogenic effects (Stearns 1992; Sinclair *et al.* 2002). Growth can display considerable intraspecific variation in response to differences in such factors as temperature and food supply (Weatherley and Gill 1987; Weatherley 1990). Winfield and Nelson (1991) described growth in temperate regions to be a function of water temperature, day length and food availability, a mixture of biotic and abiotic factors. Chub have been described as a rheophilic cyprinid, that prefer medium to fast flowing, lotic habitat conditions (Arlinghaus and Wolter 2003; Blank *et al.* 2007). They prefer the moderate current velocities that are found in the barbel and grayling zones (Cowx 2001), with preferred velocities of between 20-50 cm s^{-1} (Cowx and Welcomme 1998; Cowx *et al.* 2004), with moderate to fast flow velocities (0.15-0.75m s^{-1}) required for spawning (Arlinghaus and Wolter 2003).

The results of this study are consistent with previous studies addressing the relative influence of local versus regional factors on fish distribution and the responses of fish species to their environmental constraints, which are species specific (Pont *et al.* 2005). Chub populations in this study were shown to conform to these zonal theories. For example, in the Blackwater, Colne and Yorkshire Ouse catchments, the fastest growth rates of chub were observed in the upstream sites where greater river bed gradients would have resulted in increased flow rates than those sites downstream. This faster growth rate consequently related to a larger length at ages 1 and 3 in the Colne and Yorkshire Ouse catchments, compared with the downstream sites. It can therefore be seen that, in these rivers at least, chub prefer the upper regions where faster flow velocities occur at an appropriate temperature, in comparison to the sites further downstream, where flow regimes would be slower and temperatures warmer. These results are similar to those found by Przbylski (1995) who found the lowest values for $L\infty$, and therefore a higher growth coefficient in the upper regions of the River Warta.

Dace have been described as a common European rheophilic, lithophilous teleost species (Mills, 1981; Maitland and Campbell 1992) preferring deep, fast flowing, cool water with high oxygen levels (Blank *et al.* 2007), in the middle to upper reaches (Cowx 2001), with water velocities between 20 to 50 cm s^{-1} (Cowx and Welcomme 1998; Cowx *et al.* 2004), occupying waters in excess of 40 cm deep, with sandy substrates (Garner and Clough 1996). However, dace and chub were shown by Vlach *et al.* (2005) to associate themselves only with slower and deeper water, living only in pools, which was also noted by Lamouroux *et al.* (1999), Lamouroux & Souchon (2002) and Carter *et al.* (2004), although at a finer scale, the dace in these studies oriented to faster flowing areas at the top of the pools. The distribution of the growth parameters for dace followed the longitudinal gradient, but, as with chub, were not entirely consistent.

Dace have similar requirements to chub. One of the most important factors influencing the growth characteristics of dace was altitude. Within the Yorkshire Ouse and the rivers Blackwater and Colne, the observed growth coefficients of the dace populations, as was the case with chub from these rivers, was higher in the upper regions of the sampled areas. Preferred conditions for the growth of dace in these regions were higher altitudes with increased river bed gradients indicate cooler water temperatures occurring at higher velocities, than those encountered downstream. These results partially reflect those of Cowx (1988) who also described the preferred conditions for dace growth to occur in the upstream region of the River Exe. Cluster analysis of dace from the Blackwater catchment; however, were seen to have fast growth coefficients throughout the entire river, with the exception of two of the three uppermost sites. The differences observed between the catchments may be due to this species tolerance to environmental constraints changing between basins in relation to genetic variability among populations (Pont *et al.* 1995). The changes in growth coefficient may also be the result of human disturbances, such as agriculture, increasing nutrient load (Rahel and Hubert 1991; Harding *et al.* 1998), or urbanisation and flow regulation inducing higher water temperatures and creating lotic–lentic environments along the river (Ward and Stanford 1983), or resulting from a miscalculation during the production of length at age data.

Local success of a species is dependent on the match or mismatch between requirements and field conditions (Schiemer *et al.* 2004). Pont *et al.* (2005) found river bed gradient, size of catchment area above the site and mean air temperature to have the greatest influence on the distribution of roach in French rivers. They found roach inhabited the river reaches with the lowest gradients, in areas with the greatest catchment area above each site, where the warmest temperatures occurred and growth was fastest. This had the effect of restricting their distribution to the downstream river reaches, whereas chub and dace had a wider distribution along the rivers in question. Upstream drainage area was shown by Pont *et al.* (2005) to be of importance to roach, with increasing catchment area above each site being of increased importance. Increases in catchment area above each site would equate to decreased flow regimes, increased temperature regimes and nutrient loads, which have been linked to downstream increases in algal biomass (de Ruyter van Steveninck *et al.* 1990) and hence higher primary productivity giving these roach a larger scope for growth.

The growth of roach has been strongly linked to temperature (Goldspink 1978). As with a number of cyprinid fish species, roach prefer water temperatures in the region of 28–30°C, which are higher than those reached in most of their natural habitats in Europe (Staaks 1996). This preference may be connected to the fact that higher temperatures potentially allow for faster growth (Wootton 1990), which coincides with the highest digestive activity in the gut and the highest food conversion efficiency (van Dijk *et al.* 2002). Pont *et al.* (2005) found roach were restricted to the warmest reaches compared with chub and found mean air temperature was a key variable in explaining the geographic range of roach. Experiments on food availability showed fish prefer the patch where they obtain the highest per capita food intake (Milinski and Parker 1991; Krause 1992). In nature, however, high temperatures and high food availabilities are not necessarily always linked (Kramer *et al.* 1997; Mittelbach 1981).

In this study, roach were observed to inhabit the slow flowing, lower reaches of the catchments in question, which was consistent with Cowx (1989), where numerical dominance and or growth rate declined as conditions departed from the preferred habitat characteristics (Cowx 1989). River bed gradient was seen to effect the roach populations of the Yorkshire Ouse, as no roach were found at sites where the river bed gradient was in excess of $2^{0}/_{00}$. The high river bed gradient may have restricted these fish to the lower regions of this catchment, where reduced flow conditions, through reduced river bed gradients, in conjunction with increased catchment area above each site creating nutrient rich, warmer conditions conducive to the faster growth of roach.

The main difference between the roach populations of the Colne and Blackwater catchments and those of the Yorkshire Ouse was the ability of roach to maintain position within the rivers when river bed gradients were in excess of $2^{0}/_{00}$. The differences observed between the catchments may be due to the roach's tolerance to environmental constraints changing between basins in relation to genetic variability (Pont *et al.* 1995). Changes in the growth coefficient may also be the result of human disturbances, such as agriculture, increasing nutrient load (Rahel and Hubert 1991; Harding *et al.* 1998), or urbanisation and flow regulation inducing higher water temperatures and creating lotic–lentic environments along a river (Ward and Stanford 1983). Changing growth coefficient may also be as the result of inaccuracies in the

Environment Agency data (a number of sites were excluded from this analysis due to these inaccuracies).

From this analysis it can be seen that river bed gradient, acting upon the rivers flow dynamics, had the greatest impact on the observed within catchment growth characteristics, with the greatest growth coefficients of chub in regions where river bed gradients were above $1^{0}/_{00}$, but generally below $1.5^{0}/_{00}$. The same was seen in the dace populations, where increased growth coefficients occurred in areas where the river bed gradient produced flow dynamics ideal for faster growth leading to longer mean lengths at age 1 and 3, in regions when the river bed gradient was generally steeper than $1^{0}/_{00}$. The roach populations in this study showed the highest growth coefficients in regions were flow regimes were less than those shown as preferable to chub and dace. The highest growth coefficients for roach occurred in areas where the river bed gradient was generally low, showing this species to prefer the lower reaches of the studied rivers.

4.4.2 – Growth at the national level

Organisms exhibit tremendous variety in the way they allocate resources for growth and development, and intraspecific variation in traits of freshwater fish at large spatial scales have often been related to latitudinal clines (Blank and Lamouroux 2007). Growth rates are expected to decrease with latitude for many fish species, due to the direct effect of temperature on growth processes (Lobón-Cerviá *et al.* 1996), for example the duration of the spawning period of roach decreases with increasing latitude (Lappalainen and Tarken 2007). Ectotherms, such as fish, enduring lower mean temperatures and shorter growing seasons at higher latitudes, would be expected to show a reduction in the annual growth rate (Yamahira and Conover 2002). Fish species in the northern hemisphere with a wide distribution range have to adapt to a simultaneous decrease in the length of the first growing season and an increase in the duration of the first winter with an increase in latitude (Lappalainen and Tarken 2007). Some species adapt to this by increasing the growth rate or by decreasing the optimum temperature for growth as latitude increases (Conover 1992; Jonassen *et al.* 2000).

Helser and Lai (2004), found a significant relationship between the growth coefficient and latitude in largemouth bass, *Micropterus salmonides* (Lacepède), and implied a slower growth rate, and hence lower productivity as latitude increased. Blank and Lamouroux (2007) found six life history traits (longevity, maximal length, K, L∞, age at maturation and gonadosomatic index (GSI)) associated with latitude. Longevity increased significantly for dace and roach, in lotic habitats but not in lentic habitats, whereas chub matured at a significantly younger age, at lower latitudes. Growth coefficient (K) decreased with latitude for two of the study species, while L∞ and maximal length increased for two of the study species; GSI was also seen to increase in one of the study species, although just which species was not eluded to.

Canonical correspondence analysis of chub found longitudinal position to have the greatest influence upon the growth rate of chub from throughout England and Wales, accounting for 45.3% of the variance observed in the species-environment relationship. Rainfall averages vary across England and Wales; the Lake District being the wettest, with an average annual rainfall exceeding 2000 mm, the Pennines and the moors of south-west England receive a similar amount (Met Office 2007). This contrasts with East Anglia, much of the Midlands, eastern and north-eastern England and parts of the south-east which receive less than 700mm per annum (Met Office 2007). High precipitation in the western regions would indicate an elevated flow regime compared with the rest of England and Wales. This may explain the difference observed in the longitudinal distribution of the growth coefficient, whereby the growth coefficients observed in the east were higher than those observed in the west. Increased flow conditions effect the metabolic processes, with increasing flow increasing the metabolic demand (Deegan *et al.* 2005), and as metabolic demands increase, additional food consumption is required to maintain the growth rate (Jobling 1995).

Mean length at age 1 of chub was found to be influenced more by increased temperatures, than any other abiotic factor. Temperature is known to influence both the rate of ingestion and metabolic processes of fish, with metabolic rate increasing with concurrent rises in temperature (Jobling 1995). When comparing the lengths of chub at age 1, Prokes (1981) found a positive impact of increasing water temperature on the growth rate and stated that provided food supply was in excess of that needed for maintenance, increased water temperature would stimulate fish growth intensity. Length at the end of the first year is important to all fish populations as it is the length at the end of the first year which determines the ability of the fish to overwinter without being displaced by elevated flows encountered during the winter and are lost from the system, reducing the year class strength of that cohort.

Both oldest observed age of chub at each site and the asymptotic length were related to latitude, distance from source, wetted width and catchment area above site. Increases in asymptotic length, associated with decreased growth coefficients, were observed in the within catchment analysis of the Yorkshire Ouse and Rivers Colne and Blackwater. This was described as being a response to conditions which were less than those considered as being "preferred". Small increases in the asymptotic length and oldest age recorded at each site were observed with increasing latitude, suggesting the growth coefficient, while being related to longitudinal influences, is weakly influenced by latitude, where slower growth coefficients are seen at lower latitudes, suggesting, as with dace, chub have a preference toward cooler water temperatures.

The relationship between the growth parameters of roach and the abiotic conditions that influence their growth in England and Wales revealed wetted width and latitude as having the greatest influence. Danehy *et al.* (2004) described increases in water temperature with an increasing downstream direction, which coincided with increasing wetted widths. The growth coefficient was mainly influenced by reduced values for river bed gradient, distance from source and altitude. This shows the fastest growth coefficients were in the lowland reaches of the rivers where the flow dynamics are slowest, productivity is highest and water temperatures at their highest. Latitude weakly influenced the growth coefficient, which is similar to Pivnička (1983), who demonstrated roach as being able to reach growth maxima in all locations, suggesting geographical latitude was not the principle factor influencing their growth, but instead suggested abundance was the major factor influencing the growth rate. Similar results were seen for the mean length achieved at ages 1, 2, and 3, and can again be attributed to the lower flow regimes, higher productivity and increased temperature regimes of the lower regions of the rivers, at low altitudes. Asymptotic length was positively related to catchment area above each site, but more importantly by negative values of longitude. Higher precipitation levels in the western area of England and Wales, leading to increased river flow regimes would cause an increase in the asymptotic length observed at each site, as increased flows and a concurrent increase in metabolic demand would lead to a decreased growth coefficient.

Lobón-Cerviá *et al.* (1996) investigating spatial variations in growth rates and other life history characteristics of dace found differences between populations. They found inverse relationships between latitude and water temperature at the time of dace spawning and between latitude and the length of the growing season. The growth coefficient (K) in this study was found to be strongly related with latitude (latitude accounting for 87.7% of the variance seen in the species-environment axis), whereby increases in latitude related to decreased mean air temperatures and increased growth coefficients. These results are similar to those of Lobón-Cerviá *et al.* (1996), who found high latitude populations of dace exhibited fast growth rates, which they postulated as being an adaptation to a reduced growing season. The capacity to grow rapidly in high latitude environments was considered an adaptive response to size selective winter mortality (Conover 1990). Lobón-Cerviá *et al.* (1996) found dace at high latitudes had reduced lengths at age than their southern conspecifics, and suggested water temperature was responsible for this latitudinal variation in the growth of dace. The length at age observed in this study was not significantly related with increasing latitude, at ages 1 to 4. However the latitudinal range of sites in this study, being just a small range within the larger scale of the distribution of dace in the northern hemisphere, suggests the faster growth coefficients seen in the higher latitudes of this study area are due to temperature.

For fish species living in ecological settings where high mortality rates exist, evolution often favours a live fast, die young stratagem, where rapid growth and maturation are favoured presumably as a compensation for a reduced life expectancy (Depczynski and Bellwood 2005). The oldest age of dace recorded at each site was seen to increase with temperature within the study area, generally dace in the lower latitudes of the study area had an increased longevity (in a region where increased temperature regimes coincide with lower growth coefficients) than dace in the higher latitudes, which displayed a decreased life span. The strategy of increased growth rate where reduced longevity occurs would allow dace to reach the length at maturation at a younger age. However, as the growth characteristics used in this study were determined solely from scale reading, the principle reason being the fish populations used for study being from rivers were recreational catch and release angling takes place, where a non destructive sampling technique was paramount (Britton 2007), no estimation of fecundity or length at first maturity within these populations is known and therefore no possible relationship between latitude and the life history tactics of r or K selection can be made.

Growth of dace was primarily influenced, at a national scale, by the inverse relationship between temperature and latitude, with the fastest growth observed in the higher latitudes where lower temperature regimes exist. Chub were influenced more by longitudinal position where the slowest growth was observed in areas where increased precipitation would lead to increased flow regimes and thus decreased somatic growth due to increased energy demands for maintenance. Roach were seen to favour the conditions observed in the lower regions of the rivers where increased temperatures, increased primary production and increased wetted width would provide a larger area for growth of this species as opposed to upstream areas.

4.4.3– Influences on growth rate, and phenotypic plasticity

Ecologists and evolutionary biologists have long been interested in explaining the variability in life history traits among animal populations (Fox 1994). Fish growth has the property of "plasticity"; that is, it can display considerable intraspecific variation (Weatherley 1990) in response to differences such as variability in environmental and geographic factors, like latitude (Leggett and Carscadden 1978; Morin *et al.* 1982; Mann *et al.* 1984; Venne and Magnan 1989, Fleming and Gross 1990, Vøllestad and L'Abée-Lund 1990), thermal regime (Alm 1959; Leggett and Carscadden 1978; Mills 1988), length of the growing season (Venne and Magnan 1989), productivity and food availability (Wootton 1977; Mann *et al.* 1984; Deacon and Keast 1987; Trippel and Harvey 1989), predation (Reznick *et al.* 1990) as a response to alarm (Jachner and Janecki 1999) and degree of environmental fluctuation (Constantz 1979; Baltz and Moyle 1982; Crivelli and Britton 1987; Fox and Keast 1991).

Growth rate is a pivotal aspect of growth trajectories and life history models assume selection to favour a maximisation of juvenile growth rate (Gotthard 2001). The rationale being that individuals that maximise their juvenile growth rates, have the potential to reach the largest possible size, in the shortest possible time. Growth rates being determined directly by the quality of the environment, which in turn depends on such factors as food availability and ambient temperature (Gotthard 2001). In cyprinids, density dependent growth is most often associated with food availability (Putkis and Batsianiou 2006). Competition is a factor that regulates communities and is a major structuring force in natural communities (Bergman 1990). Vinni *et al.* (2000) demonstrated roach, bleak and white bream inhabiting the same lake had a slow growth rate, which was probably due to the low availability of animal food, indicated by the increasing proportion of detritus and plant material in the diet towards the end of the summer.

Interspecific competition for food resources often manifests in resource partitioning among coexisting species, most clearly demonstrated during times of food minima when competition is at its highest (Vøllestad 1985; Nilsson 1967; Werner and Hall 1976) and growth at its lowest. An observed reduction in growth rate was demonstrated by Cowx (1989) between the dace and roach populations of the River Exe. This was related to the subordinate species reducing its feeding diversity to avoid competition and relying more on detritus and algae. Partly decomposed organic matter of this nature has a lower nutritive value than animal prey (Bowen 1987), the assimilation efficiency of plant and algal material being between 50-60% for cyprinids compared with 80% for animal food (Persson 1983).

Primary abiotic variables controlling growth, such as temperature, length of growing season, productivity and photoperiod decline with latitude (Griffiths *et al.* 2004). Most community based models in ecology assume that all individuals within a species respond similarly to environmental conditions and therefore exert identical effects as consumers or prey; however, individuals differ among systems (Garvey *et al.* 2003). Latitude was shown to affect the growth parameters of the fish species used in this study; negative relationships were observed with increasing latitude, suggesting population productivity most likely declines the higher the latitude at which a population is found (Heslser and Lai 2004) and may be due to differences in temperature and the length of the growing season. Growing season was observed by Wilde and Muoneke (2001) to increase from north to south, as expected from latitudinal variation in solar isolation. Conover (1990) found the length of the growing season to decrease by a factor of 2.5 for American shad (*Alosa sapidissima* Wilson) and striped bass (*Morone saxatilis* Walbaum), with increasing latitude between 29°N and 46°N. Heibo *et al.* (2005) showed the growth coefficient of perch decreased with increasing latitude in the first year of life, whereas in the second year of life the growth rate increased with increasing latitude. This increase in growth rate during the second year of life was attributed to fish at higher latitudes demonstrating a trade-off between gonad and somatic production, as fish from lower latitudes reproduce earlier and thus invests more energy to gonad production (Heibo *et al.* 2005).

Conover and Present (1990) demonstrated high latitude fish having an increased growth rate within a reduced growing season as opposed to low latitude fish. This suggests that instead of being adapted for growth at low temperatures, fish from high latitudes are adapted for rapid elevations in growth rate during the brief interval of the year when high temperatures occur. Increased growth rates functioning at lower temperatures and a reduced growing season did not result in an increased length at the end of the growing season, as opposed to fish from lower latitudes, where fish from warmer climes with an increased growing season, which displayed a slower growth rate.

Predation is another important factor affecting growth rates, but only in conjunction with other factors (Holmgren and Appleberg 2001). Predators affect individual growth rates of surviving prey in two conflicting ways. First, predation acts to increase the growth rate by thinning the density of prey populations, which releases survivors from competition. At the same time, predators intimidate prey into decreasing their feeding activity and increasing refuge use, causing prey to grow more slowly (Van Buskirk and Yurewicz 1998). Maximising growth rate typically necessitates high foraging activity, which increases the encounter rate with food items, but also increases detection by predators (Lima and Dill 1990), a lowered foraging activity in response to perceived increases in predation risks therefore leads to a reduced growth rate (Anholt and Werner 1998). With predator abundance mainly affecting the maturation patterns through the effect on growth rate, there are two factors to consider, namely, for individual fish at high predation risk, it is important for the individual to grow out of the size range where vulnerability to predation is greatest and to postpone reproduction until a safe size has been attained. Secondly, for a population of fish, high predation pressure leads to an attenuation of the numbers of individuals in the population, thus lowering competition for food and increasing growth rates (Heibo and Magnhagen 2005).

A relationship between the variables of population density and growth rate has been recognised for many years (Backiel and Cren, 1967). Carlander (1966) considered population density, in relation to carrying capacity of the habitat, was the major environmental factor controlling the growth of individual fish. Backiel and Le Cren (1967) stated that in less complex communities, major changes in population density are nearly always accompanied by inverse changes in growth rate, and in many temperate waters it would appear to be natural for many species to exist in dense populations, with growth rates well below the potential for the species. The growth rate of roach has been related to fish density, with poor growth recorded in overcrowded waters, where competition for food resources is high, resulting in a stunted population (Linfield 1979). Burrough and Kennedy (1979) found several features of interest associated with sudden alterations in the growth rate of roach. A decline in growth rate in 1972 coincided precisely with the appearance of the very strong 1972 year class. Subsequent improvement in growth during 1976 immediately followed substantial mortalities amongst the roach population during the summer of 1975. These were induced as a result of parasitisation by the Pseudophyllidean cestode *Ligula intestinalis* (L.). In this situation, few resources will be used for production, since most of the available food will be required to maintain the biomass (Mann, 1967) and a low growth rate for individual fish will inevitably result. Roach are particularly prone to stunting and over-population of this type, induced by excessive reproduction (Hofstede 1974).

CHAPTER FIVE

THE ROLE OF ENVIRONMENTAL AND CLIMATIC PARAMETERS IN THE DETERMINATION OF YEAR CLASS STRENGTH

5.1 – INTRODUCTION

Cowx and Frear (2004) suggested year class strength (YCS) is an important index in the management of inland fisheries, used to show the dominance of certain cohorts in the population structure and the influence they have on the fishery at the present time and in the future. The success of a fishery depends upon the optimization of the many factors that affect the recruitment and growth of that fishery (Summerfelt and Shirley 1978). Both biotic and abiotic factors cause variation in the YCS of fish, with intra and interspecific relations of the fish and the productivity of the ecosystem being the main biotic components of population fluctuation (Karjalainen *et al.* 1996). Temperature and flow are generally accepted as being the most important abiotic factors in determining the annual variations in fish abundance in flowing waters (Grenouillet *et al.* 2001).

Early developmental stages represent a crucial period in the life cycle of cyprinid fishes and variations in mortality during this period may be critical in determining YCS (Cowx 2001). Mathews (1971) stated very heavy, possibly density dependant, mortality occurs during the first year of life, with mortality during the first two to three months being the heaviest. Flow regimes that are in excess of the critical swimming velocity, and a lack of suitable refugia also have an effect on YCS. Climatic conditions during winter also influence YCS (Flath and Diana 1985), with overwinter mortality being hypothesised as one of the mechanisms underlying recruitment variability (Toneys and Coble 1980). However, Nunn *et al.* (2007b) partly disproved this by demonstrating the strongest relationships between YCS and river discharge occur when fish are in their early (especially larval) developmental stages.

The Atlantic Meridonial Overturning Current (AMOC), which is part of the global thermohaline conveyer, and the warm surface currents within the AMOC are known as the Gulf Stream. The Gulf Stream carries vast quantities of heat north-eastwards from the Gulf of Mexico and Bahamas toward Northern Europe and Scandinavia.

This heat flow amounts to 1.3 Billion MW, and endows the UK, Scandinavia and Northern Europe with milder winter weather patterns than their respective latitudes would otherwise dictate (Cobbold 2006). Latitudinal position of the Gulf Stream, and in particular the North Wall of the Gulf Stream (NWGS) has been shown to be related to zooplankton numbers in the NE Atlantic (Taylor and Stephens 1980) the North Sea (Taylor 1995) and Lake Windermere (George and Taylor 1995; George 2000), lake nitrate concentrations in SW Ireland (Jennings and Allott 2006) and to vegetation growth in the UK (Willis *et al.* 1995). Latitudinal position of the NWGS has also been related to the growth of 0+ cyprinids (Nunn *et al.* 2007b) and the recruitment success (YCS) of cyprinids from UK freshwater habitats (Britton *et al.* 2004b; Nunn *et al.* 2007b).

The aim of this chapter was to determine the relationships between the factors that play a role in determining the YCS of roach, dace and chub from rivers throughout England and Wales. The role of river discharge over short (monthly) or protracted (seasonal) periods was tested against the YCS of roach, dace and chub in an attempt to define critical periods during the early life of these species where river discharge rate plays a part in the determination of YCS. The mean annual position of the Gulf Stream was tested against YCS in the respective years to determine its impact, acting through climatic influences, on YCS formation. In addition to the influence of the Gulf Stream on YCS, Frear and Cowx (2003) discussed a lag phase in the influence of the Gulf Stream on the YCS of roach, dace and chub. Above average YCS may be as a result of favourable growth conditions for adult fish in the previous year. Favourable growth of the adult stock would provide sufficient energy for the production of larger numbers, or better quality gametes, which in turn may lead to increased numbers of juveniles after the next spawning event and therefore an increased YCS, and this was tested.

5.2 – METHODS AND MATERIALS

5.2.1 – Calculation of cumulative flow rate above basal discharge rate

Daily mean flow data (cubic metres per second [cm^3s^{-1}]), for each river where ageing data were available, were downloaded from the UK national river flow archive (NRFA) of the Centre for Ecology and Hydrology website. Data were derived from a network of gauging stations, run principally by the Environment Agency. These data were used to calculate the cumulative number of discharge-days above the basal discharge rate (i.e. the long term mean daily discharge calculated for each month using a 35 year dataset for each river, 1970 – 2005 inclusive), analogous to the calculation of temperature degree days (Nunn *et al.* 2003).

5.2.2 – Calculation of cumulative degree days

Cumulative degree days (°C) were calculated from data from the River Trent (Environment Agency data, 1990 – 2003 inclusive) and the Yorkshire Ouse (Yorkshire Water data, 1992 – 1998 inclusive). Cumulative degree days >12°C were calculated from mean daily temperatures for each river; temperatures greater than 12°C were used because this temperature is believed to provide the greatest relation to the growth of fish (Mann 1973). Relationships between cumulative degree days for each river and cumulative flow days were investigated using linear regression in SPSS (ver14).

5.2.3 – Calculation of year class strength (YCS)

YCS estimates for roach, dace and chub were calculated from age data according to the method of Cowx and Frear (2004), for unexploited freshwater fish populations from individual surveys. The method of determining YCS proposed by Cowx and Frear (2004) was chosen over any other method as the Hellawell (1972) method as a bias is introduced by larger numbers in the younger age groups and only identifies possible strong year classes in older age groups but gives no measure of their strength. The method proposed by Linfield (1981) utilised a mean survival rate for each river, potentially introducing bias as a mean survival rate does not necessarily account for changes in mortality over time brought about by shifting biotic and abiotic conditions where as the use of a survival rate derived directly from the survey is used in the method proposed by Cowx and Frear (2004) and as such, trends are strengthened and elucidated and the YCS can be calculated from data derived from a single survey and not from multiple surveys collected on an annual or biennial basis as is required for the method adopted by Mann (1973). The number of fish in each cohort was used to determine the instantaneous mortality rate (Z) of the target population using the linear relationship between the natural logarithm of the number of fish in each age group ($\ln N_t$) against age (t) according to –

$$Z = \frac{(\ln N_t - \ln N_o)}{t} \qquad \text{Equation 5.1}$$

where the number of fish at time zero, (N_o) was calculated independently for each age group using –

$$N_o = N_t \exp Z_t \qquad \text{Equation 5.2}$$

where N_t is the number of fish at age t.

The mean number of fish in each age group (N) was determined using -

$$\frac{\Sigma^{t}{}_{max}N}{t_{max}} \qquad \text{Equation 5.3}$$

where t_{max} is the total number of age groups represented.

YCS was determined for each age group by -

$$\text{YCS} = \frac{N_o}{\overline{N}} \text{x } 100 \qquad \text{Equation 5.4}$$

Where N_o is the number of fish determined at time t_o for age group t, i.e. YCS, relating to the year of birth, is calculated as an index standardised against a value of 100. Values in excess of 100 represent strong year classes while values less than 100 represent weak year class, represented by a line across each figure at 100 (YCS axis).

5.2.4 – Relationship between YCS and cumulative flow days above basal discharge rate

Regression was used to determine whether the magnitude of flow rates during specific time periods contributed to the formation of YCS in roach, dace and chub from 32 rivers throughout England (Table 5.1). Flow data from rivers where YCS estimates were available, were sorted into monthly cumulative flow days over the period where YCS data were available, and from these data the sum of the flow days from October to February calculated to represent the winter period. As spawning of most cyprinids in rivers throughout England and Wales usually occurs from April onwards, the period from April through to March of the following year was chosen to represent the annual period when eggs and juvenile fish may be susceptible to displacement from elevated flows. Regression analysis of YCS of roach, dace and chub against cumulative flow days for each month and the winter period were performed in SPSS (ver14).

Table 5.1 – Rivers from which flow data were available and time frame over which YCS data was calculated for roach, dace and chub.

River	Roach	Dace	chub	River	roach	dace	chub
Bristol Avon	1991 – 2002	1996 – 2004	1988 - 2002	**River Kennet**	1990 - 2000	1995 - 2001	1985 - 2001
Bristol Frome	1990 – 2001	1996 – 2002	1988 - 2000	**River Lee**	1992 - 2002	2001 - 2004	1990 - 2003
Harpers Brook	1993 – 1999	1997 – 2002	1998 - 2001	**River Medway**	1993 - 2001	1998 - 2001	1987 - 2001
River Aire	1995 – 2004	1998 – 2002	1984 - 2004	**River Nidd**	1992 - 2004	1997 - 2004	1990 - 2003
River Stour	1993 – 2001	1994 – 2005	1985 - 2000	**River Severn**	1994 - 2000	-	1988 - 1999
River Anker	1995 – 2002	-	1988 - 2002	**River Soar**	1996 - 2001	1997 - 2002	1985 - 2001
River Axe	1999 – 2004	-	-	**River Tone**	1992 - 1999	1995 - 2002	1984 - 2002
River Blackwater	1993 – 2002	1998 – 2003	1986 - 2004	**River Trent**	1990 - 2001	1995 - 2005	1990 - 2000
River Blythe	1999 – 2005	1996 – 2002	1989 - 1999	**River Ure**	1991 - 2001	1998 - 2003	1983 - 1996
River Brue	1995 – 2002	-	1986 - 2003	**River Waveney**	1996 - 2005	1998 - 2005	1986 - 2005
River Cam	1995 – 2002	-	-	**River Wey**	1993 - 2003	1996 - 2004	1986 - 2002
River Chelmer	1994 – 2004	1997 – 2001	-	**River Wharfe**	1995 - 2004	2000 - 2004	1984 - 2003
River Colne	1990 – 2001	1994 – 2001	1986 - 2003	**River Witham**	1997 - 2005	-	-
River Darent	1996 – 2002	1999 – 2003	1988 - 2004	**River Wreake**	1994 - 2000	-	1986 - 1999
River Hull	1989 – 2002	1999 – 2002	-	**Warwickshire Avon**	1996 - 2002	1999 - 2002	1986 - 2002
River Ise	1995 – 2001	1996 – 2002	-	**Yorkshire Ouse**	1994 - 2001	-	1995 - 2002

5.2.5 – Relationship between mean length at age 1 of roach, dace and chub and cumulative flow days above basal discharge rate

To determine whether discharge rates contributed to the mean length at age 1 of roach, dace or chub observed in this study, linear regression analysis was used. Mean lengths at age 1 of roach, dace and chub, from rivers where flow data were available (Table 5.1), were calculated from scale reading. Flow data from rivers were sorted into annual cumulative flow days and regressions of mean length at age 1 against cumulative annual flow days performed in SPSS (ver14).

5.2.6 - Relationship between YCS and the position of the NWGS

It is widely accepted that the climate of maritime Western Europe is strongly affected by the warming influence of the North Atlantic Gulf Stream (Willis *et al.* 1995). To determine any relationship between YCS of roach, dace and chub populations from rivers throughout England and Wales and the mean annual position of the NWGS, linear regression analysis was used. YCS of roach, dace and chub from 65 rivers and canals from throughout England and Wales (Table 5.2) were available for analysis. Data for the position of the NWGS was downloaded from the Plymouth Marine Laboratory website and mean annual positions of the North Wall extracted. Positive values indicate northerly shifts and negative values a southerly shift from the mean position. Linear regression analysis of YCS of roach, dace and chub against the mean annual position of the NWGS was performed in SPSS (ver14).

Table 5.2 - Rivers from which YCS were calculated for roach dace and chub, showing time frame from which YCS data were available, to determine relationship between YCS and mean annual position of the NWGS.

River	roach	dace	chub	River	roach	dace	chub	River	roach	dace	chub
Bristol Avon	1991 - 2004	1999 - 2004	1990 - 2004	River Colne Herts	1997 - 2004	1998 - 2004	1989 - 2004	River Thurne tidal	1999 - 2003	-	-
Bristol Frome	1992 - 2002	1996 - 2004	1988 - 2002	River Cray	1998 - 2004	-	1993 - 2004	River Thurne	1997 - 2005	-	-
Fossdyke Navigation	1997 - 2005	-	-	River Dane	1995 - 2003	2001 - 2005	1995 - 2003	River Tone	1994 - 2000	1996 - 2004	1990 - 2004
Harpers Brook	1993 - 2000	1997 - 2002	1998 - 2002	River Darent	1998 - 2004	-	1993 - 2004	River Trent	1990 - 2001	1995 - 2005	1990 - 2000
Hobhole Drain	1999 - 2005	-	-	River Don	1995 - 2004	1999 - 2004	1992 - 2004	River Ure	1991 - 2001	1998 - 2003	1983 - 1996
River Aire	1998 - 2004	2000 - 2002	1990 - 2004	River Gipling	1993 - 2003	-	1988 - 2003	River Wantsum	1999 - 2004	-	-
River Alne	1995 - 2003	1997 - 2003	1994 - 2003	River Hull	1993 - 2004	-	-	River Waveney Beccles boat yard	1999 - 2004	-	-
River Anker	1996 - 2002	-	1988 - 2002	River Ise	1995 - 2002	1996 - 2002	-	River Waveney	1995 - 2005	2001 - 2005	1992 - 2005
River Arrow	1996 - 2005	1999 - 2005	1992 - 2005	River Isle	1998 - 2002	1995 - 2002	1988 - 2004	River Welland	1995 - 2005	1999 - 2005	-
River Axe	1999 - 2004	-	-	River Kennet	1990 - 2000	1995 - 2001	1985 - 2001	River Wey	1993 - 2004	1997 - 2004	1987 - 2002
River Blackwater	1993 - 2002	1998 - 2003	1986 - 2004	River Lee	1996 - 2004	2001 - 2004	1991 - 2004	River Wharfe	2001 - 2004	2001 - 2004	1985 - 1998
River Blythe	1993 - 2002	1995 - 2002	1989 - 2002	River Medway	1994 - 2003	-	-	River Witham	1996 - 2005	-	-
River Brett	1989 - 2003	1994 - 2005	1990 - 2005	River Mole	1999 - 2004	1998 - 2004	1987 - 2004	River Wreake	1994 - 2000	-	1986 - 1999
River Brue	1998 - 2004	-	1987 - 2004	River Nene	2000 - 2005	-	-	River Yare	1997 - 2005	-	-
River Bure	1996 - 2005	2000 - 2005	1988 - 2003	River Nidd	1996 - 2004	2001 - 2004	1991 - 2004	River Yeo	1997 - 2004	-	1991 - 2002
River Bure tidal	2000 - 2005	-	-	River Penk	1995 - 2002	1998 - 2004	1989 - 2002	Royal Military Canal	1998 - 2004	-	-
River Calder	1999 - 2004	1999 - 2002	1994 - 2004	River Rother	1995 - 2004	-	1992 - 2004	Sarendon Brook	1996 - 2002	1999 - 2004	1994 - 2002
River Cam	1995 - 2002	-	-	River Severn	1994 - 2000	-	1988 - 1999	Somerset Axe	2000 - 2004	-	-
River Chelmer	1994 - 2004	1997 - 2001	-	River Soar	1996 - 2001	1997 - 2002	1985 - 2001	Somerset Frome	1992 - 2004	2000 - 2004	1991 - 2004
River Chew	1996 - 2002	1996 - 2002	1991 - 2004	River Stour	1996 - 2005	1997 - 2005	1994 - 2005	Warwickshire Avon	1996 - 2002	1999 - 2002	1986 - 2002
River Colne	1994 - 2004	2000 - 2004	1988 - 2004	River Stour	1994 - 2002	2000 - 2002	-	Yorkshire Ouse	1994 - 2001	-	1995 - 2002
River Colne	1990 - 2002	1998 - 2004	1986 - 2002	River Swale	1996 - 2005	2001 - 2005	1989 - 2005				

5.2.7 - Relationship between YCS, the mean annual position of the NWGS and cumulative flow days

To demonstrate any combined influence the mean annual position of the Gulf Stream and river discharge rate have on YCS of roach, dace and chub, multiple regression analyses were used. Data for YCS of roach, dace and chub and the cumulative flow days of 32 rivers were available (Table 5.1) plus the mean annual position of the NWGS extracted from the Plymouth Marine Laboratory website (Section 5.2.6). Multiple regression analysis of YCS against cumulative flow days above basal discharge rate and the mean annual position of the NWGS were then performed in SPSS (ver14).

5.2.8 – Relationship between mean length at age 1 and the mean annual position of the NWGS

Regression analyses were used to determine any relationship between the mean length at age 1 and the position of the NWGS. Mean lengths at age 1 were determined from scale reading for roach, dace and chub from 65 rivers and canals from around England and Wales (Table 5.2) and data for the mean annual position of the NWGS extracted from the Plymouth Marine Laboratory website (Section 5.2.6). Linear regressions of the mean length at age 1 of roach, dace and chub against the mean annual position of the NWGS were performed in SPSS (ver14).

5.2.9 - Identification of a lag phase in the formation of YCS and the mean annual position of the NWGS

Climatic conditions have been shown to have a direct influence upon the formation of YCS, although Frear and Cowx (2004) suggested a lag phase may exist whereby a period of time elapses between the climatic event and the formation of the corresponding strong or weak year classes. To determine whether a lag phase exists, YCS estimates gained from data collected from scale reading were used (Table 5.2), in conjunction with data downloaded for the mean annual position of the NWGS. Linear regressions of YCS against the mean annual position of the NWGS (Section 5.2.6) from the pervious year were performed in SPSS (ver14).

5.3 – RESULTS

5.3.1 – Environmental data, cumulative flow days and cumulative degree days

A significant, although weak negative relationship was found between the temperature and discharge regimes of the River Trent ($P<0.01$). Annual cumulative discharge above the basal discharge rate accounted for 48% of the variance observed in the annual cumulative degree days (>12°C) ($R^2 = 0.4818$, Figures 5.1 – 5.2), where increases in discharge rate resulted in reduced water temperatures.

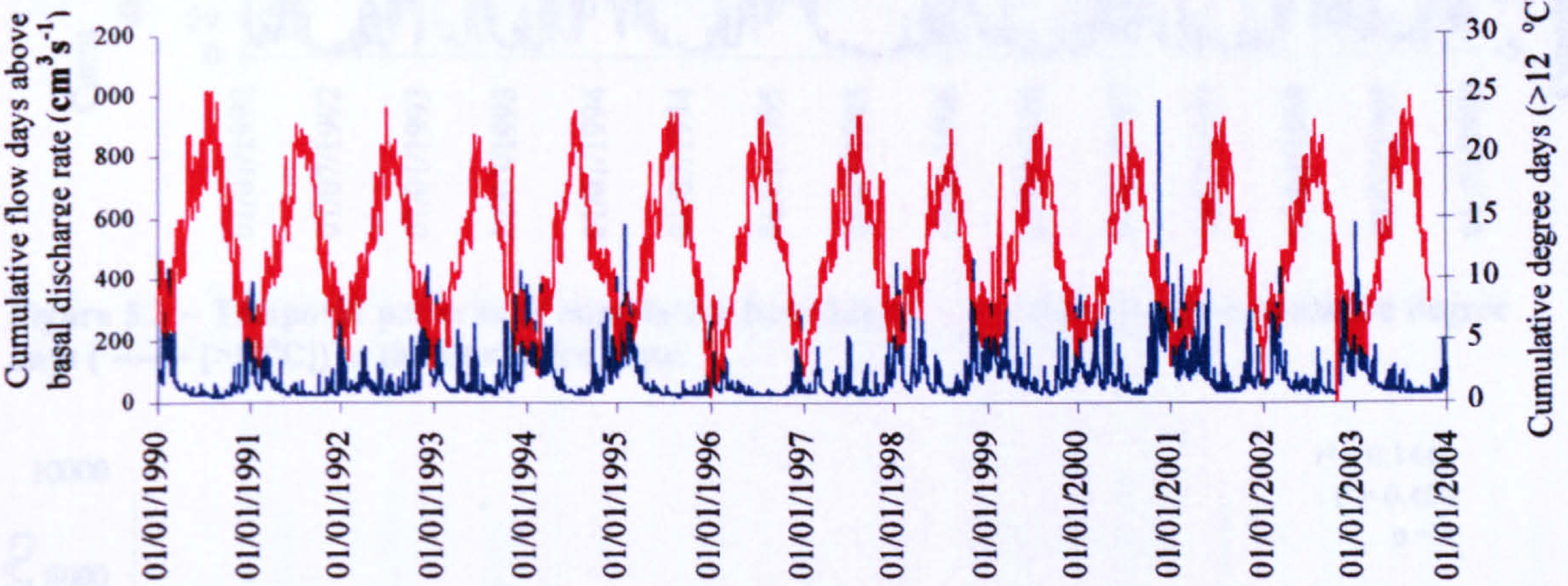


Figure 5.1 – Temporal pattern of cumulative flow days (—— [cm^3s^{-1}]) and cumulative degree days (—— [>12°C]) in the River Trent.

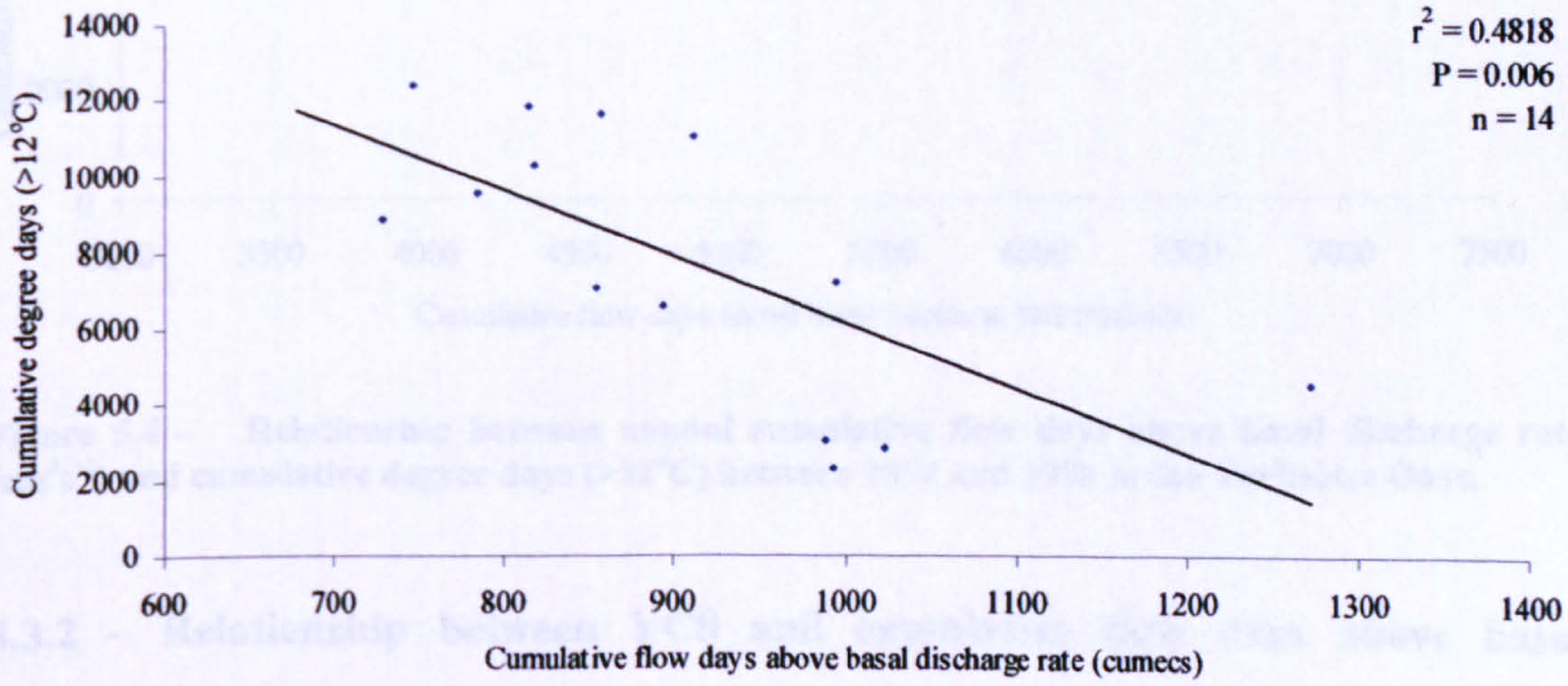


Figure 5.2 – Relationship between annual cumulative flow days above basal discharge rate (cm^3s^{-1}) and cumulative degree days (>12°C) between 1990 and 2003 in the River Trent.

A weak inverse relationship was found between the temperature and discharge regimes of the Yorkshire Ouse. Cumulative discharge above the basal discharge rate accounted for 14% of the variance observed in cumulative degree days (>12°C) ($r^2 = 0.1448$, Figures 5.3 – 5.4), whereby increases in river discharge weakly related to decreases in water temperatures.

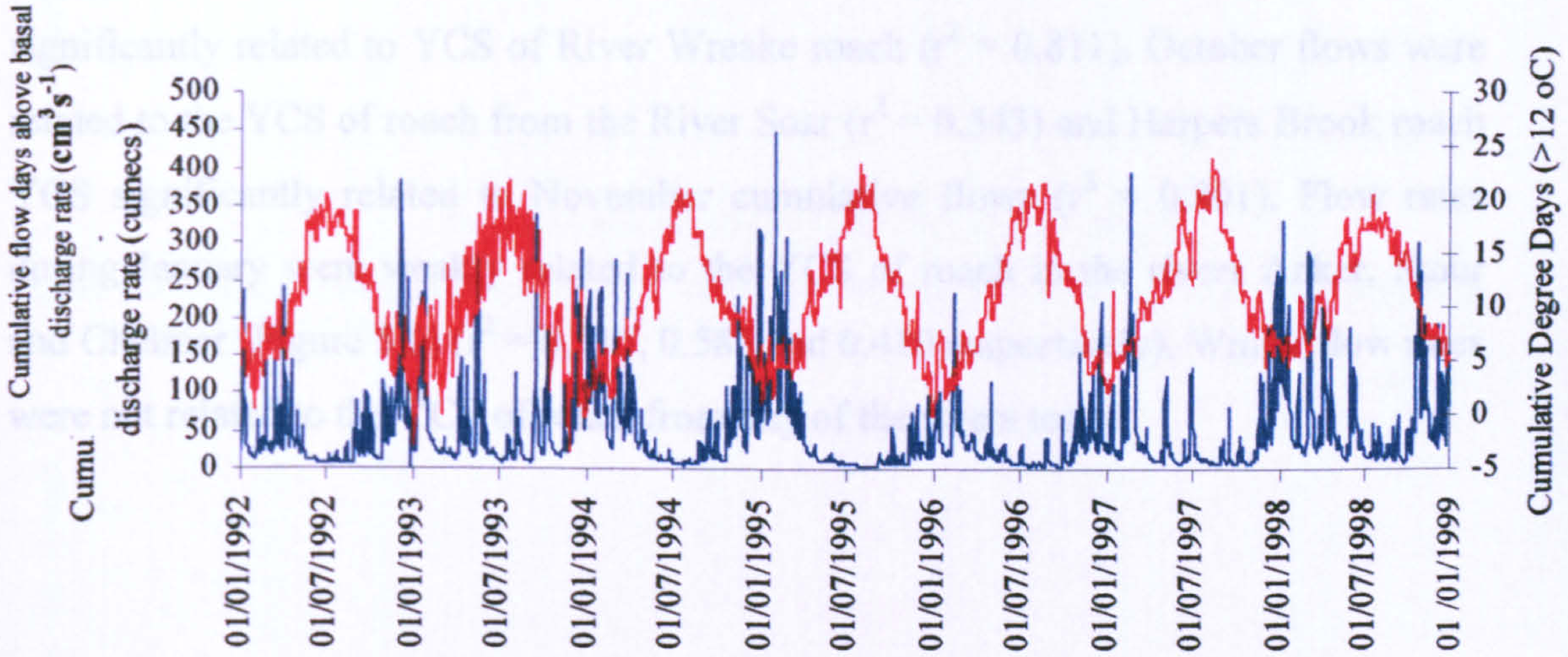


Figure 5.3 – Temporal patterns of cumulative flow days (— [cm^3s^{-1}]) and cumulative degree days (— [>12°C]) in the Yorkshire Ouse.

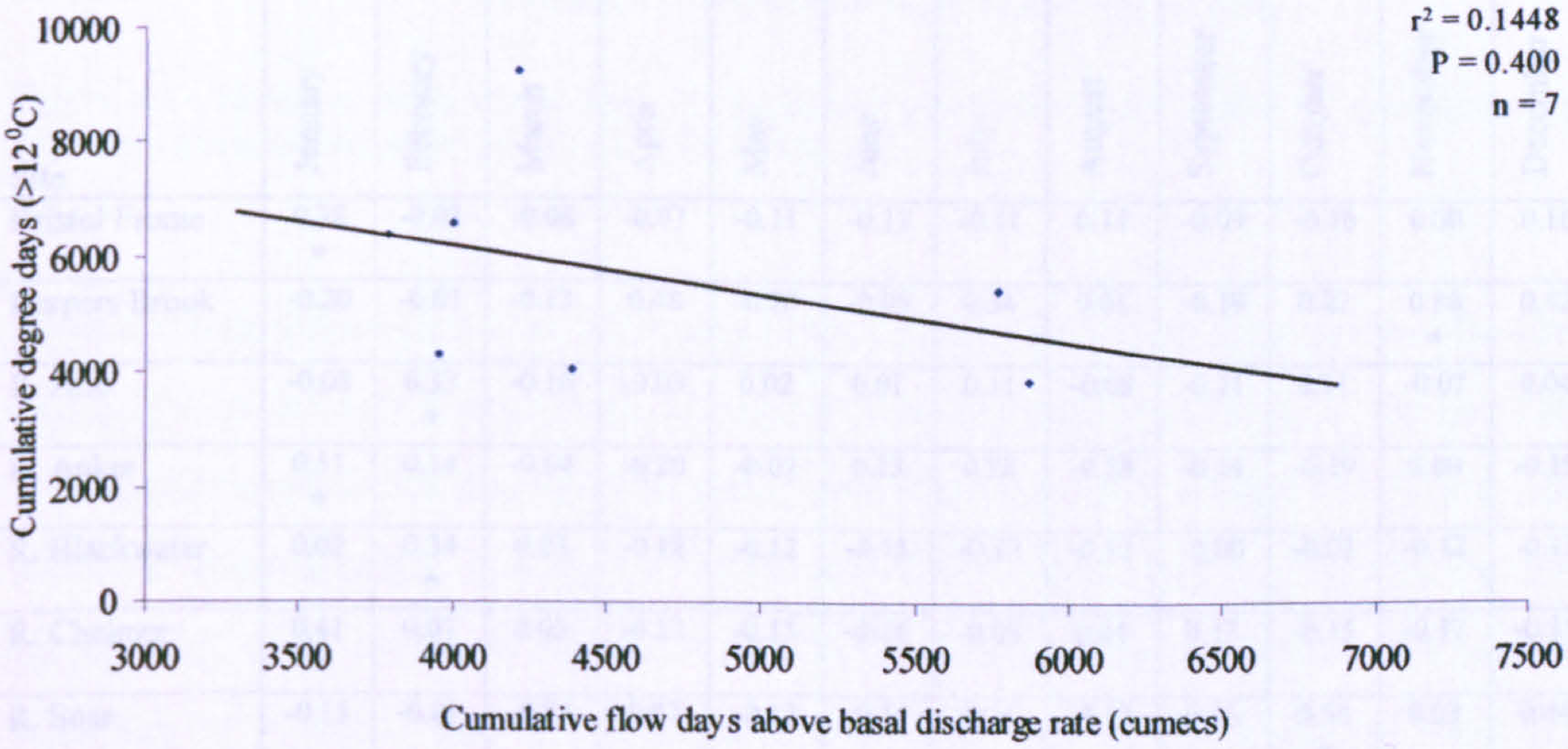


Figure 5.4 – Relationship between annual cumulative flow days above basal discharge rate (cm^3s^{-1}) and cumulative degree days (>12°C) between 1992 and 1998 in the Yorkshire Ouse.

5.3.2 – Relationship between YCS and cumulative flow days above basal discharge rate

Data from 32 rivers were used to determine relationships between YCS of roach, dace and chub and cumulative discharge rate. (Tables 5.3-5.5, Figures 5.5–5.10). Significant inverse relationships between cumulative flow days and YCS of roach from 12 rivers were found (Table 5.3). April cumulative flows were related to YCS of roach from the rivers Ure and Waveney (Figure 5.5) (r^2 = 0.452 and 0.658 respectively). The YCS of River Wey roach were related to cumulative flows during both May and June (r^2 = 0.547 and 0.487 respectively), with June flows also significantly related to YCS of River Wreake roach (r^2 = 0.811). October flows were related to the YCS of roach from the River Soar (r^2 = 0.543) and Harpers Brook roach YCS significantly related to November cumulative flows (r^2 = 0.801). Flow rates during January were weakly related to the YCS of roach in the rivers Anker, Stour and Chelmer (Figure 5.6) (r^2 = 0.515, 0.585 and 0.410 respectively). Winter flow rates were not related to the YCS of roach from any of the rivers tested.

Table 5.3 – Relationship between the YCS of roach and cumulative flow days from respective time periods from rivers across England and Wales (r^2 and P values given).

Site	January	February	March	April	May	June	July	August	September	October	November	December	Winter
Bristol Frome	0.38 *	-0.08	-0.08	-0.07	-0.11	-0.11	-0.11	0.14	-0.09	-0.10	0.00	0.16	-0.07
Harpers Brook	-0.20	-0.01	-0.13	0.48	-0.20	-0.05	0.34	0.05	-0.19	0.22	0.80 *	0.42	0.14
R. Aire	-0.08	0.33 *	-0.10	-0.03	0.02	0.01	0.11	-0.08	-0.11	0.11	-0.07	0.04	-0.12
R. Anker	0.51 *	0.14	-0.04	-0.20	-0.02	0.13	0.28	-0.18	-0.14	-0.19	0.00	-0.19	-0.13
R. Blackwater	0.02	0.34 *	0.03	-0.12	-0.12	-0.11	-0.12	-0.12	-0.09	-0.07	-0.12	-0.12	-0.07
R. Chelmer	0.41 *	0.07	0.05	-0.13	-0.15	-0.16	-0.03	0.04	0.13	-0.15	-0.17	-0.15	-0.16
R. Soar	-0.15	-0.01	-0.25	0.07	-0.12	-0.19	0.14	-0.12	0.26	0.54 *	0.03	0.44	0.22
R. Stour	0.58 *	0.16	-0.02	-0.12	-0.09	0.19	0.01	-0.11	-0.14	-0.13	0.13	-0.03	-0.05
R. Ure	-0.12	0.00	-0.04	0.45 *	-0.10	0.01	0.00	0.37 *	0.10	0.18	0.07	-0.12	0.21
R. Waveney	0.19	-0.11	-0.09	0.66 *	-0.11	-0.06	-0.12	-0.07	-0.12	-0.11	-0.12	-0.10	-0.12
R. Wey	-0.17	-0.09	0.07	0.34	0.55 *	0.49 *	0.23	-0.14	-0.12	-0.14	-0.14	-0.17	-0.16
R. Wreake	-0.04	0.12	-0.23	-0.12	-0.16	0.81 *	-0.33	-0.25	-0.24	-0.11	-0.26	-0.22	-0.23

***=P<0.05 **=P<0.01**

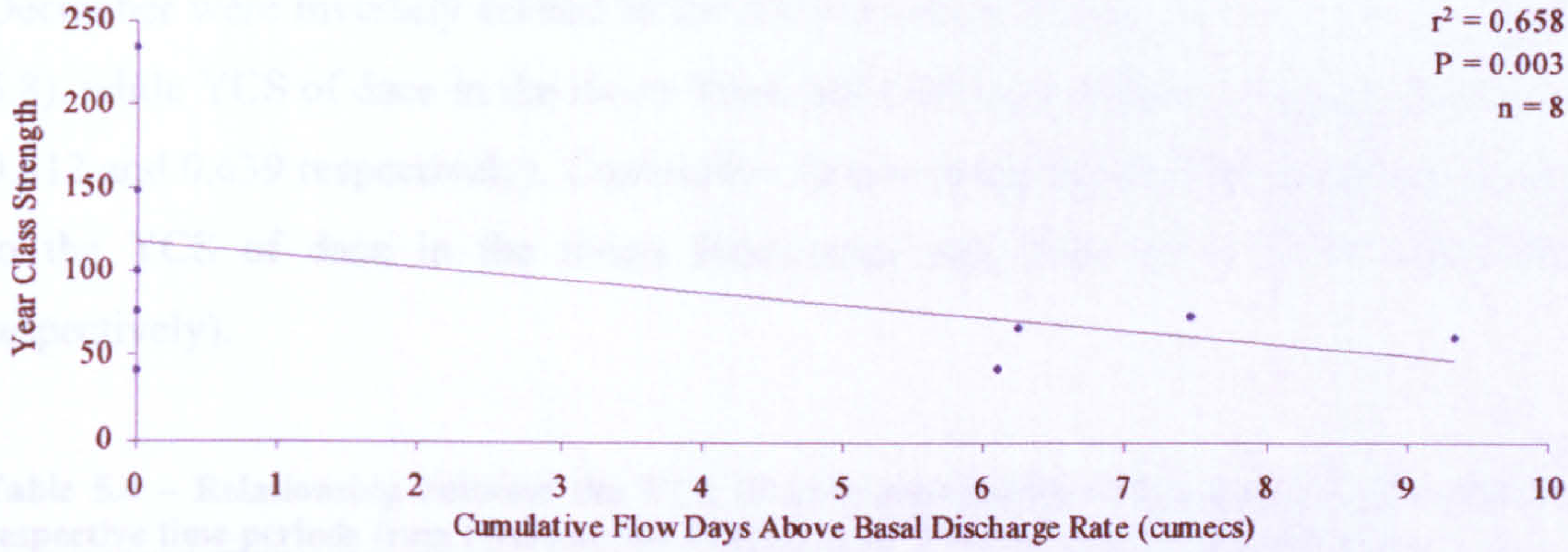


Figure 5.5 – Relationship between YCS of roach from the River Waveney and the cumulative flow days above basal discharge rate (cm^3s^{-1}) for April.

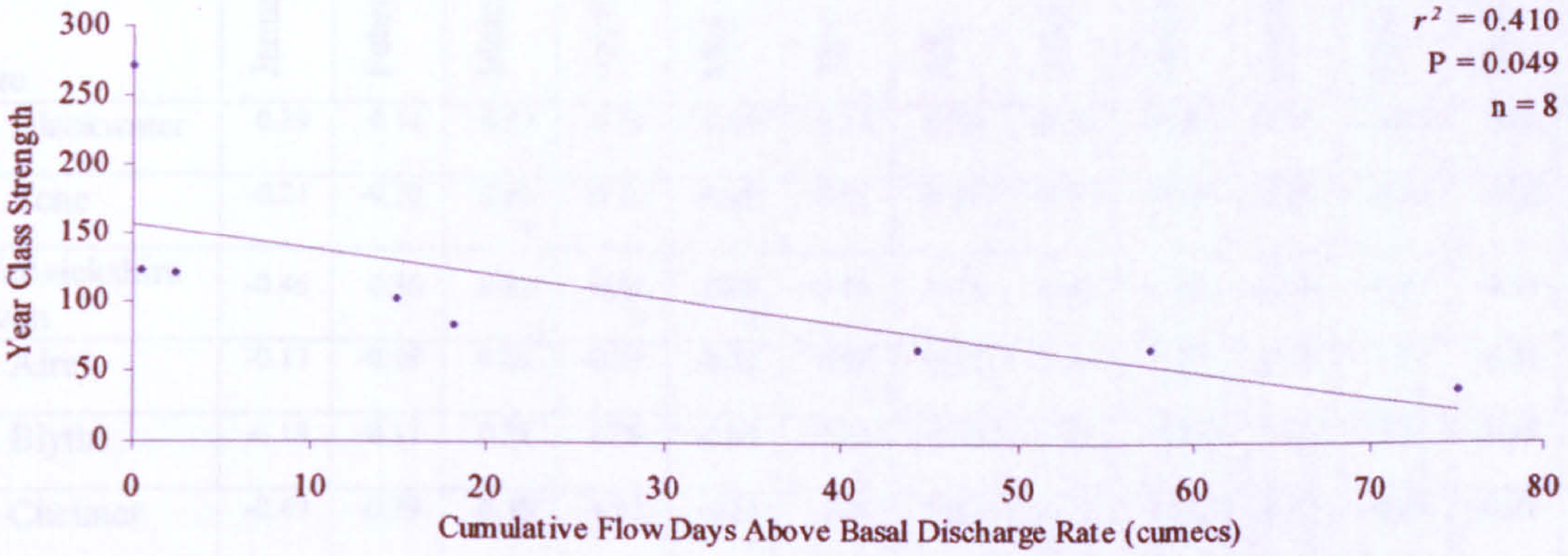


Figure 5.6 – Relationship between YCS of roach from the River Chelmer and the cumulative flow days above basal discharge rate (cm^3s^{-1}) for January.

Inverse relationships between YCS of dace and cumulative flow days at specific times during the year were found from 12 rivers from around England and Wales (Table 5.4). Cumulative flows during both April and May inversely related to YCS of dace from the Warwickshire Avon (r^2 = 0.862 and 0.997 respectively). Cumulative flows during May were inversely related to the YCS of dace from the rivers Chelmer and Waveney (r^2 = 0.891 and 0.524 respectively). Cumulative flows during June were related to the YCS of dace from the rivers Aire and Blythe (Figure 5.7) (r^2 = 0.797 and 0.667 respectively), while flows during August were inversely related to the YCS of River Soar dace (r^2 = 0.864). Cumulative flows during September were inversely related to YCS of dace from the rivers Hull, Medway and Trent (r^2 = 0.83, 0.925 and 0.510 respectively), while YCS of dace in the rivers Chelmer, Hull and Waveney were inversely related to cumulative flows during October (r^2 = 0.975, 0.910 and 0.800 respectively). Cumulative flows during November were related to the YCS of dace from the rivers Aire, Trent, Ure and to a lesser extent the R. Blythe and Waveney (r^2 = 0.713, 0.762, 0.573, 0.490 and 0.453 respectively). Cumulative flows during

December were inversely related to the YCS of River Trent dace ($r^2 = 0.590$, Figure 5.8), while YCS of dace in the rivers Trent and Ure were related to winter flows ($r^2 = 0.512$ and 0.639 respectively). Cumulative flows during March were inversely related to the YCS of dace in the rivers Blackwater and Tone ($r^2 = 0.566$ and 0.604 respectively).

Table 5.4 – Relationship between the YCS of dace populations and cumulative flow days for respective time periods from rivers across England and Wales (r^2 and P values given).

Site	January	February	March	April	May	June	July	August	September	October	November	December	Winter
R. Blackwater	0.39	0.34	0.57 *	-0.21	-0.09	-0.14	-0.24	-0.20	-0.01	-0.21	0.08	0.40	-0.02
R. Tone	-0.21	-0.20	0.60 *	-0.19	-0.18	0.31	-0.16	-0.10	0.18	-0.18	-0.10	0.28	-0.12
Warwickshire Avon	-0.46	0.36	0.33	0.86 *	0.99 *	-0.19	0.19	0.48	-0.49	-0.50	-0.47	0.43	-0.41
R. Aire	-0.17	-0.19	0.21	-0.33	-0.32	0.80 *	-0.33	-0.27	0.28	0.37	0.71 *	-0.33	0.19
R. Blythe	-0.18	0.17	0.21	0.29	-0.06	0.67 *	-0.05	0.13	-0.08	-0.06	0.49 *	-0.12	0.45
R. Chelmer	-0.49	-0.39	-0.30	-0.42	0.89 *	0.46	0.22	-0.46	0.09	0.97 *	-0.33	-0.41	-0.13
R. Hull	-0.37	0.17	-0.10	-0.26	0.46	0.69	0.46	0.41	0.83 *	0.91 *	0.55	0.68	-0.37
R. Medway	0.44	-0.48	-0.49	-0.50	0.52	-0.45	0.49	-0.48	0.92 *	0.36	0.32	0.27	0.32
R. Soar	0.19	-0.26	-0.20	0.34	0.31	0.29	-0.32	0.86 *	-0.12	-0.15	-0.20	-0.32	-0.12
R. Trent	-0.03	-0.10	-0.11	-0.02	-0.08	-0.11	-0.08	-0.07	0.51 **	-0.07	0.76 **	0.59 **	0.51 **
R. Ure	-0.25	-0.23	-0.25	-0.24	-0.11	0.21	-0.21	-0.15	0.07	-0.13	0.57 *	0.02	0.64 *
R. Waveney	-0.02	-0.15	-0.16	0.01	0.52 *	-0.03	-0.11	-0.16	-0.09	0.80 **	0.45 *	-0.16	0.25

*=P<0.05   **=P<0.01

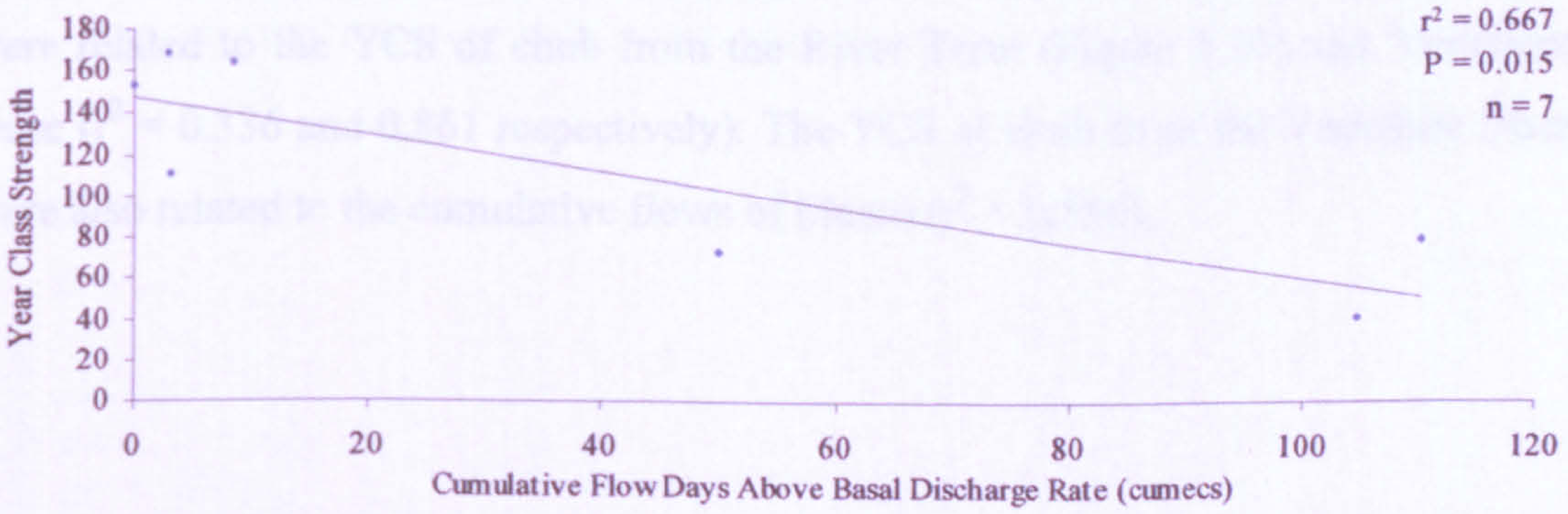


Figure 5.7 – Relationship between YCS of dace in the River Blythe and the cumulative degree days above basal discharge rate (cm^3s^{-1}) for June.

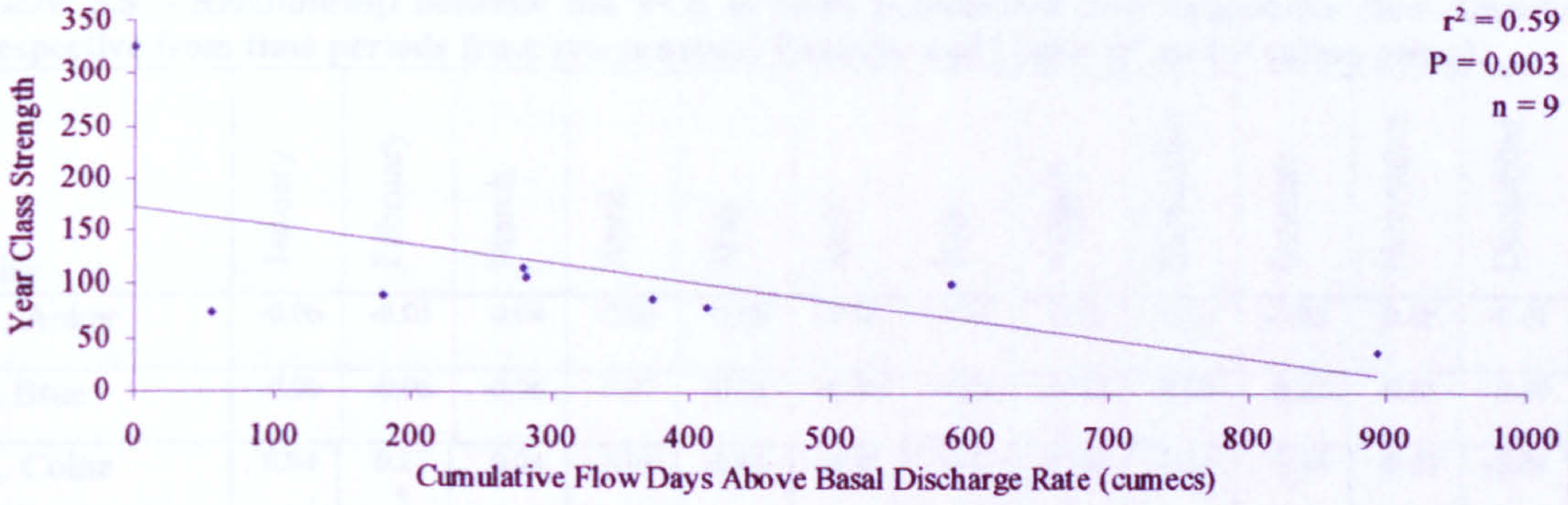


Figure 5.8 – Relationship between YCS of dace in the River Trent and the cumulative degree days above basal discharge rate (cm^3s^{-1}) for December.

Non-significant, inverse relationships were found between cumulative flow days and YCS of 11 chub populations from rivers throughout England and Wales (Table 5.5), where increased cumulative flows resulted in decreased YCS. Cumulative flows during May were weakly related to YCS of chub from the Warwickshire Avon (r^2 = 0.320), while the flows during June were related to YCS of chub from the Yorkshire Ouse and the River Waveney (Figure 5.9) (r^2 = 0.617 and 0.415 respectively). July flows were related to YCS of chub from the Warwickshire Avon (r^2 = 0.498), while September flows were weakly related to YCS of chub from the River Anker (r^2 = 0.328). YCS of chub from the rivers Wey and Wreake were weakly related to winter flows (r^2 = 0.356 and 0.355 respectively), while cumulative flows during February were related to the YCS of chub from the River Trent (Figure 5.10) and Yorkshire Ouse (r^2 = 0.336 and 0.861 respectively). The YCS of chub from the Yorkshire Ouse were also related to the cumulative flows of March (r^2 = 0.586).

Table 5.5 – Relationship between the YCS of chub populations and cumulative flow days for respective from time periods from rivers across England and Wales (r^2 and P values given).

Site	January	February	March	April	May	June	July	August	September	October	November	December	Winter
R. Anker	-0.06	-0.05	0.04	-0.05	-0.08	-0.08	0.15	0.17	0.33 *	-0.05	-0.05	-0.01	0.02
R.Brue	-0.06	-0.06	-0.06	-0.07	-0.06	-0.04	0.29 *	-0.07	-0.02	0.02	0.05	0.00	-0.02
R. Colne	0.04	0.27 *	0.04	-0.04	-0.01	-0.05	-0.05	-0.06	-0.05	-0.05	-0.05	-0.04	-0.06
R. Don	0.28 4*	-0.09	0.23	0.16	-0.09	-0.08	-0.08	-0.03	0.18	0.04	0.00	-0.04	0.01
R. Medway	0.27 *	-0.02	-0.07	-0.09	-0.09	-0.09	-0.05	-0.08	0.14	-0.07	-0.07	-0.07	-0.09
R. Trent	0.21	0.34 *	-0.11	-0.04	-0.01	0.02	0.08	-0.07	0.07	0.02	-0.06	0.17	0.07
R. Waveney	-0.07	-0.04	0.12	0.14	-0.04	0.42 **	0.14	-0.06	0.18 *	-0.06	-0.04	0.03	-0.01
R. Wey	0.06	-0.06	-0.07	-0.06	-0.05	0.03	0.12	0.17	0.09	0.07	0.16	0.15	0.36 **
R. Wharfe	0.00	-0.03	-0.05	-0.04	-0.02	0.27 *	-0.05	-0.05	0.03	0.13	0.04	-0.05	0.03
R. Wreake	0.11	-0.09	-0.07	-0.09	-0.02	-0.10	-0.10	-0.08	0.22	0.03	0.00	0.00	0.36 *
Warwickshire Avon	-0.04	-0.05	0.10	0.16	0.32 *	0.06	0.50 **	-0.10	-0.09	-0.09	-0.10	-0.05	-0.09

*=P<0.05 **=P<0.01

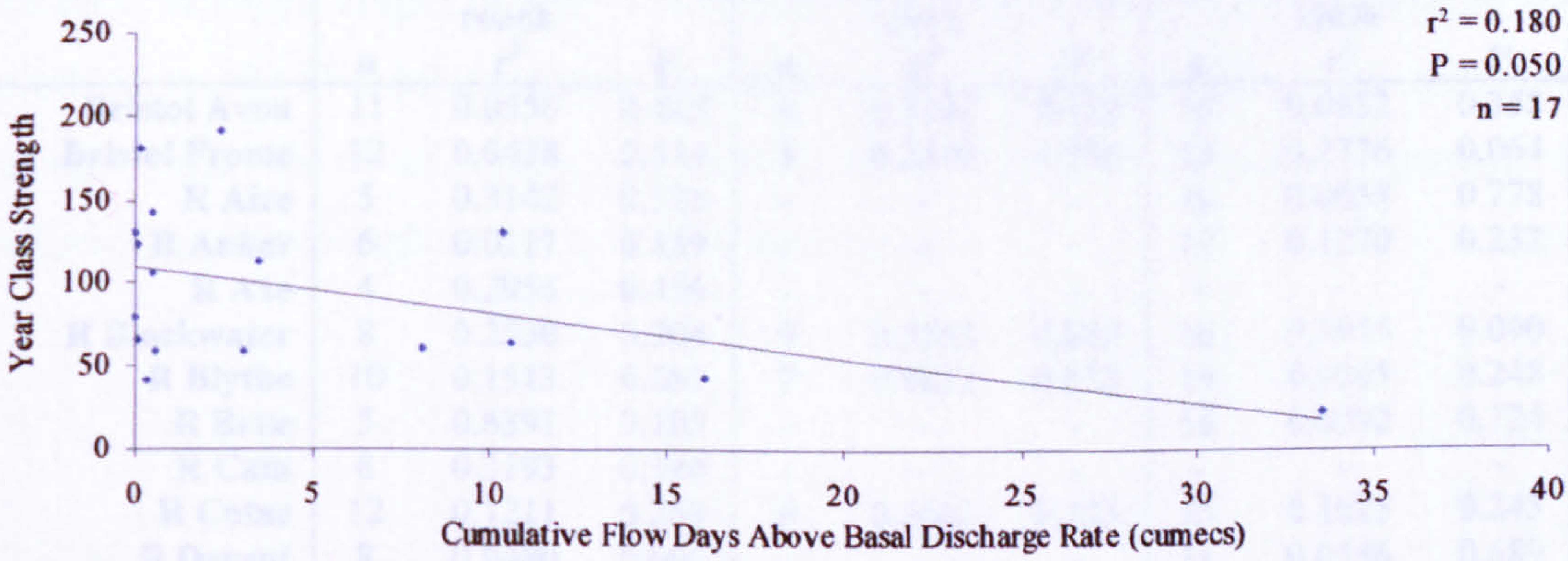


Figure 5.9 – Relationship between YCS of chub from the River Waveney against cumulative flow days above basal discharge rate (cm^{3}s^{-1}) during September.

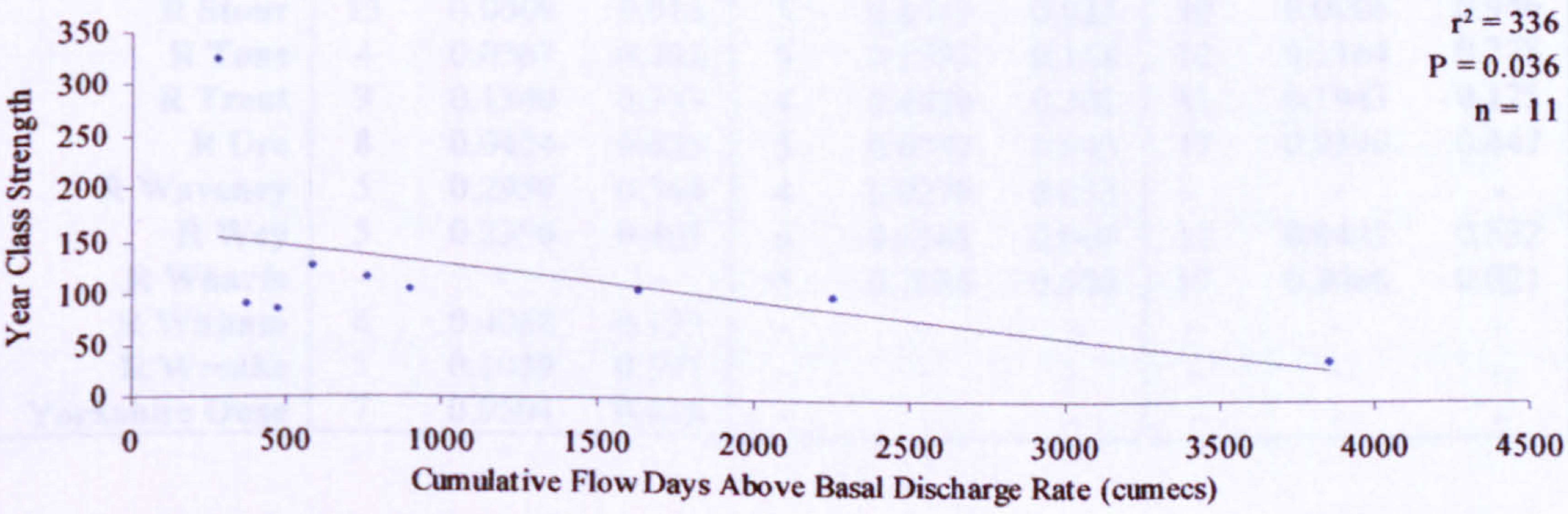


Figure 5.10 – Relationship between YCS of chub from the River Trent against cumulative flow days above basal discharge rate (cm^{3}s^{-1}) during February.

5.3.3 – Relationship between mean length at age 1 and cumulative flow days

Generally weak, non-significant relationships were found between mean length at age 1 of roach and cumulative flow from rivers throughout England and Wales (Table 5.6). In all cases the relationship between mean length at age 1 and cumulative flows was inverse, whereby increases in cumulative flow over the annual period generally resulted in a smaller mean length at the end of the first year. The strongest relationship was found in the R. Brue ($r^2 = 0.6391$; Figure 5.11), where cumulative flow accounted for 64% of the variance in mean length at age 1, although the number of observations was low ($n = 5$). As the number of observations increased in these tests, a general decrease in the variance accounted for by cumulative flow was observed. This suggests flow has an influence in determining the length of roach at the end of the first year, but is just one of a possible number of factors acting to determine the length of the individual at the end of the first year.

Table 5.6 – Relationship between mean length at age 1 of roach dace and chub and cumulative flow days.

	roach			dace			chub		
	n	r^2	P	n	r^2	P	n	r^2	P
Bristol Avon	11	0.0556	0.485	4	0.3382	0.418	15	0.0652	0.358
Bristol Frome	12	0.0438	0.514	8	0.2540	0.203	13	0.2776	0.064
R Aire	5	0.3142	0.326	-	-	-	16	0.0058	0.778
R Anker	6	0.0117	0.839	-	-	-	13	0.1270	0.232
R Axe	4	0.2956	0.456	-	-	-	-	-	-
R Blackwater	8	0.2530	0.204	6	0.5555	0.089	16	0.1915	0.090
R Blythe	10	0.1513	0.267	7	0.6832	0.022	14	0.1095	0.248
R Brue	5	0.6391	0.105	-	-	-	16	0.0092	0.724
R Cam	8	0.3193	0.144	-	-	-	-	-	-
R Colne	12	0.1211	0.268	6	0.4662	0.135	15	0.1025	0.245
R Darent	8	0.0480	0.602	-	-	-	11	0.0186	0.689
R Hull	4	0.3264	0.429	-	-	-	-	-	-
R Ise	6	0.2057	0.366	-	-	-	-	-	-
R Kennet	11	0.0003	0.957	6	0.5849	0.076	10	0.3268	0.084
R Lee	5	0.2004	0.450	4	0.7082	0.158	9	0.0482	0.570
R Medway	6	0.5704	0.083	-	-	-	10	0.5564	0.013
R Stour	15	0.0009	0.915	5	0.8517	0.025	10	0.0006	0.946
R Tone	4	0.0567	0.762	5	0.5552	0.148	12	0.1164	0.278
R Trent	9	0.1340	0.333	4	0.4870	0.302	11	0.1943	0.175
R Ure	8	0.0424	0.625	5	0.0797	0.645	17	0.0390	0.447
R Waveney	5	0.2950	0.344	4	0.0278	0.833	-	-	-
R Wey	5	0.2356	0.407	6	0.6161	0.064	17	0.0443	0.532
R Wharfe	-	-	-	5	0.1084	0.588	17	0.3066	0.021
R Witham	6	0.4068	0.173	-	-	-	-	-	-
R Wreake	5	0.1039	0.597	-	-	-	-	-	-
Yorkshire Ouse	7	0.0504	0.628	-	-	-	-	-	-

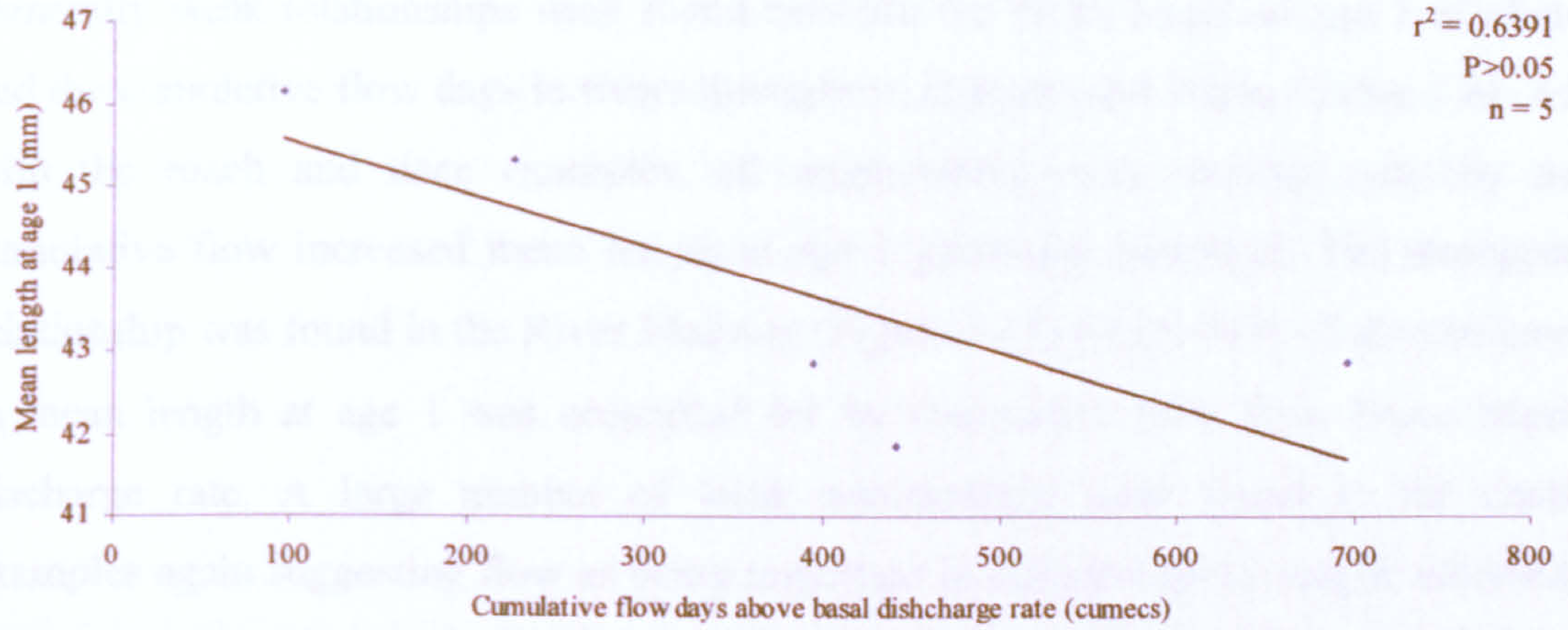


Figure 5.11 – Relationship between cumulative flow days above basal discharge rate and mean length of roach at age 1 in the River Brue.

Slightly stronger relationships were found between the mean length at age 1 of dace and the cumulative flow days in rivers throughout England and Wales (Table 5.6). As with roach, all relationships were inverse whereby increases in cumulative flow days resulted in generally smaller mean lengths at age 1. A strong relationship was found in the River Stour (Figure 5.12) where cumulative flow accounted for 85% of the variance in mean length at age 1, although again the number of observations was small (n = 5). The relationships observed in the dace examples were generally stronger than those of roach, suggesting river discharge is more important in influencing mean length at age 1 in dace than roach.

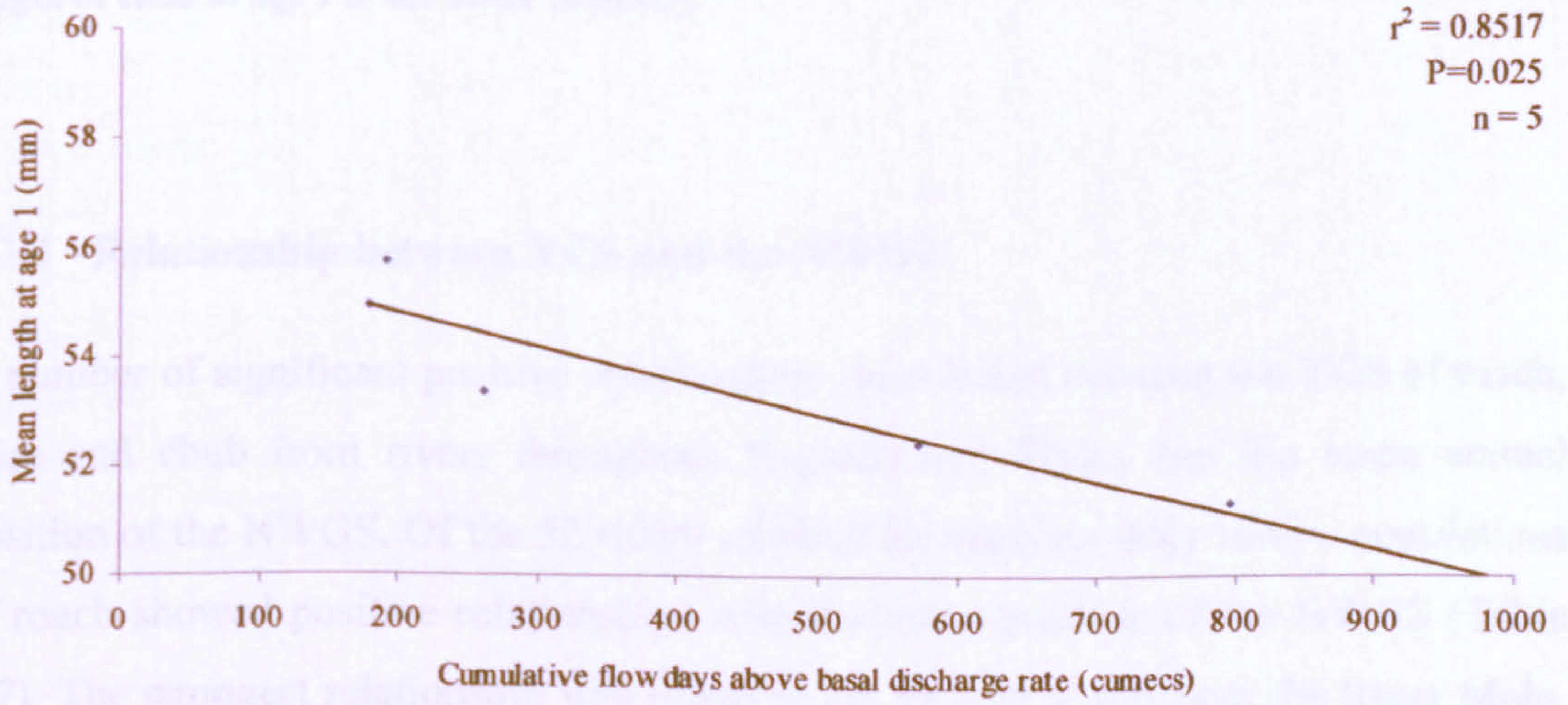


Figure 5.12 – Relationship between cumulative flow days above basal discharge rate and mean length of dace at age 1 in the River Stour.

Generally weak relationships were found between the mean length at age 1 of chub and the cumulative flow days in rivers throughout England and Wales (Table 5.6). As with the roach and dace examples, all relationships were inverse, whereby as cumulative flow increased mean length at age 1 generally decreased. The strongest relationship was found in the River Medway (Figure 5.13) where 56% of the variance in mean length at age 1 was accounted for by cumulative flow days above basal discharge rate. A large number of weak relationships were found in the chub examples again suggesting flow as being important in influencing the length achieved at the end of the first year, but is just one of a possible number of factors acting to determine the length of the individual at the end of the first year.

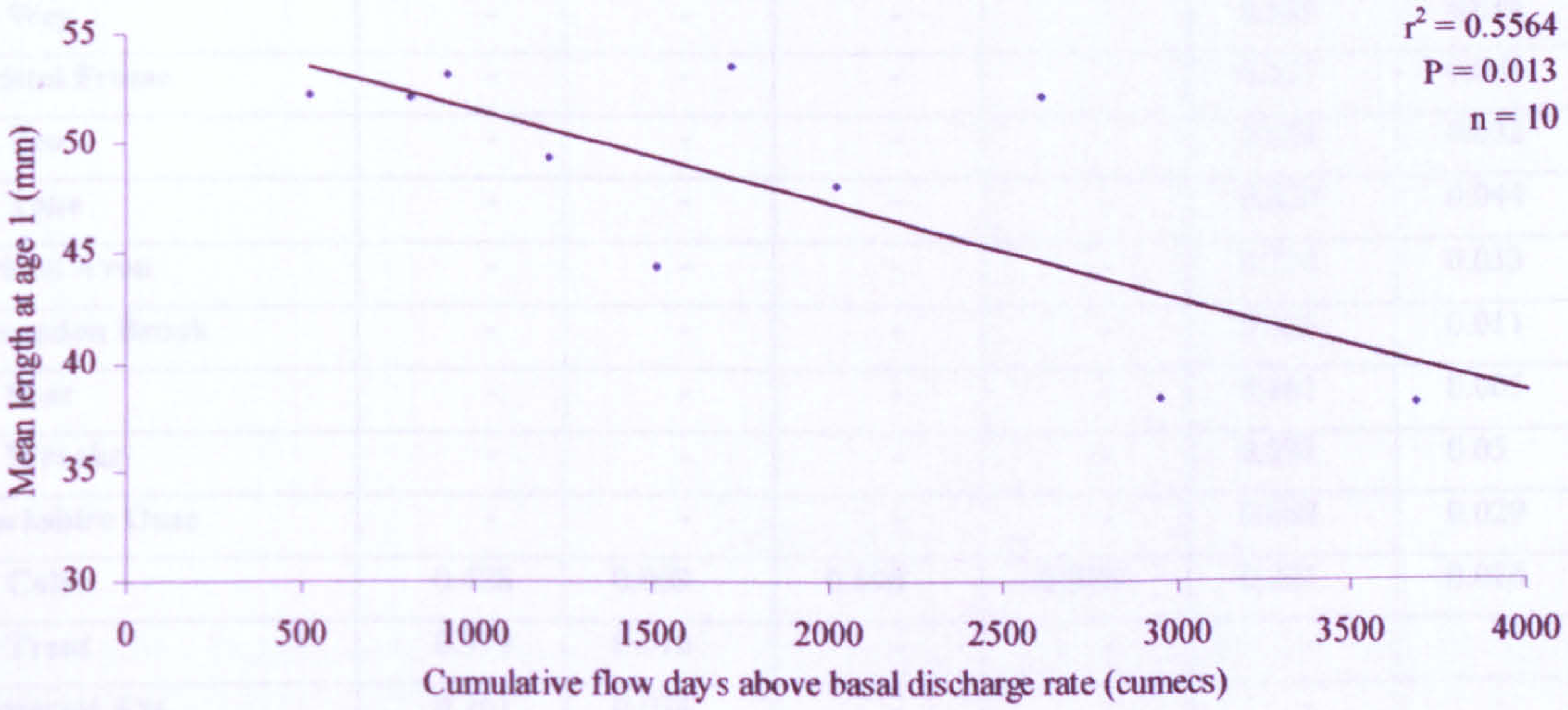


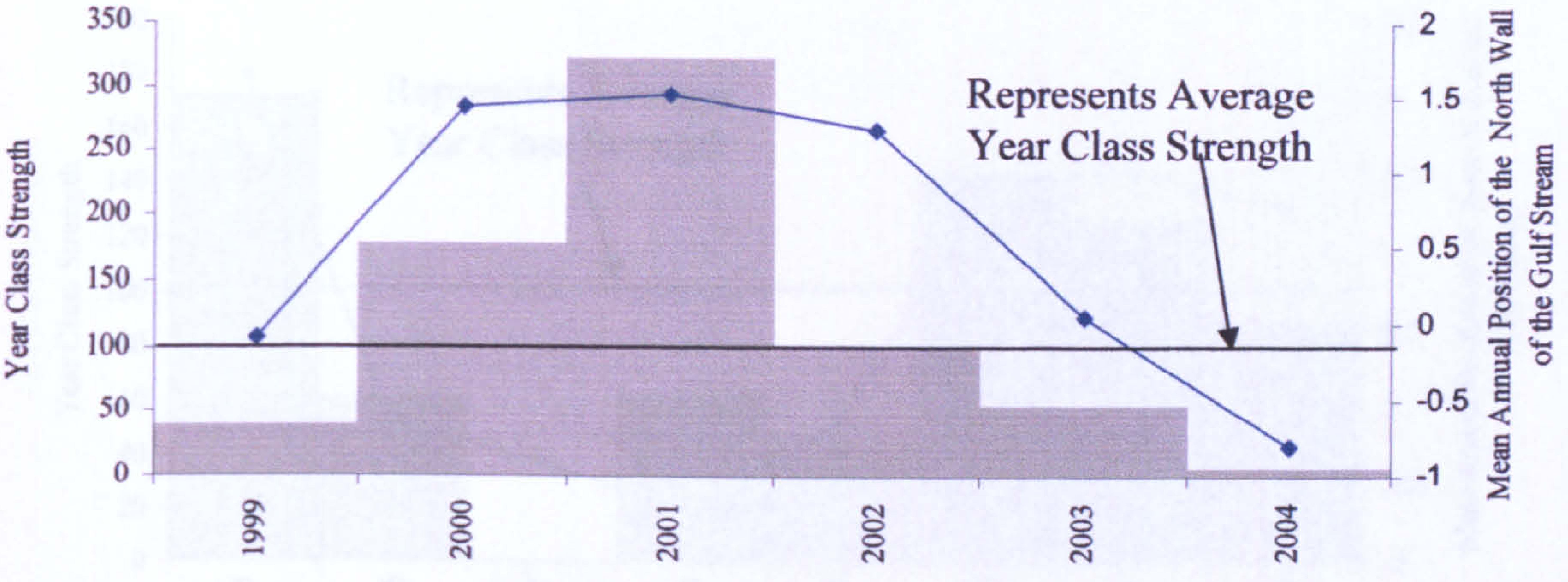
Figure 5.13 – Relationship between cumulative flow days above basal discharge rate and mean length of chub at age 1 in the River Medway.

5.3.4 - Relationship between YCS and the NWGS

A number of significant positive relationships were found between the YCS of roach, dace and chub from rivers throughout England and Wales and the mean annual position of the NWGS. Of the 52 rivers selected for analysis, only twelve populations of roach showed positive relationships with the mean position of the NWGS (Table 5.7). The strongest relationship was found in the YCS of roach from the River Mole, where 98% of the variation in YCS was accounted for by the position of the North Wall ($r^2 = 0.981$). Strong relationships also existed between the mean annual position of the NWGS and the YCS of roach from the rivers Nene, Wantsum, Colne (Herts) and the Somerset Axe (r^2 = 0.867, 0.825, 0.738 and 0.761 respectively). Weaker relationships were found in the YCS of roach from the rivers Waveney (Figures 5.14-5.15), Witham and Colne (r^2 = 0.651, 0.600 and 0.428 respectively). Of the remaining 40 rivers where roach YCS's were available (Table 5.2) no significant relationships were found.

Table 5.7 – Significant relationships between the YCS of roach, dace and chub populations from rivers throughout England and Wales and the mean annual position of the NWGS and (r^2 and P values given).

	roach		Dace		chub	
site	r^2	P	r^2	P	r^2	P
R. Wey	-	-	-	-	0.335	0.014
Bristol Frome	-	-	-	-	0.257	0.048
R. Yeo	-	-	-	-	0.654	0.032
R. Tone	-	-	-	-	0.220	0.044
Bristol Avon	-	-	-	-	0.234	0.033
Sarendon Brook	-	-	-	-	0.521	0.011
R. Soar	-	-	-	-	0.461	0.005
R. Wreake	-	-	-	-	0.291	0.05
Yorkshire Ouse	-	-	-	-	0.668	0.029
R. Colne	0.428	0.009	0.590	0.046	0.221	0.016
R. Trent	0.399	0.016	-	-	-	-
Somerset Axe	0.761	0.034	-	-	-	-
R. Wantsum	0.825	0.021	-	-	-	-
Somerset Frome	0.291	0.050	-	-	-	-
R. Mole	0.981	0.006	-	-	-	-
R. Colne (Herts)	0.738	0.018	0.665	0.050	-	-
R. Thurne	0.351	0.049	-	-	-	-
R. Waveney	0.651	0.017	-	-	-	-
R. Nene	0.867	0.045	-	-	-	-
R. Witham	0.600	0.015	-	-	-	-
R. Blythe	-	-	0.780	0.005	-	-
R. Don	0.749	0.007	0.749	0.04	-	-



Figures 5.14 – YCS of roach from the River Waveney and the mean annual position of the NWGS.

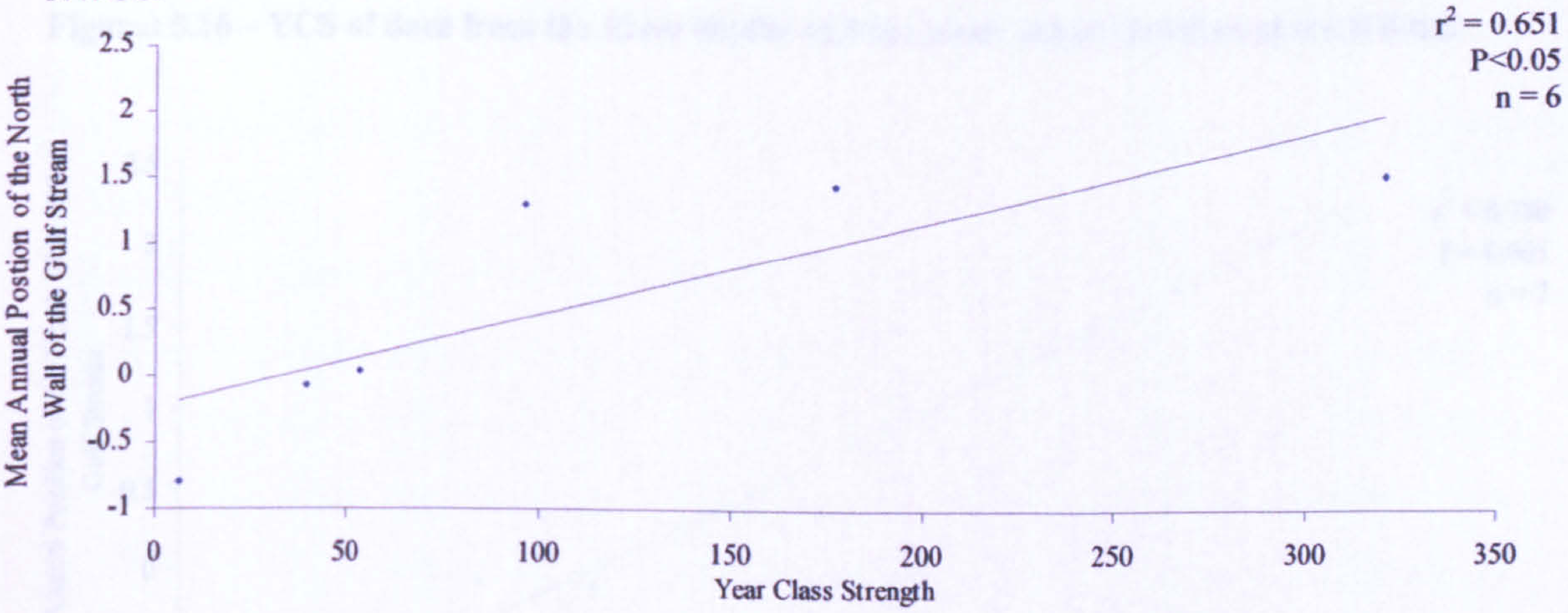
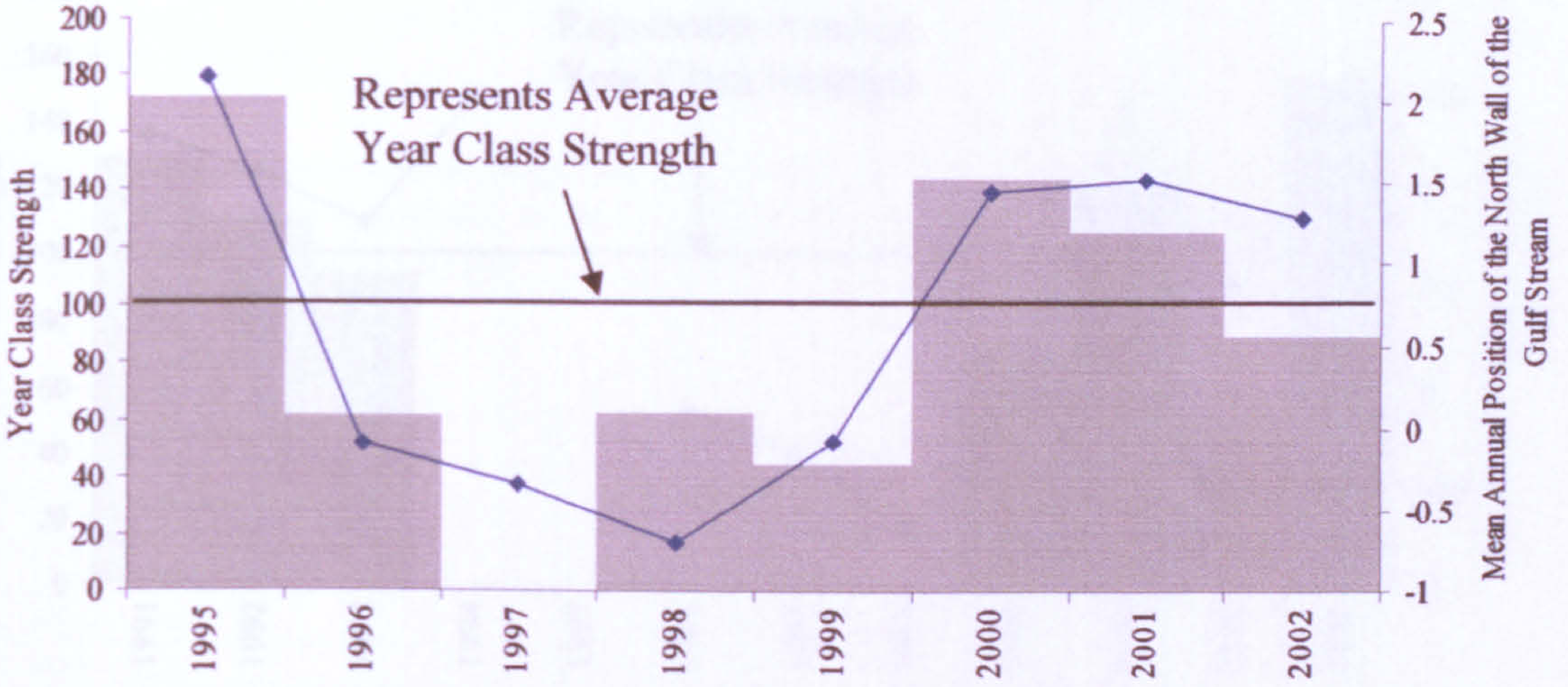


Figure 5.15 - Relationship between the YCS of roach from the River Waveney and the mean annual position of the NWGS.

Positive relationships between the YCS and the NWGS of just four populations of dace were found (Table 5.7). The strongest relationships were from the YCS of dace from the River Blythe ($r^2 = 0.780$, Figures 5.16-5.17) and the River Don ($r^2 = 0.749$). Weaker relationships were found in the YCS of dace from the River Colne (Herts) ($r^2 = 0.665$,) and the Rive Colne (Essex) ($r^2 = 0.590$). Of the remaining 48 rivers where dace YCS's were available (Table 5.2), no significant relationships were found.



Figures 5.16 – YCS of dace from the River Blythe and the mean annual position of the NWGS.

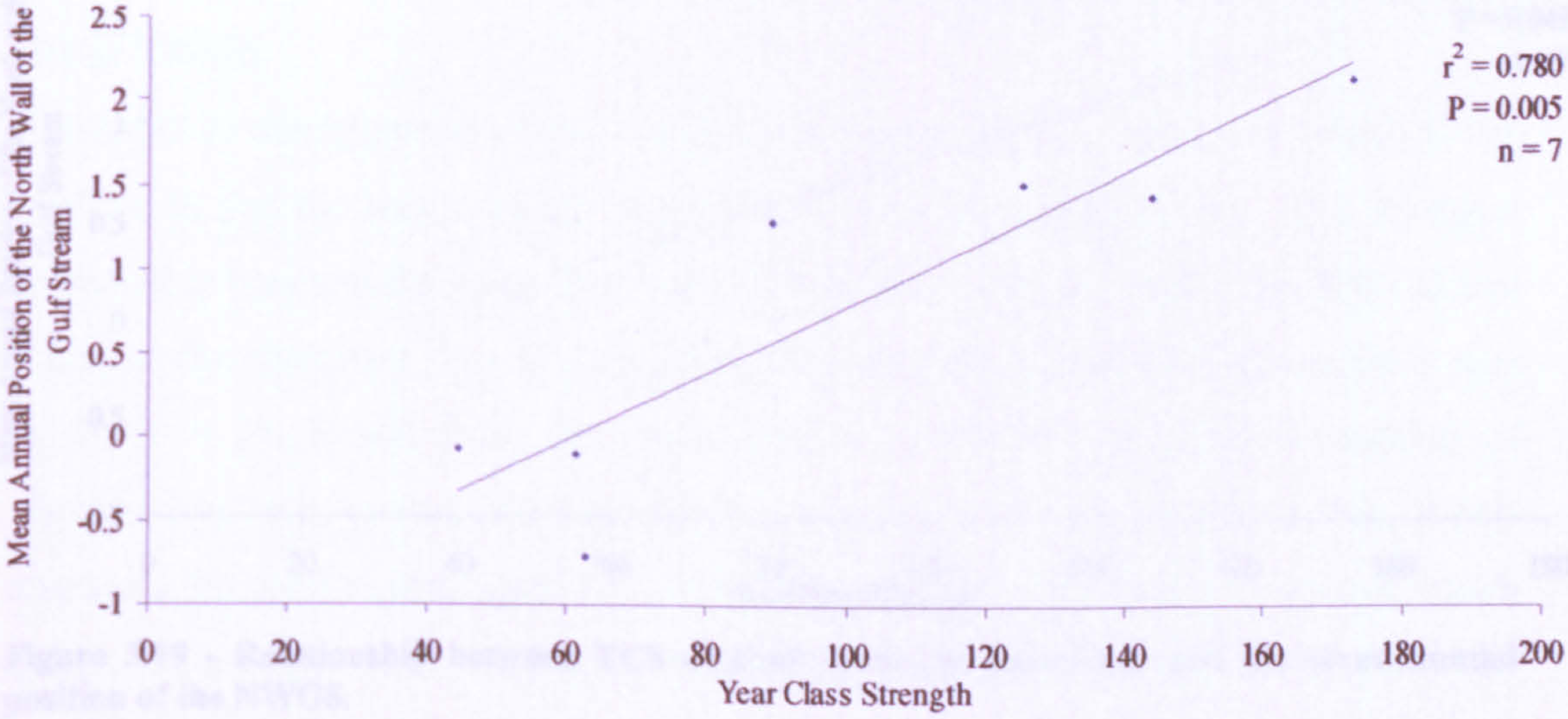
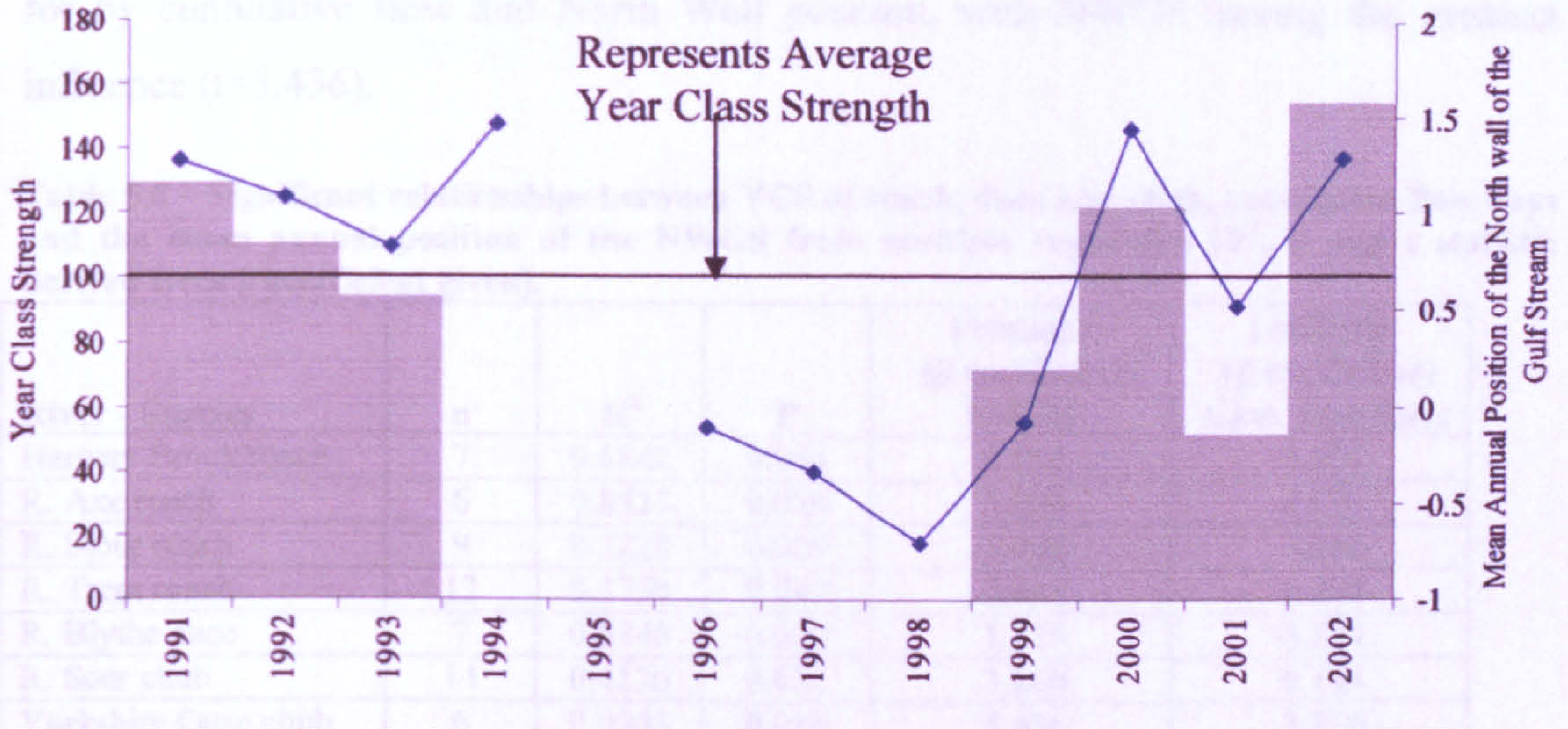


Figure 5.17 - Relationship between YCS of dace from the River Blythe and the mean annual position of the NWGS.

Chub from ten of the 52 rivers chosen for analysis had significant positive relationships between YCS and the position of the NWGS ($P<0.05$; Table 5.7). The strongest relationship was observed in the YCS of chub from the River Yeo ($r^2 = 0.654$, Figures 5.18-5.19). Weaker relationships were found between the YCS of chub from Sarandon Brook and the River Wey ($r^2 = 0.521$ and 0.335 respectively). Of the remaining 42 rivers where chub YCS's were available (Table 5.2), no significant relationships were found.



Figures 5.18 – YCS of chub from the River Yeo and the mean annual position of the NWGS.

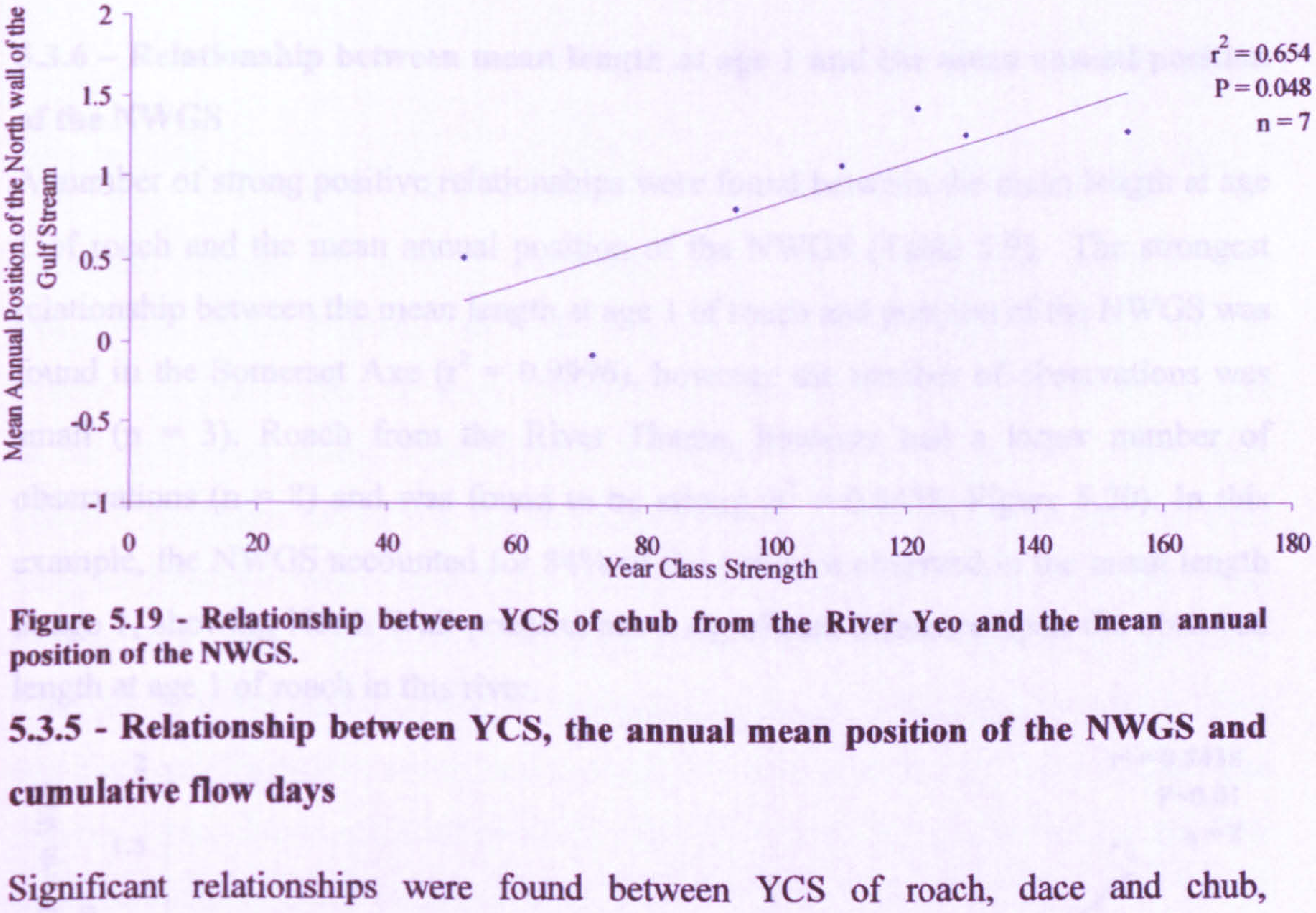


Figure 5.19 - Relationship between YCS of chub from the River Yeo and the mean annual position of the NWGS.

5.3.5 - Relationship between YCS, the annual mean position of the NWGS and cumulative flow days

Significant relationships were found between YCS of roach, dace and chub, cumulative flow days and the mean annual position of the NWGS (Table 5.8). The strongest relationship was from the R. Axe where cumulative flow and North Wall position accounted for 85% of the observed variation in roach YCS, with NWGS having the greatest influence (t=5.203). Cumulative flow and North Wall position accounted for 63% of the variation observed in the YCS of the dace from the R. Blythe, with cumulative flow days having the greatest influence (t=-3.524), while 90% of the variation of the YCS of the chub from the Yorkshire Ouse was accounted for by cumulative flow and North Wall position, with NWGS having the greatest influence (t=5.436).

Table 5.8 – Significant relationships between YCS of roach, dace and chub, cumulative flow days and the mean annual position of the NWGS from multiple regression (R^2, P and t statistic derived from β coefficient given).

River - Species	n	R^2	P	t statistic (β coefficient) NWGS	t statistic (β coefficient) Cum. flow days
Harpers Brook roach	7	0.6842	0.044	0.061	3.831
R. Axe roach	6	0.8527	0.026	5.203	-4.726
R. Stour roach	9	0.7228	0.009	-4.446	3.356
R. Trent roach	12	0.3760	0.049	-2.849	-0.794
R. Blythe dace	7	0.6346	0.050	1.129	-3.524
R. Soar chub	14	0.4126	0.021	3.260	0.144
Yorkshire Ouse chub	6	0.9003	0.015	5.436	-3.216

5.3.6 – Relationship between mean length at age 1 and the mean annual position of the NWGS

A number of strong positive relationships were found between the mean length at age 1 of roach and the mean annual position of the NWGS (Table 5.9). The strongest relationship between the mean length at age 1 of roach and position of the NWGS was found in the Somerset Axe ($r^2 = 0.9996$), however the number of observations was small (n = 3). Roach from the River Thame, however had a larger number of observations (n = 8) and was found to be strong ($r^2 = 0.8438$; Figure 5.20). In this example, the NWGS accounted for 84% of the variance observed in the mean length at age 1, showing North Wall position has a significant influence upon the observed length at age 1 of roach in this river.

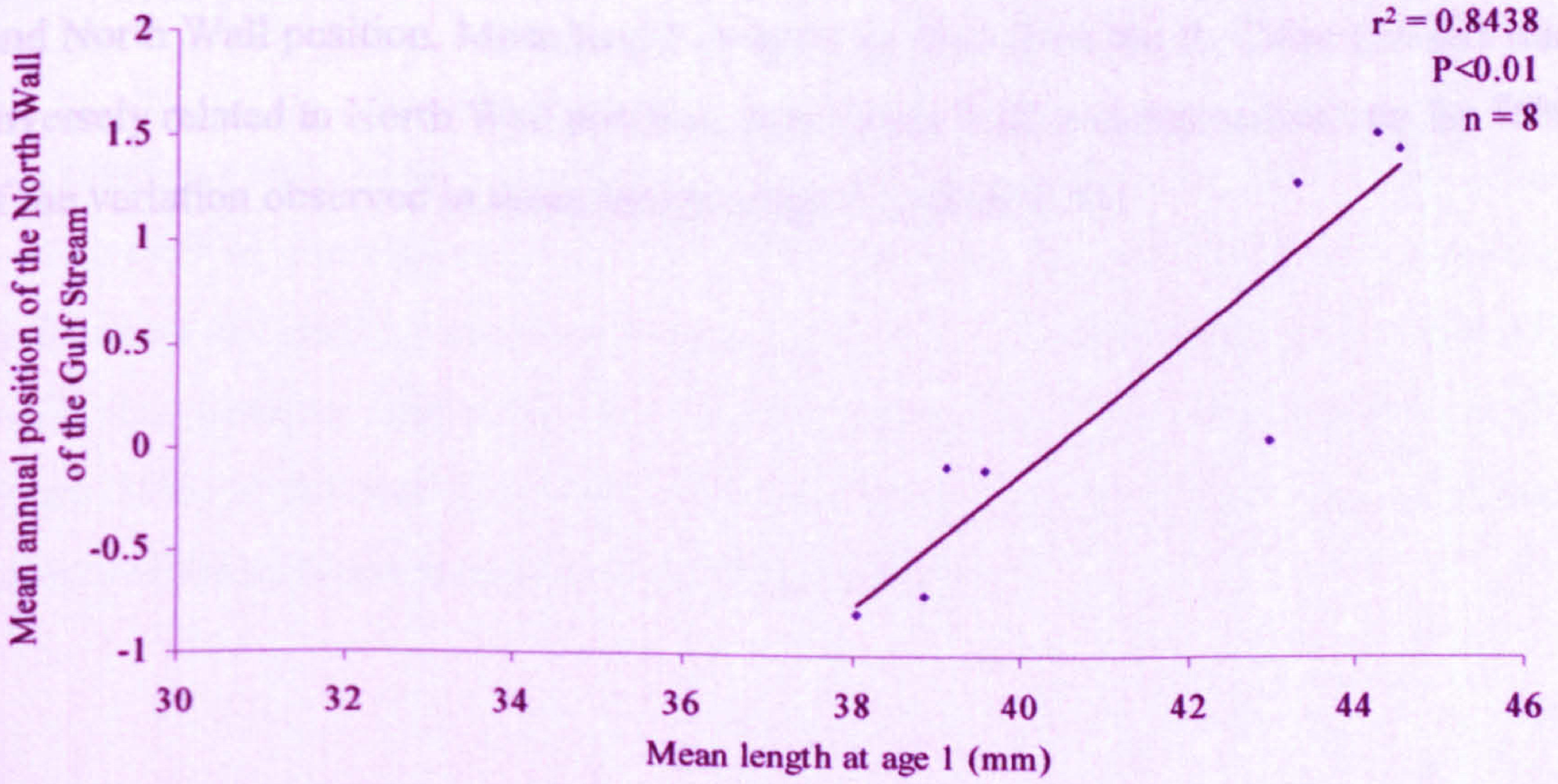


Figure 5.20 – Relationship between mean length at age 1 of roach from the R. Thame and the mean annual position of the NWGS.

Table 5.9 – Rivers where significant relationships between mean length at age 1 of roach, dace and chub and the mean annual position of the NWGS.

	roach		dace		chub	
	n	r^2	n	r^2	n	r^2
Bristol Avon	9	0.4202	4	0.1036 †	12	0.3762 *
Bristol Frome	10	0.0480	6	0.9199 **	9	0.0273
R Anker	4	0.9073 *	-	-	11	0.0293
R Blythe	6	0.7289 *	3	0.1140	9	0.0293
R Brue	5	0.2965	3	0.9998 **	12	0.1222
R Cherwell	7	0.3228	5	0.2125 †	13	0.3538 *
R Chew	5	0.4517	4	0.4865 †	-	-
R Colne	5	0.0542	6	0.7552 * †	14	0.1314
R Colne Herts	3	0.2419	3	0.3036†	14	0.1710
R Lee	3	0.0557	4	0.8549 †	14	0.1461
R Mole	3	0.0140	4	0.5456	11	0.1964
R Nene	5	0.9360 **	-	-	-	-
R Stour	4	0.9063 *	-	-	-	-
R Stour Historic	12	0.3909 *	-	-	-	-
R Thame	8	0.8438 **	-	-	-	-
R Welland	4	0.4025	4	0.9271 * †	-	-
R Wey	4	0.0056	7	0.7255 * †	15	0.1424
R Wharfe	-	-	4	0.7524 †	11	0.2147
Somerset Axe	3	0.9996 *	-	-	-	-
Somerset Frome	8	0.5062 *	3	0.1772	8	0.2568

*** =P>0.05 ** = P>0.01 † = inverse relationship**

Generally stronger relationships were found between mean length at age 1 of dace from rivers around England and Wales and the mean annual position of the NWGS (Table 5.9). The number of observations in the analyses for dace is generally low due to the short lived nature of this species. However of the analyses made, North Wall position accounted for 92% of the observed variance of mean length at age 1 of dace from the Bristol Frome (Figure 5.21). Positive relationships were not exclusive to this data set as a number of inverse relationships were found. Of the 26 tests made in this analysis, 10 rivers showed inverse relationships between mean length at age 1 of dace and North Wall position. Mean length at age 1 of dace from the R. Colne (Essex) was inversely related to North Wall position, with North Wall position accounting for 76% if the variation observed in mean length at age 1 (Figure 5.22).

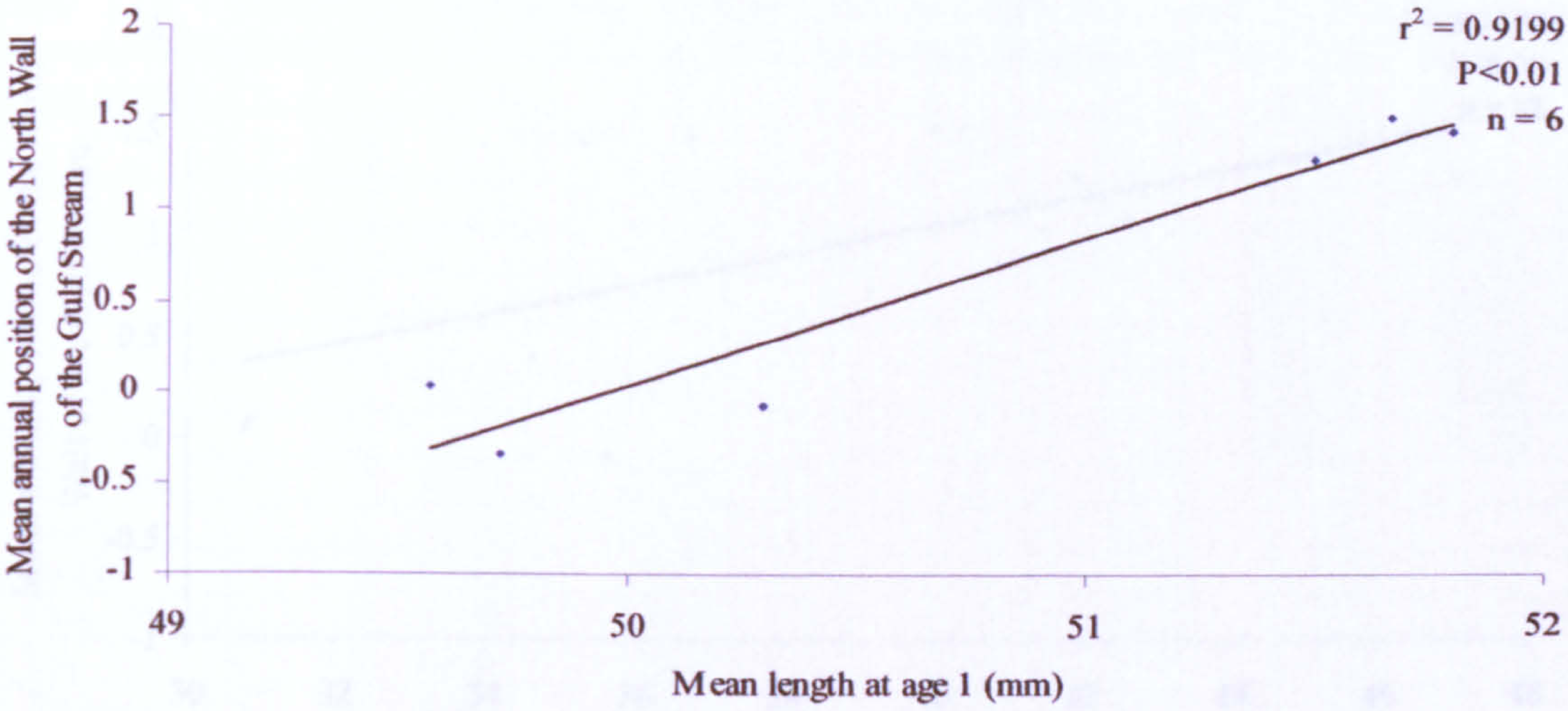


Figure 5.21 – Relationship between the mean length at age 1 of dace from the Bristol Frome and the mean annual position of the NWGS.

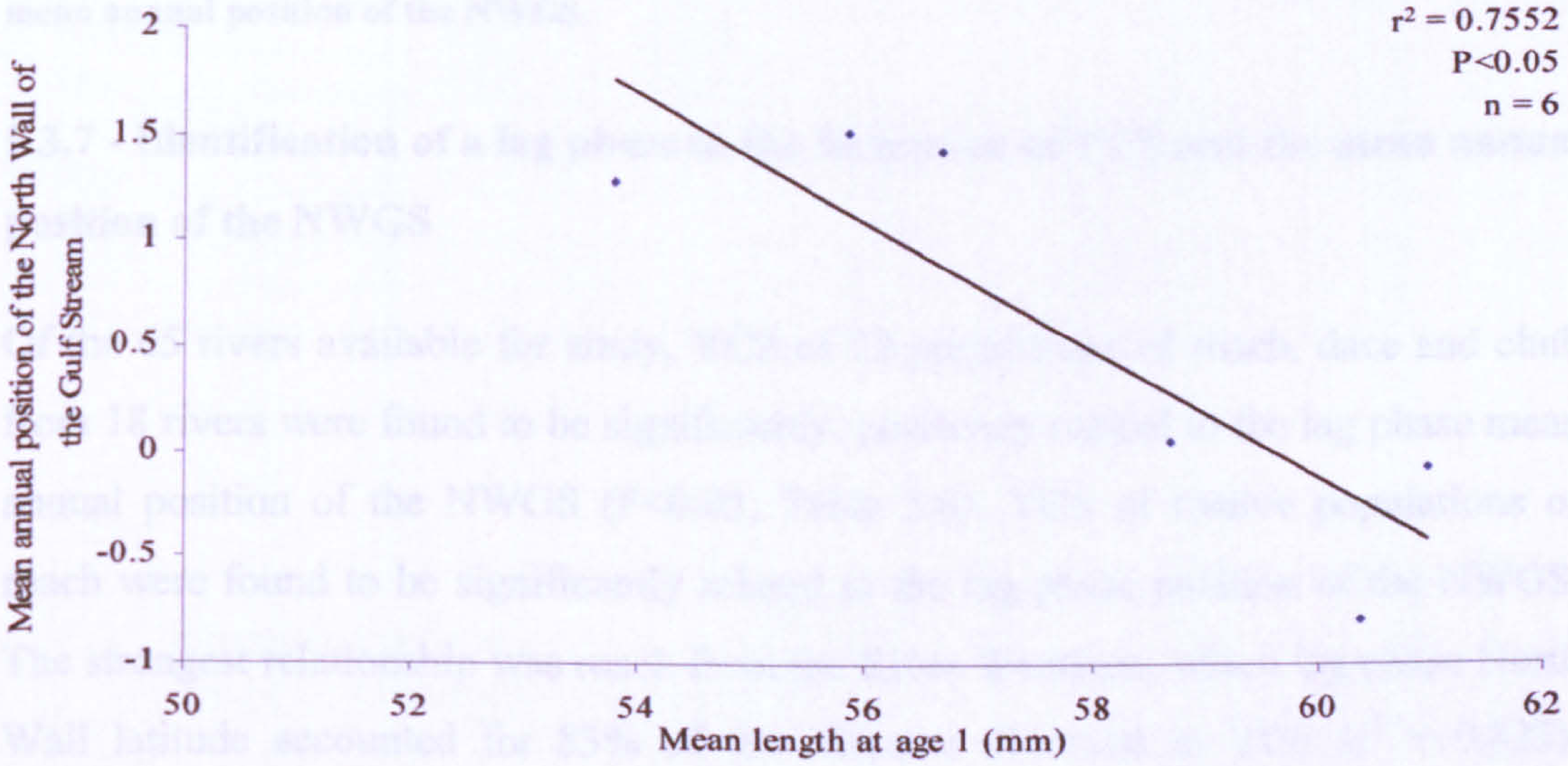


Figure 5.22 – Relationship between the mean length at age 1 of dace from the River Colne (Essex) and the mean annual position of the NWGS.

The position of the NWGS was found to have a positive effect on mean length at age 1 of chub from rivers throughout England and Wales (Table 5.9), whereby northerly shifts generally resulted in greater lengths at age 1. The relationships were generally weak, the strongest relationship was for chub from the Bristol Avon (Figure 5.23), where 38% of the variance observed in the mean lengths at age 1 of chub was accounted for by mean annual position of the NWGS.

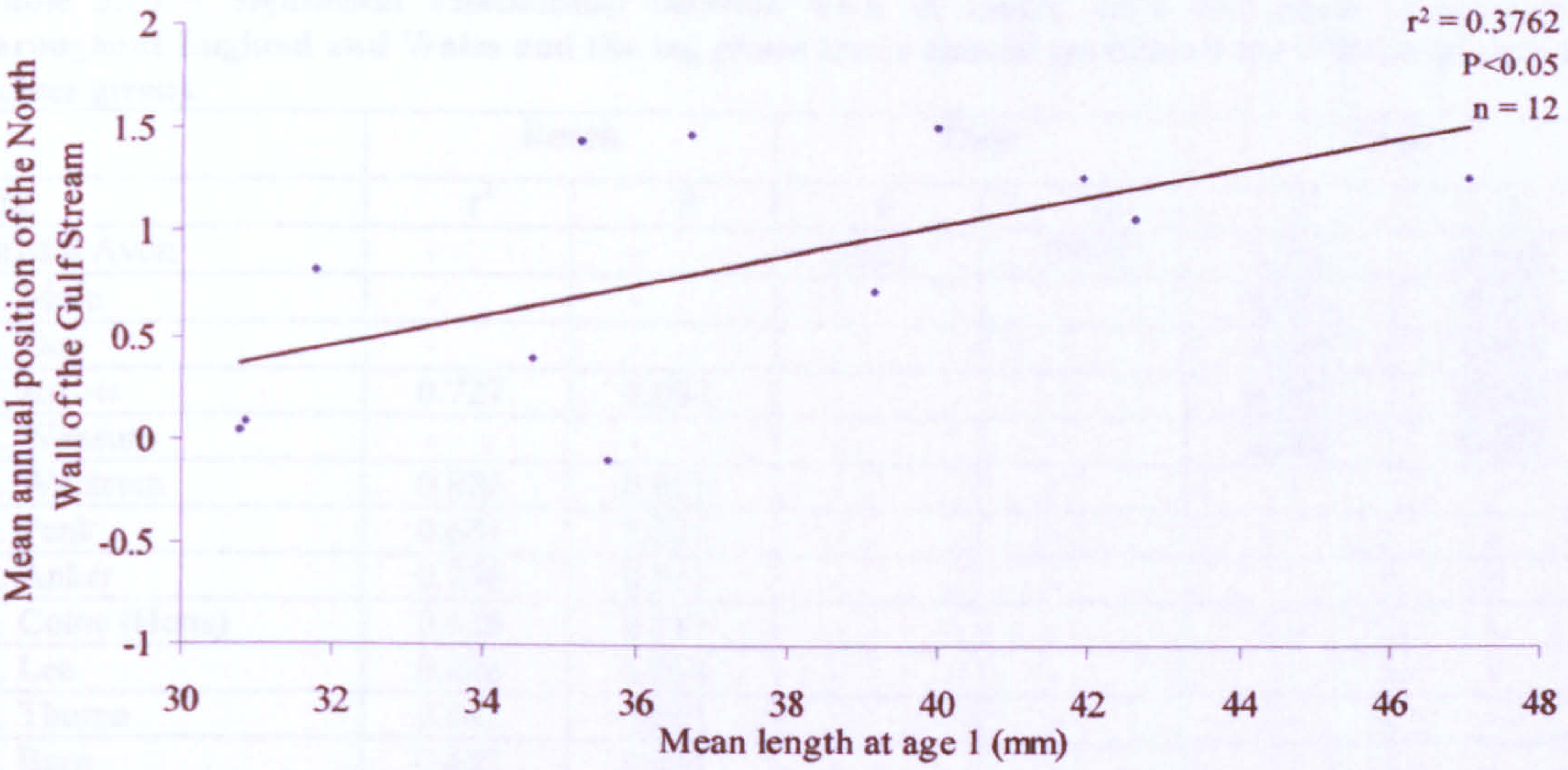


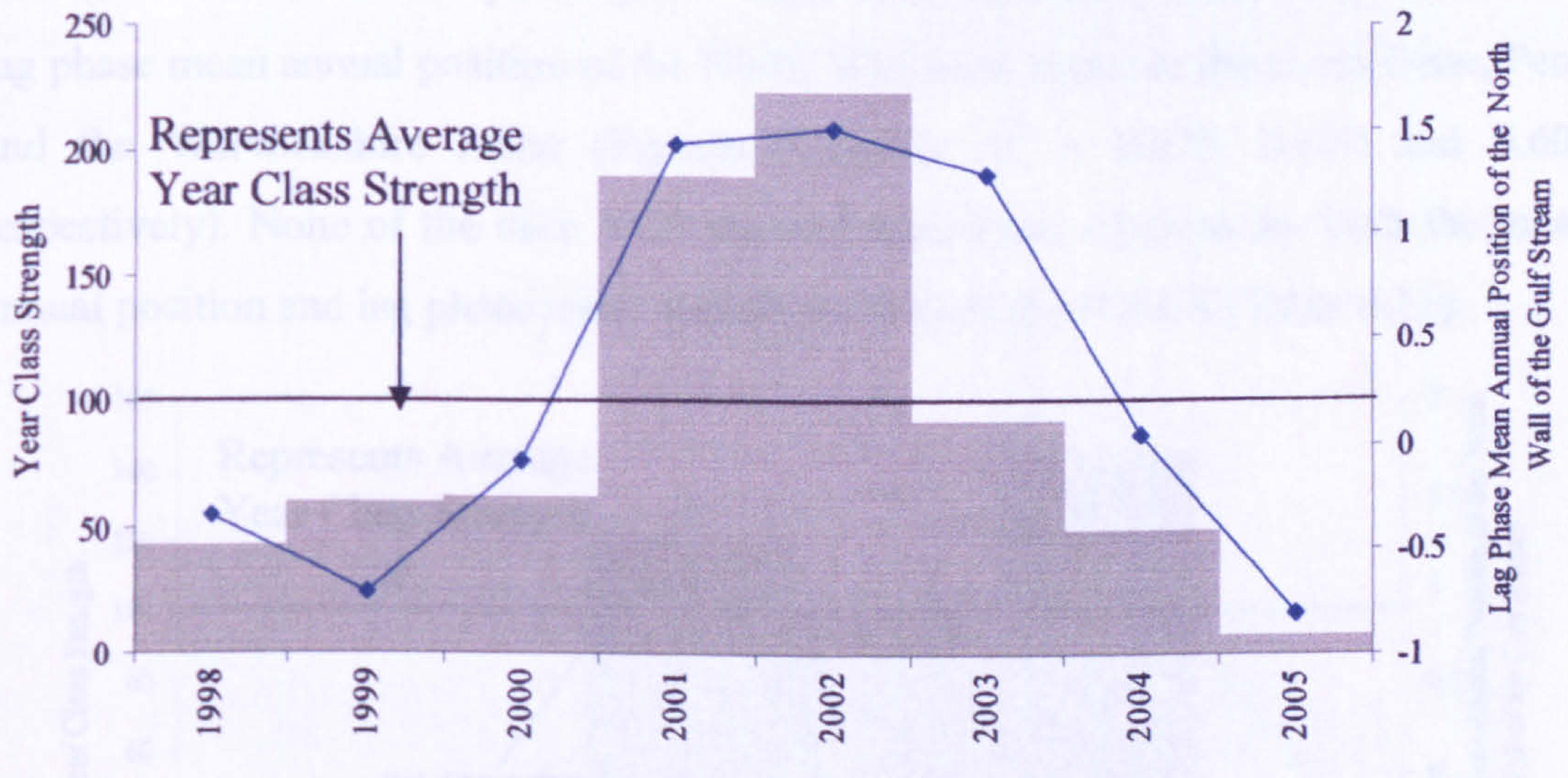
Figure 5.23 – Relationship between mean length at age 1 of chub from the Bristol Avon and the mean annual position of the NWGS.

5.3.7 - Identification of a lag phase in the formation of YCS and the mean annual position of the NWGS

Of the 65 rivers available for study, YCS of 23 populations of roach, dace and chub from 18 rivers were found to be significantly, positively related to the lag phase mean annual position of the NWGS (P<0.05, Table 5.6). YCS of twelve populations of roach were found to be significantly related to the lag phase position of the NWGS. The strongest relationship was roach from the River Wantsum, where lag phase North Wall latitude accounted for 83% of the variance observed in YCS (r^2 = 0.825). Significant relationships were found in the rivers Arrow (Figures 5.24-25) and Stour (r^2 = 0.727, 0.616 respectively). Strong relationships were also observed in the rivers Anker and Waveney roach populations (r^2 = 0.756, 0.733 respectively). Weaker relationships were found in the rivers Penk, Nene and the tidal Bure (r^2 = 0.681, 0.679 and 0.586 respectively), while the weakest relationships were found in the rivers Colne (Herts), Lee, Thurne and Bure (r^2 = 0.428, 0.426, 0.441 and 0.442 respectively). YCS of roach from the rivers Wantsum, Colne (Herts), Thurne and Nene were found to be significantly related to both the mean annual position and lag phase mean annual position of the NWGS (Table 11).

Table 5.10 – Significant relationship between YCS of roach, dace and chub from rivers throughout England and Wales and the lag phase mean annual position of the NWGS (r^2 and P values given).

	Roach		Dace		Chub	
Site	r^2	P	r^2	P	r^2	P
Bristol Avon	-	-	0.601	0.043	0.217	0.046
R. Mole	-	-	-	-	0.304	0.013
R. Don	-	-	-	-	0.117	0.049
R. Arrow	0.727	0.004	-	-	0.547	0.006
R. Wensum	-	-	-	-	0.282	0.002
R. Wantsum	0.825	0.021	-	-	-	-
R. Penk	0.681	0.027	-	-	-	-
R. Anker	0.756	0.015	-	-	-	-
R. Colne (Herts)	0.428	0.047	-	-	-	-
R. Lee	0.426	0.034	-	-	-	-
R. Thurne	0.441	0.043	-	-	-	-
R. Bure	0.442	0.011	-	-	-	-
R. Nene	0.679	0.027	-	-	-	-
R. Bure (tidal)	0.586	0.016	-	-	-	-
R. Waveney	0.733	0.009	-	-	-	-
R. Stour	0.616	0.004	-	-	-	-
Harpers Brook	-	-	0.890	0.003	-	-
R. Dane	-	-	0.675	0.050	-	-
R. Penk	-	-	0.672	0.050	-	-
R. Mole	-	-	0.877	0.004	-	-
R. Lee	-	-	0.954	0.015	-	-



Figures 5.24 – YCS of roach from the River Arrow and Lag Phase mean annual position of the NWGS.

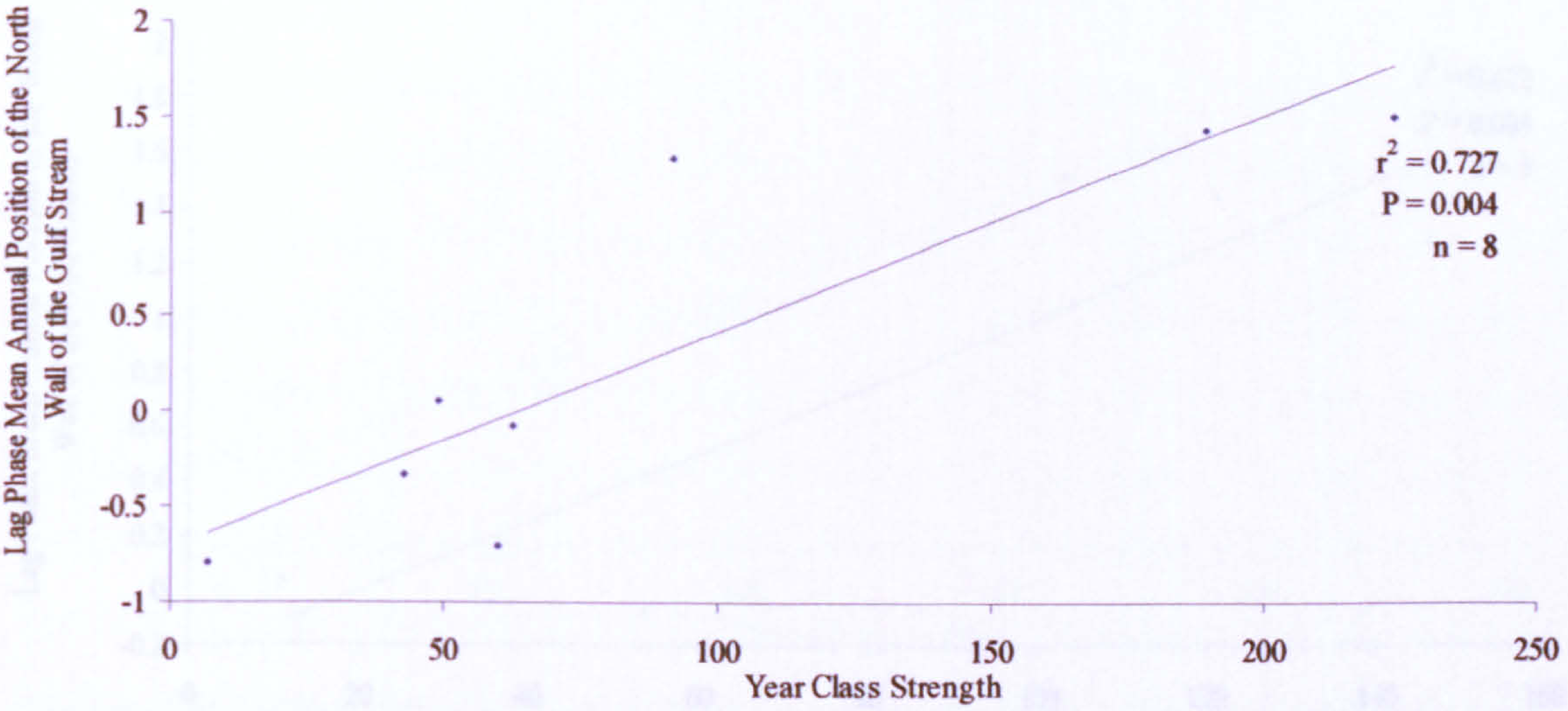


Figure 5.25 –Relationship between YCS of roach from the River Arrow and the Lag Phase mean annual position of the NWGS.

Of the 65 rivers available for study, the YCS of six dace populations were positively related to the lag phase mean annual position of the NWGS (Table 5.10). The strongest relationship was for the dace from the River Lee, where 95% of the variance in dace YCS was accounted for by lag phase mean annual position of the NWGS (r^2 = 0.954). Strong relationships were found in the YCS of River Mole and Harpers Brook dace (r^2 = 0.877, 0.890 respectively). Weaker relationships between YCS of dace and lag phase mean annual position of the North Wall were found in the rivers Dane, Penk and the Warwickshire Avon (Figures 5.26-27), (r^2 = 0.675, 0.672 and 0.601 respectively). None of the dace YCS showed significant relations for both the mean annual position and lag phase mean annual position of the NWGS (Table 5.11).

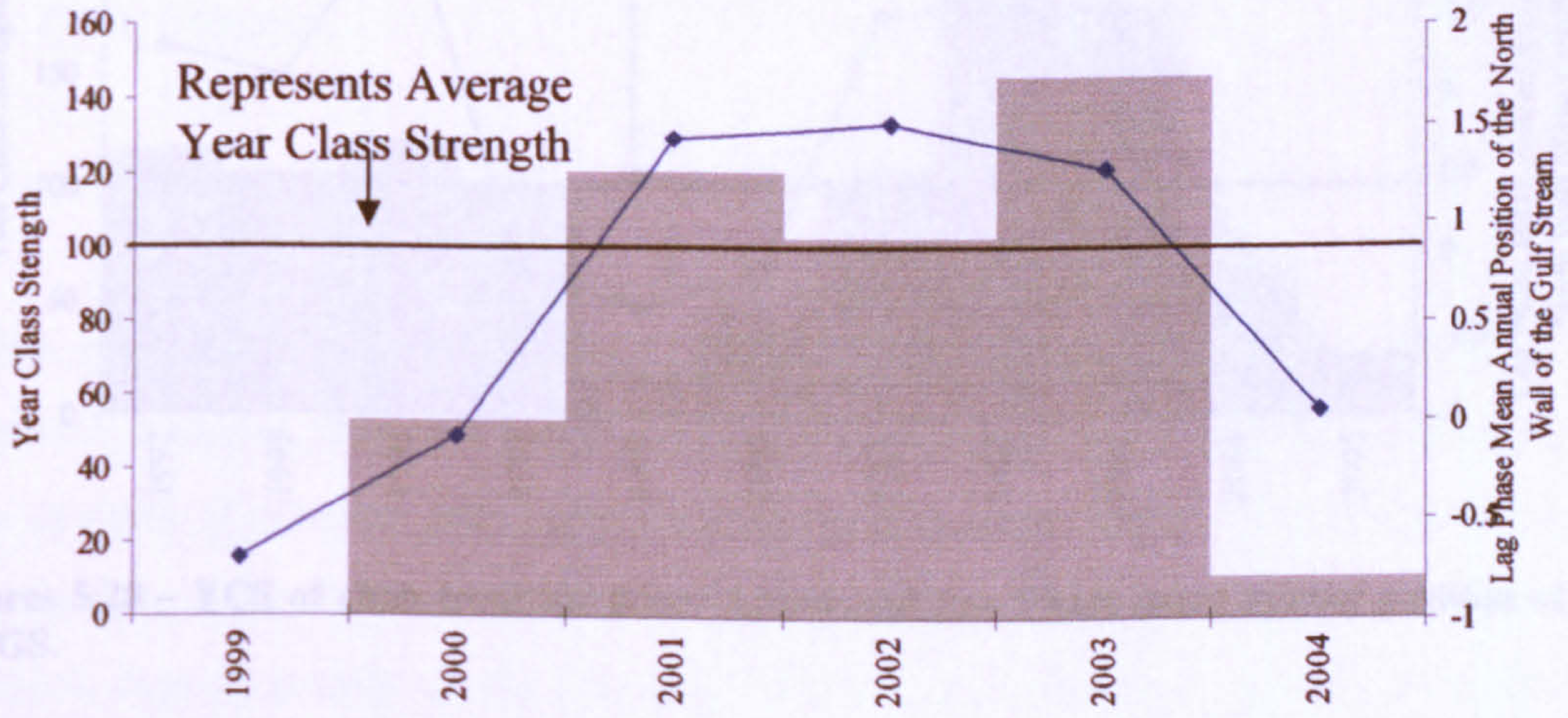


Figure 5.26 – YCS of dace from the River Penk and Lag Phase mean annual position of the NWGS.

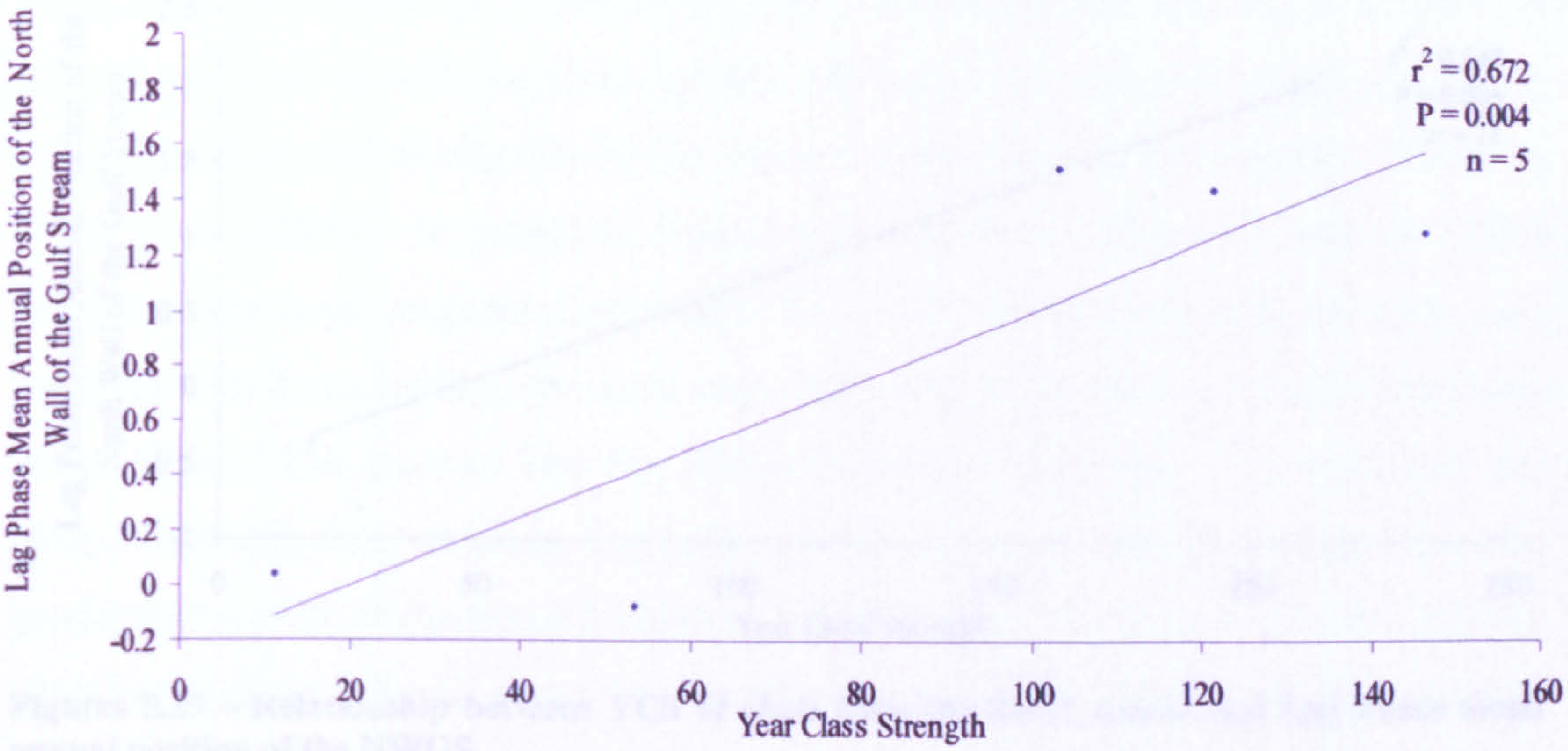
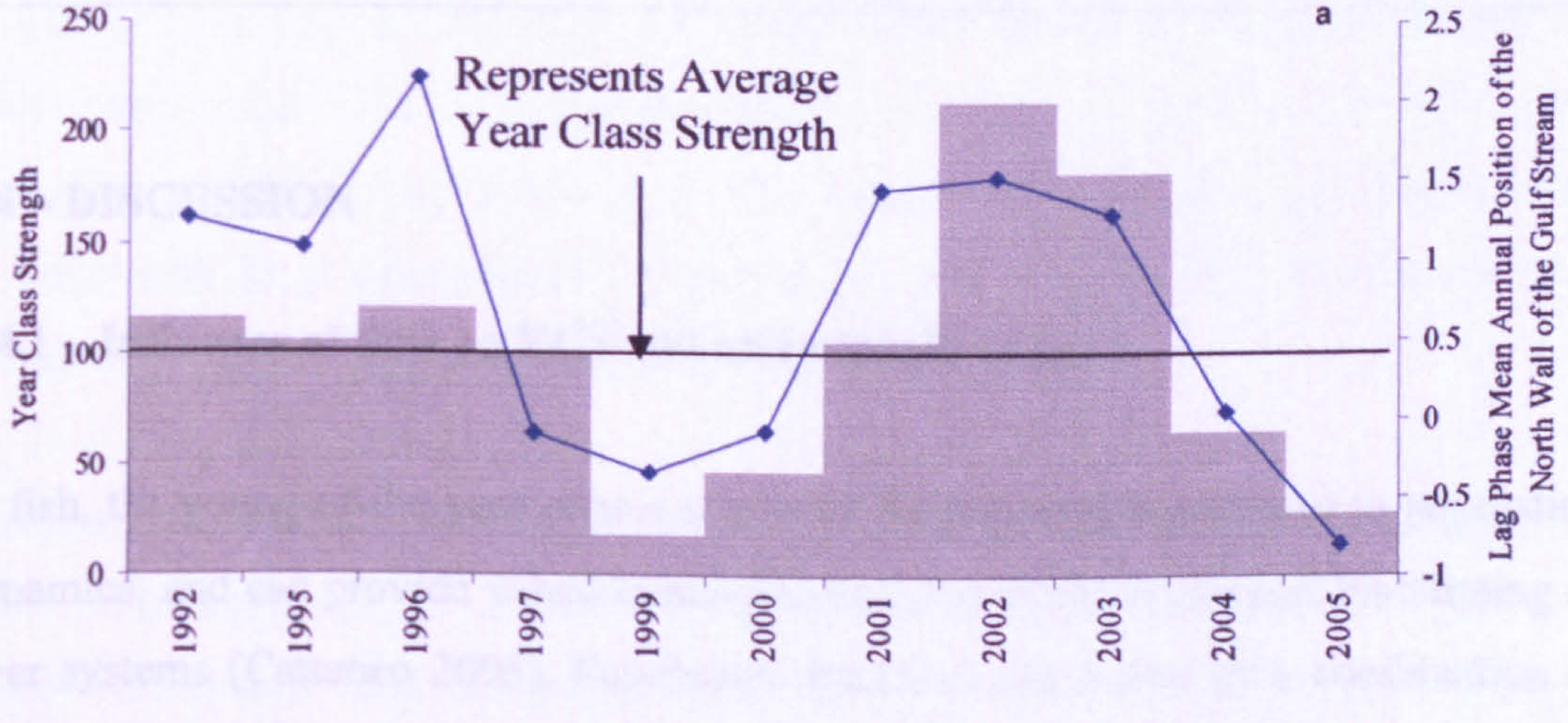
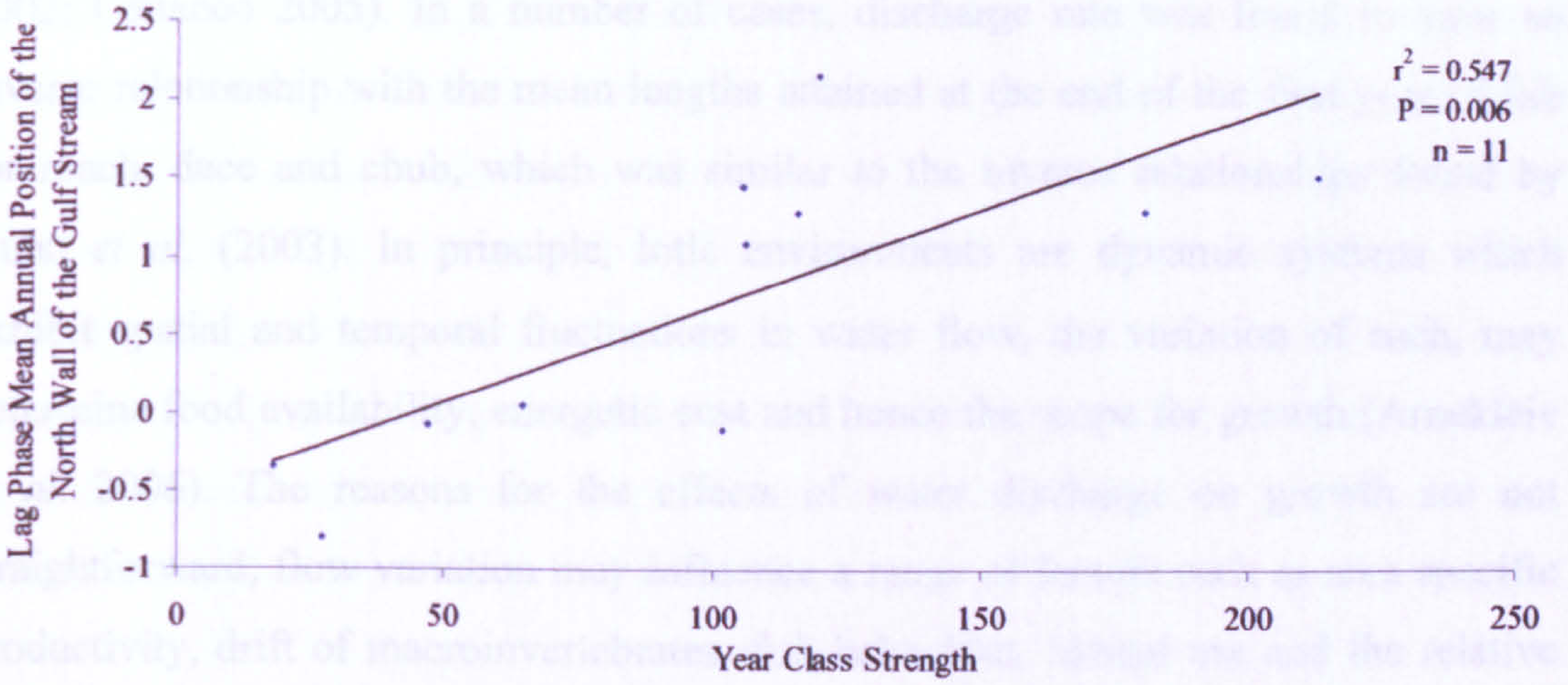


Figure 5.27 – Relationship between YCS of dace from the River Penk and Lag Phase mean annual position of the NWGS.

Of the 65 rivers available for study, YCS of chub from five rivers were found to be weakly related to the lag phase mean annual position of the NWGS (P<0.05, Table 5.10). The strongest relationship was found in the River Arrow where 55% of the variance observed in the YCS of chub was accounted for by the lag phase position of the North Wall (Figures 5.28-29, $r^2 = 0.547$). The YCS of chub from the Bristol Avon were found to be related to both the mean annual and lag phase mean annual position of the NWGS (Table 11).



Figures 5.28 – YCS of chub from the River Arrow and Lag Phase mean annual position of the NWGS.



Figures 5.29 – Relationship between YCS of chub from the River Arrow and Lag Phase mean annual position of the NWGS.

Table 5.11 – Significant relationships between YCS and both the mean annual and the lag phase mean annual position of the NWGS.

	relationship between YCS and NWGS			**relationship between YCS and Lag Phase NWGS**		
Site	n	adjusted r^2	P	n	adjusted r^2	P
River Wantsum Roach	5	0.825	0.021	5	0.825	0.021
River Colne (Herts) Roach	8	0.738	0.018	8	0.428	0.047
River Thurne Roach	8	0.351	0.049	8	0.441	0.043
River Nene Roach	6	0.867	0.045	6	0.679	0.027
Bristol Avon Chub	15	0.234	0.033	15	0.271	0.046

5.4 – DISCUSSION

5.4.1 – Influence of flow on YCS and mean length at age 1

In fish, the young-of-the-year cohort size is of fundamental importance to population dynamics, and can provide valuable insights into part of the ecological functioning of river systems (Cattanéo 2005). Population dynamics are driven by a combination of both density dependant and density independent processes, the respective influences of which depend mainly on the life stage of the fish and the environmental conditions (Elliott 1989). Amongst those factors, hydrological variability, food availability and biological interactions between individuals (competition and predation) have been demonstrated to be of major influence (Nehring and Anderson 1993; Cattanéo *et al.*

2002; Cattanéo 2005). In a number of cases, discharge rate was found to have an inverse relationship with the mean lengths attained at the end of the first year of life for roach, dace and chub, which was similar to the inverse relationships found by Nunn *et al.* (2003). In principle, lotic environments are dynamic systems which exhibit spatial and temporal fluctuations in water flow, the variation of such, may determine food availability, energetic cost and hence the scope for growth (Arnekleiv *et al.* 2006). The reasons for the effects of water discharge on growth are not straightforward; flow variation may influence a range of factors such as area specific productivity, drift of macroinvertebrates, fish behaviour, habitat use and the relative abundance or scarcity of energetically favourable habitats (Arnekleiv *et al.* 2006). Higher than average discharge rates, leading to decreased lengths at the end of the first year of life therefore have the potential to lead to reduced YCS through overwinter mortality and displacement from elevated flows as small fish are more susceptible to displacement by elevated flows.

High flows at the time of emergence have been seen to cause drastic reductions in fish larvae abundance. To accomplish their physiological activities and ontogenetic development, fish have particular habitat requirements at any given time of their biological cycle; therefore the seasonality of the flow event is of capital importance (Poff *et al.* 1997; Bunn and Arthington 2002). It is now widely recognised that the impact of hydrological events do not depend solely on their magnitude, but also on their timing relative to the developmental stage affected (Cattanéo 2005). Early 0+ stage fish are particularly sensitive to hydrological variability, owing to the inability to cope with large environmental fluctuations, for example their inability to seek refuge or withstand high current velocities (Cattanéo 2005).

Mathews (1971) estimated that between 98.1 and 99.9% of cyprinids die during the first two to three months of life. These high mortality rates have been ascribed to a number of causes such as inherent genetic traits, starvation, temperature changes, oxygen deprivation and predation (Mathews 1971). River discharge has also been shown to influence recruitment success of riverine fish populations negatively, either directly, through discharge induced mortality, or indirectly through reduced growth rates due to decreased temperature regimes, increased energy expenditure or reduced food availability (Nunn *et al.* 2003). High discharge events during the larval hatch are therefore most likely to reduce survival and account for most of the variability underlying YCS (Mion *et al.* 1998). Mortality associated with hydroclimatic events tend to select against small fish and is a key determinant of mean body size of the population attained by the end of the first summer of life (Good *et al.* 2001). While mortality in the first months of life are important in the formation of YCS, winter mortality also plays an important role in some temperate fish populations, and has been shown to be size dependant, with abundance of fish at age one being negatively related to the severity of winter flows (Hurst and Conover 1998).

The timing over which mortality occurs and over which the strength of a year class is determined, has been described as the 'critical period' in a fish's life (Mills 1982). A number of critical periods were observed in this study from a number of rivers from around England and Wales for roach, dace and chub. Of the roach populations, it was seen that two distinct periods existed where YCS were significantly related to the cumulative flows days occurring at that time, where higher cumulative flow days resulted in lower YCS. The main periods being those around the time of spawning and first emergence of larvae between April and June and the winter period between October and February. Roach in UK waters usually spawn between April and June (Frear and Cowx 2003), although the exact timing of the spawning event is climate driven, most prominently by temperature (Noges and Jävet 2005), and is therefore liable to shifts. Five populations of roach showed significant, inverse relationships between cumulative flow days occurring at the time when roach spawning would normally occur and the subsequent period when the roach larvae become free swimming and the YCS of that population may have been determined. The free swimming stage of roach from the River Great Ouse is around 6 – 8 mm total length, at an age of approximately three days (Mann and Bass 1997). At a temperature of 16°C, the critical water velocity, at which 50% of the fish population are displaced (CV_{50}) was shown to be approximately 7.2 cm s^{-1} (Mann and Bass 1997). Increased flows at this time therefore have the potential to decrease fish populations through displacement, as fish of such a small size have an inability to maintain their position within the river during periods of elevated flow, when suitable low energy habitat is not available. The YCS of roach from the River Ure, for example, were negatively related to the cumulative flows observed during April. During the period where YCS were available for study, the highest values of YCS for R. Ure roach occurred at a time when cumulative flows for those months were low. The lowest YCS were found when cumulative flows for those months were high, and the potential for displacement of young of the year roach was greatest.

Discharge has a negative influence on recruitment success of riverine fish populations, either directly through discharge induced mortality or indirectly through reduced growth at lower temperatures, discharge associated increases in energy expenditure and reduced food availability (Nunn *et al.* 2003). Higher discharge rates ultimately lead to reduced retention times for phytoplankton (Pinder 1997). Low flows, however, lead to an increased retention time for phytoplankton and the resulting zooplankton densities, which increases the fitness of 0+ fish at the end of summer, and has an important bearing on their chances to over-winter successfully (Mann and Mills 1986). Size selective over-winter mortality of many fish species and the effect this has on YCS have been discussed by many authors (Henderson *et al.* 1988; Post and Evans 1989), and attributed to such factors as larger fish having increased energy stores at the onset of winter (Kirjasniemi and Valtonen 1997; Nunn *et al.* 2003) and the ability of the larger fish to maintain position within the lotic channel (Garner 1999). The YCS of roach from the River Chelmer in this study were inversely related to the flow regimes during January. The greatest YCS value for this roach population was observed during years when cumulative flow days during January were lowest. Conversely the lowest YCS occurred when the cumulative flow days were at their highest. These results partly reflect those of Nunn *et al.* (2003) who described 'Critical Periods' as being difficult to discern, possibly due to interannual variations in river discharge relative to the timing of fish hatching, but did state that the YCS of roach from the Yorkshire Ouse showed the strongest relationship with the discharge rate during the period June to September.

Two distinct periods were observed as being negatively related to YCS in dace populations from rivers throughout England and Wales. The period between March and June was shown to be significantly related to the dace populations of eight of the studied rivers, while the period of September through to December, was seen as being significant in 13 rivers, with four of these rivers shown to have significant relationships with both of these periods. The period of time over which the first 'critical period' occurs, may be further split into the period when the loss of eggs may be the most important, and the period when the loss of larvae is most important. Mann (1981) demonstrated a four fold increase in the drift of dace eggs in the River Frome during late March and early April, when the flow increased from 1.0 to 2.3 cm^3s^{-1}. Flows during March were seen to be negatively related to the YCS of the dace populations of the rivers Blackwater and Tone, and it is at this time when it is presumed that the eggs of dace, despite their adhesive quality, may be more susceptible to displacement from elevated flows, reducing the potential number of fish available to contribute to YCS. This analysis also revealed discharge rate does not significantly or consistently determine the YCS of the fish populations in all rivers. It may be that other factors play a more important role in defining YCS of fish populations or that suitable refugium are available to those populations during high flow events enabling those populations to survive such events and contribute to their YCS.

Newly hatched cyprinids are poor swimmers, owing to their small size and lack of fully formed fins (Mann and Bass 1997) and their ability to hold station is negatively related to water velocity (Nunn *et al.* 2003). The current velocity at which 50% of the population is displaced (CV_{50}) for newly hatched dace of 8.8 mm at a temperature of 15^0 C is 5.7 cm s^{-1} (Mann and Bass 1997). Episodic increases in river discharge can therefore significantly influence YCS, density and species richness at this time by removing a proportion of the inhabiting populations via displacement. Small increases in river discharge in early summer can have severe consequences to 0+ fish mortality, as apposed to late summer increases in discharge, as fast growth during development results in a rapid decline in the susceptibility to displacement with increasing size (Nunn *et al.* 2003). Possible evidence of early post-hatch mortality was observed in this study with significant relationships between YCS of dace from the rivers Chelmer, Waveney and the Warwickshire Avon being negatively related to cumulative flow days during May and the rivers Aire and Blythe dace YCS negatively related to the cumulative flow days during June. In the River Blythe dace, an inverse relationship between YCS and cumulative flow days was found and resulted in an above average year class in 2001 when the cumulative flow rate during June of that year was very low. The YCS estimate during 2000 however, was recorded as being well below average when cumulative flows during June of that year were very high. These results indicate lower flow rates result in higher survival rates for small dace in the River Blythe at a time when they were susceptible to displacement from increased flow regimes.

Overwinter mortality of dace and the subsequent effect this has on YCS has been demonstrated in this study. High winter flows, however, may also be of benefit, as it is likely that most loose material is removed during winter floods, and as such makes suitable gravel available for dace spawning, as the presence of silt in the spawning area is detrimental to the survival of dace eggs (Mills 1981). Evidence for this may be present in the River Trent dace example. The high flow regime during December 1998 may have been detrimental to the 1998 year class, but the subsequent 1999 year class was shown to be slightly above average (YCS = 105). This above average year class was recorded despite very high cumulative flows during March and April 1999, suggesting that despite a possible high mortality rate during March and April 1999 a stronger than average year class was still evident.

The late summer months were found to be significantly related to the YCS of chub from a number of rivers. Cumulative flows during July were found to be inversely related to the YCS of chub in the River Brue and Warwickshire Avon, while September cumulative flows were inversely related to the YCS of rivers Anker and Waveney chub. A number of authors have demonstrated chub as showing a fractional or protracted spawning strategy (Nunn *et al.* 2002; Fredrich *et al.* 2003). Species that adopt a fractional or protracted spawning strategy are therefore more likely to have a greater size range of young at the end of the first growing season, as fish from later spawnings would have less time for growth before water temperatures decline (Nunn *et al.* 2002) and somatic growth slows or ceases. High flow events during the late summer period may therefore be detrimental to the survival of these later spawnings as data from the River Waveney suggests. YCS for chub during 2001 was 22, when 33.6 cumulative discharge days were recorded during September of that year. During 1992, however, when 2.5 cumulative discharge days were recorded during September, YCS was 191. It may therefore be that the progeny from these later spawning events, when able to survive through their first winter, contribute significantly to the chub populations of these rivers, and when high flows and reduced temperatures occur during their early life, removing at least a proportion of them from the system, poor YCS are the result. In many cases however, no relationships were found between YCS of roach, dace and chub and cumulative flows. In these cases it may be that factors other than discharge rate, such as habitat quality and availability of refugium, food availability and quality and predation pressure all have a greater affect on the YCS of these fish, however as these influences were not investigated they could only be speculated upon.

5.4.2 – The influence of Gulf Stream latitude on YCS and mean length at age 1

The British Isles, lying in the mid-latitudes, lie in a path of mass air convergence between warm tropical airflow and cold polar airflow (Aire 2000). In general, the British climate is relatively mild for its latitude as it is influenced by the Gulf Stream (Aire 2000). Year to year variations in the latitude of the NWGS have been observed, with northerly displacements accompanied by significant reductions in cyclone numbers in the northernmost regions of the Atlantic in spring, summer and autumn, and although changes around the British Isles were generally small, they consisted of a lower frequency of storms accompanied by significant reductions in atmospheric pressure (Taylor 1996).

Interannual variation of YCS and mean lengths at age 1 of roach, dace and chub were observed in this study from rivers across England and Wales with significant relationships existing between the YCS and the latitudinal position of the NWGS. In addition to this, discharge regimes of a number of rivers were also related to the position of the NWGS and in a number of cases, significant relationships existed between the mean annual position of the North Wall, the cumulative discharge regime of the river and the YCS for one of the inhabiting species.

A significant relationship existed between the cumulative flow days for February in the River Colne and the mean annual position of the Gulf Stream, with North Wall latitudinal position accounting for 17% of the variation observed. Within the same river the YCS of the roach population were significantly related to cumulative flow days in February and the mean annual position of the Gulf Stream. These relationships reveal a distinct, direct relationship between the YCS of roach from the River Colne and the climatic factors that influence their recruitment success. The analysis reveals an increased ability to overwinter successfully with northerly shifts in the Gulf Stream, presumably from improved prevailing weather conditions leading to lower flow regimes and increased temperatures. This would have increased the ability of the fish to utilise the available resources to maximize their growth potential and therefore their ability to overwinter and contribute to their specific year classes. Conversely, southerly shifts in the NWGS were related to increased discharge rates in the River Colne and a reduced recruitment success, presumably from a decreased ability of the roach to overwinter, due to increased river discharges during February.

Positive relationships between the growth of the study species and the mean annual position if the NWGS were not exclusive to this study as a number of inverse relationships were observed in the dace populations studied. For example, dace from the R. Colne, Essex were observed as showing a decrease in the mean length at age 1 with northerly shifts in the NWGS. Within the same river northerly shifts in the North Wall were positively related to the YCS of not only dace, but also roach and chub. Increased numbers of fish persisting through the first year of life would lead to an increased level of competition for available resources during that first year. Increased competition may therefore be the major factor leading to a decreased mean length at the end of the first year of life. Like most small fish species, dace often reside in large, often dense shoals and, when present in large numbers can significantly reduce the resources available, not only to themselves, but also to other co-habiting species (Kennedy and McCarthy 1965; Cowx 1988). In a number of cases, however, the inverse relationship between mean length at age 1 was not accompanied by an increased YCS associated with Gulf Stream position. In these cases in may be that a northerly shift in the North Wall, which reduces the flow rate and increases air and therefore water temperatures, shifted the prevailing conditions away from those preferred by dace. Cowx (1988) described dace as having a preference toward faster flowing, cooler, well oxygenated waters, as was also demonstrated in this study (Chapter 4).

Positive relationships were observed for the lag phase mean position of the NWGS and YCS estimates of roach, dace and chub. The association of a lag phase between the positions of the NWGS was observed by Frear and Cowx (2003) who described an association between a lag phase for North Wall latitude and strong year classes in the rivers Colne and Blackwater. From this study, five chub populations, 12 roach populations and six dace populations were found to show similar trends. The effect this lag phase has upon the populations in question may be due to the condition factors associated with the adult populations which in turn leads to an increased fecundity (Cowx 1990). The years in which northerly shifts were observed in the North Wall's latitudinal position provides the adult population with conditions that are conducive to an increased condition factor through reduced flow conditions and warmer water temperatures. Low flows and increased temperature conditions increase metabolic rates in fish (Giller and Malmqvist 1998), while increased phytoplankton retention times inevitably increase the food base (Lieberman *et al.* 2001). Increased condition factors sequentially lead to increased energy available for the production of gametes and therefore a higher fecundity. A high fecundity, of high quality eggs, may lead to an increased number of larvae after the next spawning event, therefore producing better than average YCS as larger numbers of larvae, if factors like increased competition do not impact the population in any significant way, would be available to contribute to the YCS of the population in question. Although as the method of capture used in this study was non-destructive and all fish were returned to their respective water courses, no fecundity or egg quality condition measures were available so this theory cannot be substantiated.

Relationships between the YCS of the populations in question were not restricted to either the latitudinal position of the NWGS or to the lag phase position of the NWGS, as relationships with both in specific rivers were observed. Roach populations from the rivers Wantsum, Thurne, Nene and Colne (Herts) and the chub population from the Bristol Avon were seen to have significant relationships between the mean annual position and the lag phase mean annual position of the NWGS. This study demonstrates northerly shifts in the mean annular position of the NWGS have the potential to have a two fold effect upon a fishery. Providing young of the year fish have conditions which are conducive to good growth, enables them to attain a length at which displacement through high winter flows is less likely. In addition, northerly shifts in the Gulf Steam provides conditions for the adult stock of the river, which enables them to maximize their potential fecundity measures leading to a potentially increased number of larvae in the following year, increasing the potential of that cohort to produce a strong year class, which ultimately enriches the fish populations in question.

CHAPTER SIX

GENERAL DISCUSSION

6.1 Introduction

Scales from more than 76,000 fish from 13 species and over 250 surveys were used to determine age and growth in this study. Scales were used as the method to determine age, as opposed to any of the other calcified structures, as the fish populations used for study were from rivers where recreational catch and release angling takes place, and thus a non destructive sampling technique is paramount (Britton 2007). The determination of age and growth of fish from hard structures in temperate waters is a classical procedure used in fisheries science (Musk *et al.* 2006), for many years. Validation of the use of scales to determine age in fish began in the late 1800s (Jackson 2007) and has been achieved and reviewed by many authors (Cragg-Hine and Jones, 1969, Klumb *et al* 1999a and b; Panfili and Tomás, 2001) because a reliable and easily applicable technique was needed to age fish to aid effective management of natural populations (Hirethota and Schindelholz 2006). Due to the extensive nature of the validation studies outlined above in identifying appropriate marks within the calcified structures studied, the assumption was made that growth checks observed on the fish scales used in this study was due to a seasonal interruption in growth only occurred on an annual basis and it was felt that validation of the technique, in the case of this study, was not warranted. Fish ageing is important as it increases understanding of life history traits and population growth parameters such as growth rate, age at maturity, mortality rates and year class strengths (Gledhill 2007). However, to gain length at age data it is important to identify an appropriate structure from which growth data can be extracted and then determine the best method of estimation (Chapter 2).

Growth rate often provides a useful index of performance in freshwater fish (Elliott and Hurley 2003). Evaluation of population growth data is an important aspect of stock assessment and comparative tools enhance their evaluation (Britton 2007). Standard growth indices have been used to assess growth performance of fish populations; but the first standard growth curves in the UK were based on low numbers of populations from rivers (Hickley and Dexter 1979; Hickley and Sutton

1984) and the ensuing years have seen physical, chemical and biological changes within these rivers (Environment Agency 2001, 2005a, 2005b, 2007). Changes in species composition and or growth rates of inhabiting fish species have occurred as a direct result of water quality improvements, habitat improvements through rehabilitation programmes and thus standard growth curves need to be updated on a periodic basis (Chapter 3).

Comparison of growth characteristics of one or a number of species at a small (catchment) of large (national) scale has been attempted by a number of authors (Cowx 1988, 1989; Przbylski 1995; Nunn 2003; Pont *et al.* 2005), but the evaluation of growth performance across a wide number of rivers throughout England and Wales has not previously been achieved. Longitudinal changes in the growth of a number of species in a number of river courses was observed and was similar to the results of Cowx (1988) and Przbylski (1995) and the influence of latitude was similar the findings of Lobón-Cerviá *et al.* (1996) (Chapter 4). The mean annual position of the North Wall of the Gulf Stream has been shown to influence plankton species composition in the coastal areas around the UK (George and Taylor 1995), the growth patterns of vegetation in Britain (Willis *et al.* 1995) as well as populations of fish species in rivers from around England and Wales (Frear and Cowx. 2003; Britton *et al.* 2004; Nunn *et al.* 2007b). In this study the Gulf Stream was found to influence both year class strengths of fish in a number of rivers and the lengths attained at the end of the first year of life (Chapter 5). Northerly shifts in the North Wall of the Gulf Stream provide conditions conducive to faster growth of young of the year fish, which possibly increases the ability of young of the year fish to overwinter resulting in increased survival and strong year classes (Chapter 5).

6.2 – Efficacy of back-calculation methods in gaining length at age estimates

It is generally accepted that the growth of calcified structures in fish, such as scales, vertebrae and fin spines, are related to the growth of the whole fish, with seasonal changes in growth in temperate regions producing growth checks or annuli (Ottaway and Simkiss 1977). The ageing of fish is based principally on the interpretation of features on the calcified structures (Bagenal and Tesch 1978), but is prone to error due to the subjective nature of the interpretation of the features on the scales (Mann and Steinmetz 1985, Britton *et al.* 2004). The technique of ageing fish also suffers from the misinterpretation of checks that form on the calcified structure due to a temporary cessation in the growth pattern, giving rise to false checks (Ottaway and Simkiss 1977). Interpretation is also made difficult when annuli overlay each other at the scale margin, a common feature in the scales of older fish (Musk *et al.* 2006), especially bream and chub (*pers. obs.*), although through experience and a stringent quality control procedure any possible misinterpretation was minimised.

To extract length at age data from the measurement of checks on hard structures, a number of back-calculation methods can be used. Back-calculation of fish length has been widely used to increase the number of observations in length-at-age data or to estimate lengths at age, and is based on the assumption that somatic growth in fish is proportional to the growth of its bony structures (Horpilla and Nyberg 1999); the question is how precise is the information and which method best extracts it? (Francis 1990). Back-calculated fish lengths, determined from a number of methods and compared with a known observed mean length at age, identified the Hile method to be the most consistent for providing accurate length at age data from fisheries surveys. Other methods chosen for the determination of the efficacy of back-calculation methods showed a similar degree of accuracy on occasions but lacked precision, as mean length at age estimates were, on occasion, close to the observed, but the Hile method produced the closest length at age estimate the most. A number of tests gave a length correction factor, used in the back-calculation of length at age data, that were too large or negative, and therefore unreasonable as a correction factor. This was found, especially for bream, mainly due to a lack of certain size groups within the data, i.e. when sufficient numbers of larger fish were caught there was a lack of the smaller size classes, and a variance in the size of scale taken from those larger fish produced trend lines that did not compute an accurate intercept with the length axis. A larger, more represent able sample, encompassing a large proportion of the length classes would be needed before back-calculation of this species be performed.

6.3 – Growth standards

Standard growth curves for roach, dace, chub and bream were first developed in the late 1970s (Hickley and Dexter 1979) although due to data availability, were calculated from a small number of populations. Many changes have occurred in rivers over the ensuing years, which have been reflected in changes in the growth characteristics of roach, dace, chub, pike and bream (Chapter 3). The original standard growth curves were considered, by this author, to no longer represent the standard growth characteristics of fish populations today. Standard growth curves were developed in this study for comparison with the original growth standards and those produced by Britton (2007). Standard growth curves produced in this study were similar to those of Britton (2007) for most of the species tested, but significant differences were found when compared with the original standards. Many studies have shown changes in water quality, habitat (Environment Agency 2001, 2005a, 2005b, 2007) and the growth characteristics of fish in rivers throughout England and Wales (Britton 2007). Changes in the growth characteristics such as the initial slowing of the growth rate observed in roach and dace are more likely caused by increased competition from previously suppressed species like chub (Cowx and Broughton 1986), which tended to exhibit an initial increase in growth rate.

6.4 – Comparison of growth characteristics

Roach, dace and chub within the Colne, Blackwater and Yorkshire Ouse catchments exhibited growth characteristics that changed in a longitudinal direction along the course of each river. The morphology and hydrology of rivers change from upstream reaches that are generally characterised by fast flowing, cool waters, to slower flowing, warmer waters that typify the lower reaches. Each species had preferences toward different physical environmental characteristics resulting in faster growth rates, which slowed as the physical environmental character of the river departed the optimum. Roach preferred the lower reaches of each catchment, defined by reduced river bed gradients, wider wetted widths and larger catchment areas above the site at a greater distance from source, where warmer, slower flowing, nutrient rich waters occur (Pont *et al.* 2005). Conversely, dace and chub prefer areas with greater river bed gradients at higher altitudes with smaller catchment areas above each site, suggesting these species prefer faster flowing water with cooler temperatures in areas where nutrient loading is less (Arlinghaus and Wolter 2003; Blank *et al.* 2007).

Geographic position was found to have a strong relationship with the growth of the study species, in a similar vein to the longitudinal growth patterns in rivers. Roach displayed faster growth in the lower latitudes and dace the higher latitudes of the study area while chub preferred the higher latitudes and the easterly longitudes. A mean air temperature difference of 2°C was observed between the northerly and southerly latitudes showing small differences in temperature, in conjunction with other physical or biological factors such as flow of food availability, were enough to influence the growth of roach, dace and chub. Increased flow conditions have an affect on the metabolic processes of fish (Wooton 1990), whereby increases in flow increase the metabolic demand thus leaving less energy for somatic growth.

6.5 – The role of environmental and climatic parameters in the determination of year class strength

The timing over which mortality occurs and over which the strength of a year class is determined, has been described as the 'critical period' in life of fish (Mills 1982). Distinct critical periods were identified for YCS of roach, dace and chub in this study, when flow rates were influential in the formation of YCS, namely the time around spawning and first emergence of larvae and the winter period for roach, dace and chub and the late summer period for chub. Newly hatched cyprinids are weak swimmers (Mann and Bass 1997) and flows greater than critical water velocities (CV_{50}) at the time of emergence reduce YCS through displacement, when sufficient low energy habitat is not available. The late summer period, critical in the formation of YCS in chub, may be due to the fractional spawning strategy demonstrated in chub by Nunn *et al.* (2002). Chub from later spawnings would be smaller than those from earlier spawnings as they have had less time for growth (Nunn *et al.* 2002). Favourable flow regimes during the late summer period may provide the progeny from these later spawning events, when able to survive through their first winter, the possibility to contribute significantly to the YCS of chub.

Mean annual position of the North Wall of the Gulf Stream was found to affect the YCS of roach, dace and chub in many rivers throughout England and Wales. Northerly shifts in the North Wall results in increased atmospheric temperature regimes from increased sunshine hours and decreased rainfall (Willis *et al.* 1995).

Northerly shifts were related to decreased flow regimes and increased water temperature regimes, which, in turn lead to greater mean lengths at the end of the first year of life for roach, dace and chub, increasing the ability of the fish to overwinter and increase YCS. Indirect affects of the North Wall of the Gulf Stream, were manifested in a lag phase between the mean annual position of the North Wall of the Gulf Stream and the YCS of roach, dace and chub. It was postulated that favourable atmospheric conditions associated with northerly shifts in the North Wall would increase the condition factor of the adult stock, leading to an increased fecundity and/or better quality eggs. The increase in the number or quality of gametes produced may then contribute to the observed increases in YCS, however as no fecundity or gamete quality assessment was available this could not be substantiated.

6.6 - CONCLUSIONS AND RECOMMENDATIONS

Efficacy of back-calculation methods in producing mean length at age data from routine fisheries surveys

The correction factor used in the determination of length at age data represents the length at which the first scales are laid down on the fish. The derivation of the correction factor used in the back-calculation of length at age data varied over a wide length range. **It is recommended that an estimation of fish length at scale squamation, for as many species as possible, be made through the microscopic examination of stained samples of juvenile fish collected on a daily basis be made. Collection of juvenile fish using micro-mesh hand or seine nets, immediately after hatching from a number of rivers and/or laboratory reared fish would provide an appropriate length for use as a correction factor.** Accurate ageing of fish is of paramount importance to fisheries evaluation as it forms the basis for a wide range of techniques that are applicable to fish resource assessment and management and therefore all steps should be taken to increase the accuracy of back-calculated length at age data. Determination of the length at scale squamation from a number of habitats may even allow for the production of a standard correction factor for each species, if the range of fish lengths at scale squamation is sufficiently small to allow such an estimate.

Fractional spawning has been identified in a number of species inhabiting the rivers of England and Wales (Nunn 2005; Bolland *et al.* 2007). Species such as chub were found to persist through the first year of life at a length where the squamation of scales has not yet begun or is at stage where the first annuli could easily be missed (Nunn 2005). **It is recommended that 0+ fish species identified as having a protracted or fractional spawning strategy be analysed to assess the impact of over-wintering of fish at or below the length of scale squamation and the impact this has on the reliability of ageing fish from scales.** Comparison of data gained from scale reading against that gained from otoliths from the same fish could then be used to identify any error from scale reading to be calculated. Improving the accuracy of scale reading would ultimately reduce any miscalculation of age and avoid incorrect assessment of such techniques as year class strength estimations and mortality assessments on which management decisions are made.

Standard growth

Standard growth curves for roach, dace, chub and pike produced in this study were similar to those of Britton (2007), but significantly different to those produced by Hickley and Dexter (1979) and Hickley and Sutton (1984) and attributed to a number of possible causal factors. **It is therefore recommended that standard growth curves produced in this study are used as an appropriate comparative data set at present. It is also recommended that the standard growth curves are recalculated every ten years, this period of time would allow for any changes in the physical, chemical or biological structure of any habitat or population that may have an effect upon the growth rate of any inhabiting fish to manifest and be identifiable.** The periodic recalculation of standard growth curves would then enable comparison of length at age data to an appropriate set of length at age data, which reflects the growth of those species at the time of capture.

Comparison of standard growth rates of roach, dace, chub and pike from this study, and Britton (2007), with the standard growth rates produced by Hickley and Dexter (1979) and Hickley and Sutton (1984) showed significant differences. The change in growth characteristics must be as a result of physical, chemical and/or biological changes within the respective systems. **It is recommended that further investigations are made into the causal factors that have changed the growth characteristics of the fish populations in question.** Factors such as water quality improvements and changes in trophic status, resulting in the expansion of previously suppressed species (Cowx and Broughton 1986), habitat rehabilitation (Environment Agency 2001, 2005a, 2005b, 2007) and alien species introductions (Korsu 2008) have been linked to changes in fish growth rate. An evaluation of any historic changes in fish lengths at age or species composition in combination with changes in concentrations of nitrogen and phosphorus or trophic status that have occurred in rivers throughout England over the ensuing years would provide evidence into the causal factors behind any changes in the growth characteristics of the fish populations identified in this study. An evaluation of the responses of the fish species may then be used as a reference when changes to the environment are planned or detected in the future.

To further the use of standard growth curves, an adaptation of the methods used in this study to include only sites from specific catchments could be made for individual catchments. **It is therefore recommended that standard growth curves are produced per catchment using as much data as is possible, for as many species that are available, to produce robust catchment level standards.** The use of standard growth curves produced for a specific catchment may highlight changes in the growth characteristics of any particular species at any particular site faster than when using national standards as the variance in the length classes identified as showing slow or fast growth would be smaller and more specific to that catchment allowing for any causal factors to be highlighted.

The use of national growth standards is only of limited use and provides a standardised baseline dataset for making comparisons to that national standard but makes no predictions as to the expected growth rates of a fish species from differing environments at differing latitudes or altitudes, or when prevailing weather conditions differ due to such factors that influence the prevailing climate like position of the Gulf Stream. **It is therefore recommended that predictive growth models be made that encompass environmental differences associated with altitude and latitude which then adapts the growth outputs according to such influences as Gulf wall**

position. Determining growth parameters of fish from as many sites as possible from over as wide an area as possible would be needed along with prevailing weather conditions, water temperature (although altitude may be used as a surrogate for water temp.) and discharge rate, from those sites on an annual basis along with the altitude and latitude. An annual growth increment, possibly for each age class of each species, could then be used to construct a model showing the growth characteristics over that area at that time considering latitude and altitude. If done over a number of consecutive years the inclusion of Gulf Stream position could be included and correlated to the growth characteristics via an analysis of growth increment change and prevailing weather conditions, after the correlation of Gulf Stream position and prevailing weather patterns has been determined. This would enable researchers to predict the growth of a species in the future

Growth variation of roach, dace and chub – catchment and nationwide

Growth characteristics of dace showed strong relationships with the physical environmental variables used in this study at the catchment level; roach and chub however, were found to have weaker relations. This suggests variables other than those used, have a stronger influence upon the growth characteristics of roach and chub at the catchment level. **It is recommended that an expansion of the variables used to determine the drivers behind the growth of roach and chub is made.** The inclusion of accurate water temperature and flow measures and the expansion of the data to include such information as trophic status, concentrations of pollutants, a dietary analysis and densities of each species would increase the understanding of the growth of roach and chub in these rivers. The inclusion of water quality would allow for an assessment of anthropogenic impacts and any influences this has on primary productivity and subsequent influences this has on food quality and quantity, while density measures and a dietary analysis would allow for an assessment of inter and intra specific competition on the growth characteristics of roach and chub.

Comparison of growth characteristics of roach and chub against the physical environmental variables at the national level were found to be weak, although were stronger for dace. **It is recommended that an expansion of the study area used in the determination of growth patterns of roach, dace and chub be achieved.** The area used for this study constitutes a small fraction of the global distribution of roach, dace and chub and the variation in growth characteristics within the small area used were such that discrete variation in the growth characteristics of these species with geographic position were not entirely gained. Roach, dace and chub are distributed across the whole of Europe from England and France in the west to the Urals in the east and south into northern Asia (Jiří Čihař 1999). Examination of the growth characteristics of roach, dace and chub across their entire distribution may allow for variations observed over larger areas to reduce the impact of variance in the growth characteristics over smaller areas.

The Water Framework Directive is a piece of legislation produced by the European Commission to provide a major driver for achieving sustainable management of water in the UK and a number of other member states. It requires that all inland and coastal waters within defined river basin districts must reach at least good ecological status by 2015 and defines how this should be achieved through the establishment of environmental objectives and ecological targets for surface waters. The improvement in ecological status through such actions as habitat and water quality improvement may influence the growth of the inhabiting fish populations. Increases in biodiversity may increase competition from sympatric species, which has the potential to change the growth characteristics of the inhabiting species. **It is recommended that growth characteristics of fish populations in all improved rivers are monitored to identify change.** Identification of changes would allow factors that influence the growth characteristics of the inhabiting fish populations to be identified and how each species has adapted to change. If biodiversity increases, there is a possibility it could manifest in a reduction of the growth rate of the fish that already inhabit that area, if the species moving in inhabit the same niche. If an alteration of the growth rate occurs, there may also be the possibility that life history traits other than the growth rate may also be affected, such as length or age at maturity. Changes in the growth characteristics over time would also make the growth standards inaccurate as a comparative data set, therefore increasing the need for updated growth standards when such comparative data are needed.

Growth characteristics identified in this study represent just a small portion of the species found in rivers throughout England, and, with the exception of growth, did not include any information regarding other life history traits. **It is recommended that the growth characteristics studied are expended to include such life history traits as size or age at maturity and fecundity, encompassing a larger number of species, including those used in this study, be made especially for species where little is known of their growth.** From an ecological view point, Cowx (2001) identified that little information has been documented on the growth of ruffe, *Gymnocephalus cernuus* (L.) especially from rivers. Data acquisition for ruffe and other important angling species such as barbel, salmon, perch and pike or more environmentally sensitive species such as grayling, was however low from fisheries surveys. Identification of sites where these species are known to inhabit would allow for an increased effort to be made in order to gain sufficient data to determine the growth characteristics and determine life history traits. Determination of the growth and life history traits would allow a wider perspective into how the environment within which these species are found affects them, which could be utilised in future studies to help identify possible impacts, if for example, habitat improvements are planned.

This study identified the physical environmental characteristics that influence the growth characteristics of roach, dace and chub at the catchment and national levels. To increase the knowledge of the plastic and dynamic nature of growth between fish species, an analysis of the interactions between sympatric species through a range of habitats from the same or different rivers would benefit. **It is recommended that a comparative analysis of the growth characteristics between sympatric species and the affect one species has on growth characteristics of another is made.** Comparative analyses of an index of growth, such as percentage standard growth, of sympatric species through a range of habitats could be used to identify competitive influences one species has on another. Through the identification of specific habitat types, densities and the feeding interactions of those species within each habitat a number of questions can be posed, namely does the presence of one species affect the growth characteristics of another species in one habitat in a similar way as the same species in different habitats or in different rivers and how do the growth characteristics change when one of those species is missing and what is the effect on the growth characteristics when the dominance of the species is reversed?

Influence of climate on growth and year class strength

The influence of northerly shifts in the mean annual position of the Gulf Stream was not shown to have a positive relationship with the growth of all species, as dace in a number of rivers were shown to have smaller mean lengths at the end of the first year when northerly shifts in the North Wall occurred. **It is recommended that further investigations into the climatic factors controlling mean length at the end of the first year and the subsequent effect this has on year class strength, especially in dace, be conducted.** Northerly shifts in the Gulf Stream's North Wall have been shown to create a milder climate (George 2000); investigations should therefore determine any trends in length at age 1 of dace, in conjunction with density estimates, food availability and the affect North Wall position has on prevailing weather conditions to elucidate whether reduced lengths at the end of the first year is due to increased competition for available resources or whether the prevailing conditions depart the preferred, as dace prefer cooler, faster flowing, well-oxygenated waters.

Recent studies have focused on a number of aspects relating to climate change (Hulme 2005) and the potential impact on fisheries (Ficke *et al.* 2007). One aspect shows Atlantic meridional overturning circulation and in particular the cold water flowing from the Arctic has slowed by around 30% since 1992, although at present, heat transport in the Gulf Stream has remained almost constant (Bryden *et al.* 2005). Models have predicted a possibility that, although unlikely, a reduction in the heat transfer within the Gulf Stream is possible, which would result in reduced atmospheric temperatures across Northern Europe. This study has shown mean annual position of the Gulf Stream to be significantly related to the year class strengths of roach, dace and chub populations from a number of rivers throughout England and Wales. **It is recommended that investigations into the influence of the Gulf Stream on the year class strengths of fish populations from England and Wales be continued.** Any reduction in the heat flow from the Gulf Stream would cause a reduced atmospheric temperature regime which, in turn, could influence the year class strengths of fish in rivers throughout England and Wales through reduced growing seasons and therefore smaller mean lengths at the end of the first year, which could reduce the ability of the fish to overwinter.

A lag phase in the mean annual position in the North Wall of the Gulf Stream has been demonstrated to have a positive effect on the year class strengths of roach, dace and chub. **It is recommended that further investigations into the mechanisms that determine year class strengths of those populations thought to be influenced by a lag phase in Gulf Stream position be carried out.** Specifically, as northerly shifts in the mean annual position of the North Wall creates a milder climate over Northern Europe creating conditions conducive to the growth of the adult stock. Increased energy available for growth leads to increased condition factors and ultimately increases in fecundity and/or the production of higher quality gametes for the following spawning event. A clearer perspective of the mechanisms underlying increases in year class strength one year after the favourable climatic event could therefore be made through determining the fecundity and/or quality of gametes produced by the adult stock through identification of spawning sites and collection of spawned eggs.

Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level. Global surface temperature increased 0.74 ± 0.18 °C between the start and the end of the 20th century. Climate model projections reports indicate that the global surface temperature is likely to rise a further 1.1 to 6.4 °C during the 21st century, with concurrent rises in the temperature regimes of freshwater bodies. An increase in global temperature will cause a change the pattern of precipitation, changes in the frequency and intensity of extreme weather events, and changes in agricultual yields and therefore possible changes in agricultural practices and impacts to nutrient loads in freshwater bodies. **It is reconmended that fisheries monitoring is continued, in conjunction with assessing climate change and the impacts of any future climate change to the fish populaqtions in rivers nationally, if not globally, be assessed to determine the extent, if any, of changes in growth rate, species composition and recriutment success.** Through the monitoring of prevailing climate in conjunction with the results of historic assessments of climate, future trends can be identified. These trends can then be used to assess any changes that have occurred in the same time frame, where possible, through the assessment of growth rate and YCS and with the results of future fisheries monitoring, an assessment of any changes in growth rate or species composition can be made. Assessments could also be made as to which species would be impacted most, for instance, grayling are considered to be a species that have specific habitat requirements and are not generally found in areas where conditions differ greatly from their habitat requirements. Current fisheries monitoring conducted around England do not specifically target this species and as such little is known about their current status, in relation to other species, adaptation or an expansion of current fisheries monitoring practices could be made to specifically target this, or other species, to determine the effects, if any, of climate change.

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Apendix 1 - List of rivers and species used to determine growth standards

	roach	dace	chub	brown trout	pike	perch	bleak	gudgeon
20ft Drain	*							
Abbey Fields	*							
Barton Broad	*					*		
Bollin drought				*				
Bourne EAU	*							
Bradshaw brook				*				
Bristol Frome	*	*	*			*		
Cam Lodes	*							
Chelmer and Blackwater Canal	*	*						
Coley Brook	*							
Cut-Off Channel	*							
Darent and Cray	*	*	*	*	*	*		*
Ehterow Drought				*				
Fossdyke Navigation	*							
Frome Chew and Parrett	*	*						
Gt Ouse	*	*	*			*		
Harper Brook	*	*	*					
Hobhole Drain	*							
Hurst Brook				*				
Kings Barn Farm		*						
Lodden Catchment	*	*	*	*				
Mid Avon	*	*	*					
Mid Bristol Avon	*	*	*			*	*	*
Mid Medway	*	*	*				*	*
Mor brook				*				
New Forest Life				*				
Old Bedford Delph	*							
Ouse Ely	*						*	*
Peover Eye	*			*		*		
R Cherwell							*	
R. Aden							*	*
R. Aire	*	*	*	*				*
R. Alne	*	*	*					
R. Anker	*	*	*					
R. Arrow	*	*	*					
R. Blackwater	*	*	*			*		
R. Blythe	*	*	*					
R. Brain	*	*	*					
R. Brett	*	*	*					

Apendix 1 - Continued

	roach	dace	chub	brown trout	pike	perch	bleak	gudgeon
R. Brue	*		*		*	*		
R. Bure	*	*	*		*	*		
R. Bure Scarrow Beck				*				
R. Calder	*	*	*	*				
R. Cam	*							
R. Cherwell	*	*	*		*	*		*
R. Chew	*	*	*	*				
R. Colne	*	*	*		*			
R. Colne Herts	*	*	*			*		
R. Dane	*	*	*			*		*
R. Deben	*	*			*			
R. Derwent				*				
R. Dibb				*				
R. Don	*	*	*	*				
R. Douglas	*	*	*					
R. Dove				*				
R. Eden							*	
R. Eden	*		*		*	*		*
R. Erewash	*	*	*					
R. Etherrow			*					
R. Evenlode	*	*	*	*	*	*		*
R. Frome			*	*		*		
R. Gipping	*		*					
R. Hull	*	*	*	*				
R. Ise	*	*	*					
R. Isle		*	*					
R. Kennet	*	*	*		*	*	*	*
R. Lark	*							
R. Leam	*	*	*					
R. Lee	*	*	*					
R. Lodden					*	*		
R. Manifold				*				
R. Medway				*	*			*
R. Meese	*	*						
R. Mole	*	*	*		*	*	*	*
R. Nene	*						*	*
R. Nidd	*	*	*					
R. Noe				*				
R. Onny				*				

Appendix 1 - Continued

	roach	dace	chub	brown trout	pike	perch	bleak	gudgeon
R. Pant	*	*	*	*				
R. Penk	*	*	*					
R. Perry		*	*					
R. Plym				*				
R. Ray					*	*	*	*
R. Ray Wilts	*	*	*					*
R. Reabrook		*	*	*				
R. Rother	*		*	*				*
R. Sett drought				*				
R. Severn	*		*				*	*
R. Sheaf				*				
R. Soar	*	*	*			*		
R. Stour	*	*	*					
R. Swale	*	*	*	*				
R. Tavy				*				
R. Thame	*	*	*		*	*	*	*
R. Thames	*	*			*	*		
R. Thurne	*					*		
R. Tone	*	*	*	*				
R. Trent	*	*	*					
R. Ure	*	*	*	*		*		
R. Wandle	*		*					
R. Wantsum	*							
R. Waveney	*	*	*		*	*		
R. Welland	*	*						
R. Wensum					*	*		
R. Wey	*	*	*		*	*		
R. Wharfe	*	*	*	*				
R. Witham	*							
R. Wreake	*	*	*					
R. Wye millers dale				*				
R. Yare	*					*		
R. Yarrow	*	*	*					
R. Yeo	*		*		*			
R.. Camel				*				
RMC and Marshes	*				*			
Roman River	*	*	*	*				
Sarendon Brook	*	*	*					
Sloop						*		

Appendix 1 - Continued

	roach	dace	chub	brown trout	pike	perch	bleak	gudgeon
Somerset Axe					*			
Somerset Frome	*	*	*	*	*	*		
Stour Lower	*	*					*	*
Stour Middle		*						
Sussex Ouse	*		*		*			
TWARP	*	*	*		*	*	*	*
Tyne tunnel				*				
Upper Avon	*	*	*			*	*	*
Upper Bristol Avon	*	*	*	*				
Wensum Central	*		*					
Wey Catchment	*	*	*	*			*	*
Yorkshire Ouse	*	*	*		*	*		*