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1 Executive Summary and Recommendations

This study was initiated to address the perceived decline in adult trout numbers in Dartmoor streams. In this document we have explored the national importance of Dartmoor brown trout, their habitat and their conservation value. The state of trout stocks in the upper tributaries of the Dart are considered and habitat plus fish numbers reviewed. Through statistical analysis of the data collected in part of this work, correlations between habitat and fish numbers are made. Growth rates of Dartmoor brown trout are evaluated and compared to other rivers and historical data. A tagging study is undertaken to assess the extent of brown trout populations on Dartmoor and further studies initiated to this end. Possible causes for the perceived decrease in the number of adult brown trout in Dartmoor Rivers are identified. Recommendations are made for physical works on the Upper Cherry Brook to improve adult brown trout numbers. Finally, recommendations are made for further refinement of the management of brown trout stocks.

Recommendations:

- Improve degraded adult trout habitat. *e.g.* areas not suitable for juveniles or fry of brown trout or Salmon. There are several pools on the Upper Cherry Brook which are clearly degraded adult trout habitat. We recommend the exclusion of stock from the immediate vicinity of these areas and their exclusion from the river channel above these sections. This would serve to increase most of the factors correlated with the adult brown trout abundance in this study. The mechanism for this and the implications will be decided in discussions with Dartmoor National Park ecologists, which are already planned. Fencing is the obvious solution but more subtle methods may work. *e.g.* Off stream drinking with incentives such as salt licks. Once riparian vegetation has reached a certain level of succession it will form its own barrier.

- Buffer the flows in ditches draining forestry plantations and maybe treat them for acidity using low-tech, flow-responsive methods as outlined in Arnold *et al*. (1988). This may increase energy flux into the ecosystem by increasing primary productivity.

- Add features to runs to improve the visual isolation of juvenile trout and increase the carrying capacity of a section. This can be achieved using carefully placed brush or boulders following the procedures outlined in the Environment Agency guidance manual ‘Restoration of Riverine Trout Habitat’ (Summers *et al*.,1996). The statistical models can be used to assess the amount of instream cover required in a section and tailor works accordingly.

- Promote the catch and release of all breeding aged trout caught on Dartmoor streams. Dartmoor trout are thought to be sexually mature at 3+. In the Upper Cherry brook the mean size of 3+ trout is 19.7cm and range 16 to 22cm. Therefore, trout of approximately 16 cm and above should not be killed.

- Create a protocol for recording angling effort and catch so results are nationally comparable. This may be an increasingly important tool for fisheries management in the future given the possibility of reductions in the Environment Agency's budget for fisheries. This also serves to promote the role of angling in conservation.

- An intensive study of river chemistry (such as that undertaken by Cornwall EA on the Small Brook) to investigate pH fluctuations in Dart Tributaries with and without connections to forestry plantations.

- Further trout tagging in conjunction with the planned genetic study of Dartmoor brown trout to increase our knowledge of the spatial extent and the level of reproductive isolation of trout populations. With this quantified, habitat can be managed over the full range of the population using models such as the one detailed in this study and HABSCORE to stabilize and manage the population. Life tables and other dynamic models can be used to keep yields high and safe guard the population.

- Examine and include further sections of Dartmoor rivers in the models outlined in this study to increase their predictive capabilities and the range of their application.

- Controlling stock access to spawning reaches especially when eggs are green and vulnerable to vibration.

- Further investigate changes in flow on the in the upper East Dart.

2 Introduction

2.1 General Introduction

Concern has been mounting over recent years for the state of stocks of brown trout (*Salmo trutta*) in tributaries of the Upper Dart. Regular anglers perceive a decline in the numbers of large brown trout caught on the Upper Dart. Concerns over the rivers and streams on Dartmoor are also brought to light in the Dartmoor Biodiversity Action Plan. One of the proposed actions in this document is the analysis of the habitat requirements of important riverine species and the instigation of an ongoing monitoring program for important species and their habitats. The document highlights the necessity for this research to be carried out for the Atlantic Salmon and for Otters and also names wild trout, bullheads and watervoles as species deserving attention. The Devon Wild Trout Project (Phase I), commissioned by the Environment Agency and the Wild Trout Society, aimed to assess the populations of trout in several Devon rivers. Brown Trout numbers in the Upper Dart were found to be declining based on the results of the electrofishing data routinely recorded since 1965 by the Environment Agency. The main aim of this study is therefore to look for causes for the decline and suggest strategies for mitigation.

2.2 Dartmoor and The River Dart

Dartmoor is the largest area of moorland in the south of England. It is formed from a granite batholith that rises to 618m above chart datum. The boundary of the Natural Area roughly follows the National Park boundary, designated in 1951. The Natural Area covers over 1000 km^2. Dartmoor is an area of open moorland with high rainfall and acid, nutrient-poor, peaty soil. The main land uses are hill livestock farming (sheep, beef cattle and dairy) tourism and recreation, military training, forestry, china clay extraction, water supply and there are several substantial coniferous forestry plantations. Dartmoor is the largest expanse of unglaciated upland in Great Britain, and the largest granite surface in England.

The Moor is divided into three large SSSIs (Site of Special Scientific Interest) and a fourth, smaller SSSI at Tor Royal Bog (EN,DNPA, 1991). Dartmoor entered the ESA (Environmentally Sensitive Area) scheme in 1994. Land entered into this ESA scheme must comply to prescribed practices of stocking, winter feeding and fertilizer applications. The more rigorous the husbandry the greater the compensation. However, common land constitutes over 90% of the open moorland on Dartmoor and there is difficulty in getting common land into the ESA scheme. Wolton *et al*. (1994) have shown that large areas of the common land are adversely affected by overgrazing and burning.

The River Dart catchment has an area of approximately 475 km^2. The Upper River Dart rises on South East Dartmoor and comprises two major tributaries, the East and West Dart which rise at approximately 550 m above chart datum. Other large tributaries of the Upper Dart are: Swincombe; Blackbrook; Cowsic; Cherrybrook; Walla Brook.

The Upper Dart tributaries flow south and east over the granite batholith of Dartmoor. The East and West Dart converge at Dartmeet (SX672 731). Below Dartmeet the River Webburn joins the main river. In this section the river flows over the shale and sandstone of the Culm Measures. There are no major aquifers within the catchment and most of the water storage in the upper catchment is in wetlands and bogs. Immediately below Dartmeet the river is bordered by mature deciduous broadleaf forest and as the river moves into the lowlands below Buckfastleigh, the riparian land is more intensively farmed and populated. Most of the rivers within the upper catchment conform to the RE1 class of the Rivers Ecosystem Classification (Water of very good quality suitable for all species). Industry in the catchment, apart from agriculture and tourism, is very limited. The mean daily discharge rate of the river as monitored from Austin's Bridge is approximately $11 m^3 s^{-1}$. The Q95 (the flow rate which is exceeded for 95 % of the time) is approximately $1.5 m^3 s^{-1}$.

2.3 Introduction to Brown Trout Evolution and Ecology

Part of the rationale for this study is to broach the perception that brown trout are a near ubiquitous species of resilient and adaptive fish and therefore not of high conservation value. The marching paradigm that perpetuates this attitude is out-dated, and recognized as so in the case of many other species. The need for *in-situ* conservation and management of brown trout wherever they occur is paramount. Invoking the genetic evidence best emphasizes the point. In a review of the literature on the genetic variation and techniques for it's measurement in brown trout, Ferguson (1989) brought to light some important facts. His major conclusions were that there is abundant genetic variation in the European brown trout. The individual populations sampled possessed only a fraction of the overall diversity of the species. He concluded that the brown trout metapopulation (all the polymorphic ecotypes of brown trout from all the various environments where they are found) is subdivided into a large number of reproductively isolated, genetically unique populations within, as well as among catchments. He adds that many genetically unique populations have been lost in the last century and emphasizes the need to conserve the remaining genetic diversity. These populations are an irreplaceable resource for the management of sport and commercial fisheries and of great conservation value. Genetic variability also enhances a species' ability to survive adverse conditions over evolutionary time scales. The degree of variation found in the electrophoretic studies reviewed by Ferguson indicates that the brown trout is one of the most polytypic vertebrates on earth. The ecotypes of the brown trout may represent an incipient stage of specieation as suggested for the guppy and some isolated populations of gobies (Endler, 1986; Miller, 1986; Miller, 1987; Magurran *et al*., 1992).

It is possible that a proportion of the genetic variability of brown trout may be due to genetic drift in reproductively distinct populations and not natural selection (Fergurson, 1989; Harvey & Pagel, 1991). However, there is evidence to show physiological and morphological differences between populations of salmonids (see

Elliot, 1994). Indeed, over 50 species of brown trout were recognized in the last century. Some authors have linked phenotypic differences to genotypic differences in salmonids (Ricker, 1972; Tsuyki & Williscroft, 1973; Ihssen & Tait, 1974; Tallman, 1986; Child, 1984; Furguson & Mason, 1981; Furgason, 1986,1988, 1989; McVeigh & Furguson, 1988; Northcote & Kelso, 1981; Cross, 1988). Notwithstanding this, comparatively few of the many phenotypic differences noted by authors are unequivocally linked to genetic differences and it is clear that more work is required in this area (Taylor, 1991). It is a formidable task to link a genetic variation with a phenotypic trait and explain its ecological significance even in the simplest of structures in a simple organism (Beard *et al*., 1999; Bright & Walsby 1999). As pointed out by Mayr (1975), success is the result of the combined effect of all the measured differences and other unmeasured differences and in the real world each organism in a population has a thousand traits in which it will be superior or inferior to the mean of the population. The probability of its success is dependent on the number of these superior traits.

Brown trout were originally indigenous to Europe but during the last glaciation the northern ice sheets restricted their distribution. As the ice sheets receded, brown trout have recolonised the rivers. Populations on Dartmoor were unaffected by the ice and therefore may have had a long period of isolation for genetic differentiation to occur. The populations may represent ancestral genotypes, which are of great conservation value.

The importance of conserving unique gene-pools is paramount as such gene-pools may provide material for aquaculture and restored habitats that once constrained populations of wild brown trout. This genetic information also has clear implications for stocking policy. Restocking should only be performed with trout reared from the indigenous population with its optimum genotypes for a particular locality. This opinion is reinforced by recent genetic work on brown trout in the Tajo and Duero basins in Spain where, due to the introduction of stock brown trout of non local provenance, native, genetically distinct populations have been lost (Machordom *et al*., 1999). Many authors comment on the competitive stress placed on indigenous populations of brown trout by stocked fish (Hesthagen *et al*., 1995, 1999; Weiss & Schmutz, 1999) and the deleterious effects of stocked brown trout on populations of other resident fish (Dewald & Wilzbach, 1992; McIntosh *et al*., 1994).

Industry on Dartmoor has radically affected the water quality of the rivers draining the area; their upper reaches were streamed for tin as far back as the 14th Century. The practice of tin streaming turned the rivers into open mining waste adits. The period of streaming can be traced using sediment cores from ancient riverbeds. Unnaturally high levels of metal deposits and the skewed distribution of the particle size fraction in the cores mark the periods of intense mining activity. The level of metal pollution and siltation were so intense that one of the first ever pollution abatement laws was passed in the mid fifteen-hundreds. The law was passed to prevent the siltation of harbours at the mouths of the rivers draining Dartmoor. The level of siltation must have been very high to require such extreme steps. It is hard to believe that a visual predator like the brown trout could have survived in the affected rivers. It is likely that over this period, brown trout sought refuge in the smaller moorland tributaries that were unworkable for tin. This would further increase the genetic distinctiveness of separate populations. The surviving fish in the headwaters would, in all likelihood have recolonised the rest of the river. This pattern of recolonisation has been documented in wild brown trout populations in other heavily disturbed rivers (Beaudou *et al*., 1995).

As previously discussed, brown trout are genetically highly variable. The genetic differences can occur over relatively small spatial scales. It is likely that some genetic differences encode subtle phenotypic differences, which have been advanced in the reproductively distinct populations to increase fecundity. However, most reviews of the habitat preferences of brown trout have pooled data from many sources. Thus the documented habitat preferences of brown trout are applicable only to a hypothetical generic brown. In reality, at a local scale, the habitat preferences, growth rate, behaviour and ultimately, the life history of trout can vary between neighboring streams providing the trout are reproductively isolated (Elliot, 1989; Grant & Kramer, 1990; Elliot *et al*., 1992; Elliot, 1994; Heggenes, 1996; Heggenes *et al*., 1999). Trout may freely intermingle as juveniles and adults but may remain reproductively isolated by virtue of their accurate homing to natal tributaries for spawning.

The broad preference range of brown trout detailed in the literature represents the preference range of the whole metapopulation. The preference range of a single sub-population of brown trout is within these limits. The habitat preferences of a population of brown trout is best described as a multidimensional hypervolume

(Hutchinson, 1957). Each dimension is an environmental variable, which could potentially limit the success of the brown trout. To understand and manage a specific population of brown trout, the tolerance range of the fish to changes in the important variables must be measured.

Generally, habitat selection is the manifestation of a trade-off between energy intake and risk, or cost. Trout feed predominately on drifting invertebrates. They employ a sit and wait strategy where they hold station in low currents, conserving energy, and pick drifting food items from nearby, fast flowing water (Le Cren, 1973; Elliot, 1967). This relationship is elegantly described by the optimal foraging theory (*sensu* Hart, 1993). The potential energy intake and costs change over space and time in a river due to physical and chemical heterogeneity in both dimensions (Leopold *et al*., 1964; Hynes, 1970; Vannote *et al*., 1980). A further level of complexity in the habitat preference of brown trout is their aggressive territoriality whilst feeding. To avoid aggression they require visual isolation from one another and from other sympatric species (Kalleberg, 1958). Also the habitat requirements of trout change diurnally, seasonally and ontogenetically.

What follows is a brief description of the preferred summer daytime habitat of different age groups of brown trout. The values presented are taken from several studies on brown trout from different streams. One must remember that a population of trout from a particular river may be optimally adapted to live somewhere within these limits. Although able to survive in the full breadth of conditions described, living outside their evolved optimum entails a cost.

2.3.1 Fry.

Trout fry are comparatively weak swimmers and prefer to hold station in slow water (0-20 cm s^{-1}). After emerging from eggs they stay within the gravel until their yolk store is depleted. They swim up to the surface during the early morning and drift and swim with the current until they settle in areas with shallow, slow-flowing pockets in the stream-bed where they can shelter and feed on drifting invertebrates. However, fast water brings more food so these pockets must be in close proximity to the faster currents in shallower waters (current velocity increases exponentially with distance from the streambed due to diminishing frictional forces). Suitable areas are generally in quite shallow water; this also lowers the risk of trout fry being eaten by larger fish, which live in the deeper water. Fry also require cover habitats in which to hide from danger. These, by preference, should be near the feeding stations. Cover can be gaps between boulders and cobbles in the main stream, gaps in undercut banks or shelter under overhanging vegetation. Generally, suitable habitat for fry is found in small shallow streams (<30 cm deep) and occasionally in the shallow margins of larger streams.

2.3.2 Juveniles

Juvenile trout are stronger swimmers than fry and prefer water with a current velocity of 0-40 cm s^{-1}. They can hold station in faster water but are still comparatively weak swimmers. Again, they feed on drifting invertebrates and therefore need to be close to fast flowing water. Their body is larger and longer and they are therefore able to take prey items in the feeding current whilst waiting in positions, comparatively further away from the feeding current, which results in lower energetic costs without decreasing food intake. The manifest result of this is that they tend to hold station further off the streambed in deeper (<50 cm) faster water compared to fry. Trout, as mentioned, are aggressively territorial whilst feeding. They will show aggression towards any other fish within their field of view. As juveniles hold station further off the streambed whilst feeding they can see further than fry and have proportionately bigger territories. Visual isolation is therefore a strong determinant of juvenile carrying capacity in otherwise suitable habitat. Juveniles, being larger, also need larger cover structures compared to fry. They will seek refuge in undercut banks and in bank-bound tree roots by preference.

2.3.3 Adults

Adult trout are faster swimmers again but still slow compared to other salmonids (10-80 cm s^{-1}). Again they feed on drifting invertebrates in nearby, fast flowing water. They occupy deeper water than fry and juvenile trout (30-100 cm). Cover is also very important for adult trout but they will feed further away from cover than fry or juveniles. Cover structures need to be larger to suit their larger bodies. Adult trout will also lie in deep water far from cover structures but where cover is maintained through depth and cryptic skin coloring; most trout darken with age becoming increasingly cryptical in the surroundings of their preferred habitat. They also have been found to feed frequently at night further enhancing their concealment. There is no good correlation with streambed substrate in their preferred habitat. This variable seems to be secondary in importance. The territory of adult fish is larger again, than juveniles. Adults are generally found in larger deeper streams although, large fish are often found in small streams providing they are slow, deep, narrow and have plenty of bank cover.

2.3.4 Spawning habitat

Generally for adult trout to spawn they must migrate to areas where the conditions are suitable for the female to excavate a redd. The gravel must be small enough (coarse sand to small cobble, 5-50mm), and loose enough for the female to excavate. The current velocity must also be quick enough to move the excavated gravel downstream (20-40 cm s^{-1}). Good spawning reaches also need low silt loading and high dissolved oxygen levels. It will come as no surprise that the most of the suitable areas are found towards the headwaters of a river system.

A further requirement of all the life stages is that all these habitats are roughly contiguous within the system and that the passage of fish between them is not restricted. A stream will generally have a continuum of habitat (Vannote *et al*., 1980). Suitable habitat for spawning and fry will be found towards the headwaters. More large trout habitat will be found the further down the stream you go.

Source references for habitat data:

(Baldes & Vincent, 1969; Bovee, 1978; Loar, 1985; Heggenes & Traaen, 1988; Heggenes 1988, Näslund, 1989; Greenberg *et al*., 1996; Mäki-Petäys *et al*., 1997; Bardonnet & Heland, 1994; Heggenes 1998; Heggenes *et al*., 1999)

2.3.5 Changes with time.

The previously described 'preferred habitats' of the different life stages of the brown trout are relevant only in the summer time, during the day. As mentioned, trout habitat preferences and behaviour also change diurnally and seasonally. At night, in the summer, trout seek slower water near banks and in back eddies and slacks. The nightime habitat must provide security through cover and water velocities of near 0.0 m s^{-1}. Although some studies show feeding at night in the summer via epi-benthic foraging.

During the winter brown trout generally decrease feeding markedly; they also become nocturnal. This switch occurs when the water temperature drops below approximately 8^{o}C (Metcalfe & Thorpe, 1992; Heggenes & Saltveit, 1990). During the day, young trout seek shelter in the streambed. To permit this, the streambed must be loose and have hollows and gaps. Trout also shelter in the banks, or in vegetation in the stream. If these forms of shelter are not available in sufficient quantities, trout may seek shelter in pools where they school gregariously. Aggressive, territorial behaviour does not occur in the absence of competition for food. Larger trout may also remain in the pools or seek solitary shelter. At night they emerge from their winter shelter positions and take up positions in faster water, near or on the stream-bed. To complement their nocturnal behaviour trout undergo a shift in their visual apparatus to make their vision more light sensitive, presumably to aid night-time drift feeding.

2.4 Experimental design and analysis

The preceding text tells us that Dartmoor rivers are unique. We also know that brown trout from different environments could be optimally adapted through natural selection to better suit the conditions in those environments. There is more chance that natural selection will have led to adaptation in populations that have been reproductively isolated for extended periods. We also know that the habitat requirements of trout change from day to night, season to season and as they mature.

The objective of this study is therefore initially to find out what river-features are correlated with the abundance of trout of different ages, specifically on Dartmoor. Changes in these river-features over time may alter trout numbers. However, there is no accurate historical record of the river-features and there are only fairly unreliable recordings of fish numbers with which to compare present day figures. It is therefore necessary to shift the analysis to a spatial rather than a temporal comparison. This is performed by statistically testing which river-features or combinations of river features in Dartmoor streams are correlated with increasing or decreasing trout numbers. From the results of the statistical analyses the relationship between the important habitat features and numbers of trout of different ages can be mathematically modeled. The modeling process is described more fully in the following section.

Once it is established which river-features appear to dictate the abundance of trout of different ages, we can look for the causes of changes in these river-features and suggest methods for mitigation. Mitigation methods can be implemented on stretches of streams for which there is good *a priori* baseline data and the population can be monitored for changes. This monitoring will aid the understanding of the potential causal links in the relationship between river-features and trout numbers.

It is important to note that frequently, local in-stream habitat is the product of catchment-scale processes. An assessment of macro-scale habitat features is therefore also necessary to help in the interpretation of the meso-scale habitat assessments. Macro scale habitat features and fish accessibility were recorded in this study. Trends in River flow dynamics are also assessed and discussed with relevance to the trout populations.

2.5 Habitat modeling

Mathematical models relating fish populations to habitat availability have been used with great effect for predictive impact analysis (Bovee, 1982; Milner *et al*., 1985). HABSCORE is a static model of physical habitat use (Heggenes, 1996) developed by Milner, *et al*. (1995) and used extensively by the fisheries departments of the Environment Agency, nationally. HABSCORE is based on the derived relationships between different aged fish and quantitatively measured variables. The model requires quantitative measurements of specific habitat river-features (referred to as variables from hereon) from an unknown section of river. From these the model will produce a prediction of the numbers of trout of different ages you would expect to find in the river were it pristine, *i.e.* not affected by any artificial constraints and where recruitment is not limiting. There are many other models available which perform similar functions in a variety of ways (Barnard, 1992). They appear to perform quite well with one significant limitation. Models perform poorly when used to predict trout numbers in streams further away (both geographically and in functional morphology) from those in which they were calibrated (Bernard, *et al*., 1995; Barnard & Wyatt, 1995). This is due in part to the subtle changes in the pervading influences with geographical range, which are not included in the empirical formulae comprising the models. Also the decrease in accuracy may be related to the increasing genetic divergence of trout from further afield both in the spatial sense and in terms of the duration of their reproductive isolation. Differences certainly exist in the genetic profiles of trout from different streams within catchments and between catchments. As discussed previously, it is likely that these genetic differences have phenotypic manifestations, which may lead to differences in physiology, behaviour or life history, which will affect the optimal habitat profile of the trout.

HABSCORE is being tailored to increase its transferability from a regional to a national scale by including in the suite of sites used to calibrate it, a larger and more diverse selection of rivers. However, for this study a separate static habitat model was produced specifically for, and calibrated with Dartmoor rivers. This allowed the precise tailoring of the model to include habitat variables peculiar to Dartmoor and the tailoring of more general habitat variables to better suit the situation on Dartmoor. Once the protocols for recording habitat features are established the model can be added to quickly and easily, improving the accuracy of the predictions. The model also allows us to predict the impact of mitigation works on rivers. Thus our mitigation work can be designed to increase a specific proportion of the population by a prescribed amount.

Adult brown trout are known through radio telemetry studies to move up to half a kilometre up or down a main river diurnally (Bridcut & Giller, 1993). Other studies have shown that brown trout may move as far as 2km away if there is a lack of suitable habitat locally (Fausch *et al*., 1995) although this was fairly exceptional. Bridcut & Giller (1993), confirmed these movements and added that all fish showed some site fidelity at either a micro-habitat or macro-habitat level during their monitoring but most fish moved away from the monitored stretch altogether after three to four months.

To successfully manage a population of trout as described in the preceding paragraph it important that the spatial limits of a reproductively distinct trout population are defined. The habitat within the area defined can then be managed to enhance and stabilize the population as a whole. Otherwise, by altering habitat in one area to relive a perceived local bottleneck in the trout numbers one could be instigating limitations on the breeding population as a whole at another level. This is stressed with relevance to the management of a population of brown trout by Addicott *et al*. (1987). The potential watershed scale of habitat dispersal must be acknowledged to successfully manage a population (Näslund, 1993) and similarly, the distinctiveness of subpopulations within the catchment. The problem of defining the spatial limits of a subpopulation is addressed in the Cherry Brook Trout Marking Study, described in section 6 of this report.

2.5.1 Variable selection

The first stage in creating a habitat preference model is the selection of suitable variables, which are deemed the most likely determinants of trout abundance. Different studies emphasize the importance of different variables in controlling the distribution of different aged trout. Trout micro-position is well correlated with water velocity at the snout of the fish and this has lead to some good models predicting the microposition on trout in stable situations. On a meso-scale, most studies indicate that water depth is the strongest determinant of trout habitat preference; this is followed closely by water velocity, changes which usually correlate with changes in depth. Other studies favor particle size as the strongest determinant, which is itself related to the previous two factors. Other authors rate the importance of cover above other determinants and some regard chemical factors as having a pervading influence, particularly pH and the presence or absence of metal ions. Others again regard biological factors as dominant determinants of trout abundance. Most studies recognize that habitat preferences are size structured among trout populations. One vexing inconsistency among studies is that most don't lend themselves to comparative quantitative analysis due to their semi-quantitative often subjective methods of variable measurements, or the recording of only a few of the many variables which may be influencing the population.

Furthermore there is an apparent lack of recognition or clarity in distinguishing density dependent and density independent processes. Adverse water chemistry will affect individuals of a fish population in a similar way at any density although density differences may exacerbate the effects. The population is unlikely to reach a level where resources such as habitat availability are limiting its expansion if chemical factors are controlling fish abundance. In the absence of chemical adversity or other density independent factors (and where ample recruitment is measured or assumed) the population will probably be controlled by density dependent processes such as competition for space or food through intraspecific competition. The density is controlled by the extent of resource availability. Biotic factors, such as interspecific competition or predation, are likely to increase the strength of density dependent population control by limiting a resource such as food or space or creating more competition for the resource of safe habitat or cover. These differences are recognized in this study.

Variables measured in this study were selected on the basis of an extensive review of the relevant literature which was based on the work of the following authors: Fausch & White, 1981; Kennedy & Strange, 1982; Milner *et al*., 1985; Heggenese *et al*., 1993; Greenberg, 1992; Bain, 1995; Baran *et al*., 1995; Fausch *et al*., 1995; Heggenes *et al*., 1995; Orth, 1995; Heggenes *et al*, 1996; La Voie & Hubert, 1996; Naslund *et al*., 1998; Mäki-Petäys *et al*., 1997; Sundbaum & Näslund, 1998; Hesthagen *et al*., 1999; Bremset & Berg, 1997; Eklöv *et al*., 1999; Heggenes *et al*., 1999.

It appears that certain variables and combinations of variables are of different degrees of importance to different aged trout from different rivers in different environments. Therefore, most of the variables reported as important in the cited literature were initially incorporated in the methodology. The selected variables and their dimensions are listed in the next section, along with the quantitative and repeatable methods for their measurement.

3 Methods for Habitat Suitability Assessment

Initially, 71 reaches were chosen, which have been regularly, quantitatively electrofished since 1965 by the Environment Agency. The 71 reaches were narrowed down in number to 40 on the basis of their accessibility and size. Eighteen reaches were finally selected via a random process. All eighteen reaches were between 65 and 110 m long and comprised a variety of flows and channel forms.

The locations of the 18 study reaches are depicted on Map 1 in Appendix I, along with grid references. Photographs of the top and bottom ends of the reaches are shown in Figures 1 to 18 in Appendix I.

A suite of physical habitat variables was measured quantitatively at each site. Values of a suite of chemical variables were also obtained for each site from water quality data, routinely recorded by the Environment Agency, and through site sampling (for BMWP scores). The selection of these physical and chemical variables was based on a literature survey of similar experiments and discussions of their design. The process of variable selection is described in the introduction.

Some subjectivity may be involved in the assessment of some of the habitat features, such as fish cover, but it was our aim to make the survey as repeatable as possible. To this end, each variable and the protocol for its measurement is described in Table 1.

Measurements of each reach were taken from sequential 10 m sections until the whole reach was covered. Transects were taken perpendicular to the bank at even distances along sections. The results are tabulated and graphed for each reach in figures 19 to 36 in Appendix II.

The response variables (numbers of brown trout of different sizes) were sampled by the Environment Agency using electrofishing apparatus. A 240 V, 500 W bank mounted generator producing pulsed direct current with a frequency of 100 Hz with a single anode was used. The sampling methods of Bird (1996) were emulated. Sampling was conducted over May and June whilst rivers were at summer base flows. Numbers of all size trout were recorded from each reach. Other species of fish were recorded as present or absent.

The habitat surveys were performed in summer low flows at roughly the same time of year in which the Environment Agency perform their routine salmonid population monitoring. At this time of year trout are feeding and behaving territorially and the rivers are discharging at their lowest annual rates. We therefore assumed that if habitat availability were limiting the population it would be doing so at this time of year. Walkover surveys of the rivers indicate that there are large areas of suitable spawning habitat accessible to trout from the Dart rivers that are included in this study.

Table 1. The selected variables, their dimensions and the methods of measurement.

Variable	*Units*	*Methods of Measurement*
		Physical Variables
Total wetted area	m^2	The sum of the areas of all the 10 m sections in each reach. Calculated using 5 width measurements per 10m section.
Mean stream width	m	The mean of all the width measurements in each reach.
Mean stream depth	m	The mean of 3, 5 point river transects for depth in each 10 m section.
Current Velocity	s /10m^{-1}	The current velocity recorded using a digital flow metre held at a quarter of the total depth from the surface. The means of 3, 5 point river transects for each 10m section of the reach were used.
Discharge	$m^3 s^{-1}$	Derived from the mean velocity, the mean width and the mean depth of each reach.
Riffle area	ratio to total area	The surface area of each flow type in each 10 m section was estimated by eye and is given as a ratio of the total surface. The mean for each reach was derived from the mean for all the sections.
Run area		
Glide area		
Pool		
Slack water		
Sinuosity	ratio total length to straight length	Direct measurement
Bank characteristics	m^2	The area (beneath at least 10 cm depth of water) overhung by the bank. Measured using a 1 m rule with a 10 cm L bar attachment.
Overhang/refugia	m^2	The area overhung by vegetation on the bank (beneath at least 10 cm depth of water). Measured using a 1 m rule with a 10 cm L bar attachment.
Woody debris	m^2	The area (beneath at least 10 cm depth of water) overhung by woody debris whether in the bank or in the river. Measured using a 1 m rule with a 10 cm L bar attachment.
In stream refugia	m^2	The area (beneath at least 10 cm depth of water) overhung by objects within the stream (not attached to the bank) or overlain by roughened, broken water.
Fines (silt and sand <2mm)	ratio to total area	Substrate was measured and classified according to a modified Wentworth scale. The surface area of each substrate type (or that covered by macrophytic vegetation) was measured across three 10m wide transects in each 10m long section. The mean for each reach was derived from the mean for all the sections and given as the ratio to the total area.
Small gravel (2-40mm)		
Large gravel (4cm-10cm)		
Cobble (10cm-30cm)		
Boulder (>30cm)		
Bedrock		
		Bilogical
Macrophytes		
Number of other fish species found	n	EA electrofishing survey
Grazing pressure	1-10	Estimated by eye *e.g.* 1= lush ungrazed vegetation (>20cm high); 5=tightly grazed sward (<3cm high). 10 = bare soil/sand.
BMWP	Arbitrary units	1 minute standard kick samples at the down river end of each reach. A 250 µm mesh net was used to sample. All samples were preserved in alcohol, and then spread in 1200 cm^2 trays divided into 12, 100cm^2 areas. Each area was studied for 5 minutes. All macro-invertebrates found were identified to family level and recorded Samples were scored using the Biological Monitoring Working Party (BMWP) score system.

Chemical Variables		
Conductivity	μ/CM	EA water quality measurements
Dissolved O_2	%	EA water quality measurements
Dissolved O_2	mg l^{-1}	EA water quality measurements
Ammonia (N)	mg l^{-1}	EA water quality measurements
BOD mg l-1	mg l^{-1}	EA water quality measurements
pH	pH units	EA water quality measurements
Calcium	mg l^{-1}	EA water quality measurements
Response Variables		
Trout Fry	100 m^{2-1}	Electrofishing
Trout Par	100m $^{2-1}$	Electrofishing
Mature trout (>15cm fork length)	100m^{2-1}	Electrofishing

4 Methods for Statistical Analysis of Brown Trout Abundance

The initial trout data set contained 30 physical and chemical independent variables. These data were collected for three dependent variables (abundance of fry, par and adults) in eighteen different reaches. Due to the number of independent variable exceeding the number of independent observations (i.e. number of rivers), the number of variables used in any given analysis had to be greatly reduced. This was achieved by (a) classifying independent variables as either 'physical' or 'chemical' and carrying out separate analyses on these classes, and (b) combining several related variables into one variable. For instance the pH and calcium (Ca^{2+}) chemical variables were converted to a single chemical variable, the ratio of Ca^{2+} ions to H^{+} ions. Ca^{2+} : H^{+} is a commonly used variable in similar studies (Turnpenny, 1989). Combining related variables also served to considerably reduce collinearity. The variables used in the study are described in Table 20. The chemical variables were deemed to be density independent factors and the physical variables were deemed to be density dependent factors.

Table 20. The combined variables used in the statistical analysis.

Physical Variables	*Code*
Total wetted area	[*wetted*]
Mean depth	[*depth*]
Velocity	[*velocity*]
(riffle area + run area)/(glide area + pool area)	[*riffrun*]
Fines (silt)	[*fines*]
(sm. gravel + lg. gravel)/(rocks + boulders)	[*gravrock*]
Macrophytes	[*macroph*]
Overhang	[*overhang*]
Woody debris	[*woody*]
In-stream refugia	[*refugia*]
Chemical Variables	*Code*
Conductivity	[*conduct*]
Dissolved O_2	[*oxygen*]
Ammonia	[*ammonia*]
BOD	[*bod*]
Ca^{2+}: H^{+}	[*Ca2*]
BMWP score	[*bmwp*]

The effects of these two classes of independent variables on the abundance of trout fry, par and adults were assessed using multiple regression. For each combination of dependent and independent variables, two analyses were carried out: (1) a confirmatory analysis in which all predictor variables were included in the model, (2) a stepwise multiple regression to produce a regression equation with only a subset of the available variables, but hopefully high predictive power. In the stepwise regression, terms were included in the model when $p<0.1$ and excluded when $p>0.2$.

To use the particular statistical analyses the data must conform to certain conditions. In all analyses, the residuals were tested for normality, the partial regression relationships were checked for approximate linearity, and the variables were tested for colinearity. Unless otherwise stated, these conditions were met for all analyses.

4.1 Physical variables

4.1.1 Fry

4.1.1.1 Confirmatory analysis

The confirmatory model explained around three-quarters of the variance in the dataset ($R^2_{adj} = 0.715$), and produced an overall significant regression ($F_{10,17}=5.26$, $p=0.019$).

However, only the *gravrock* term is a significant predictor ($t=2.613$, $p=0.035$) of fry abundance in this model.

4.1.1.2 Stepwise regression

This approach revealed that significant predictive power could be gained by a model with just three independent variables:

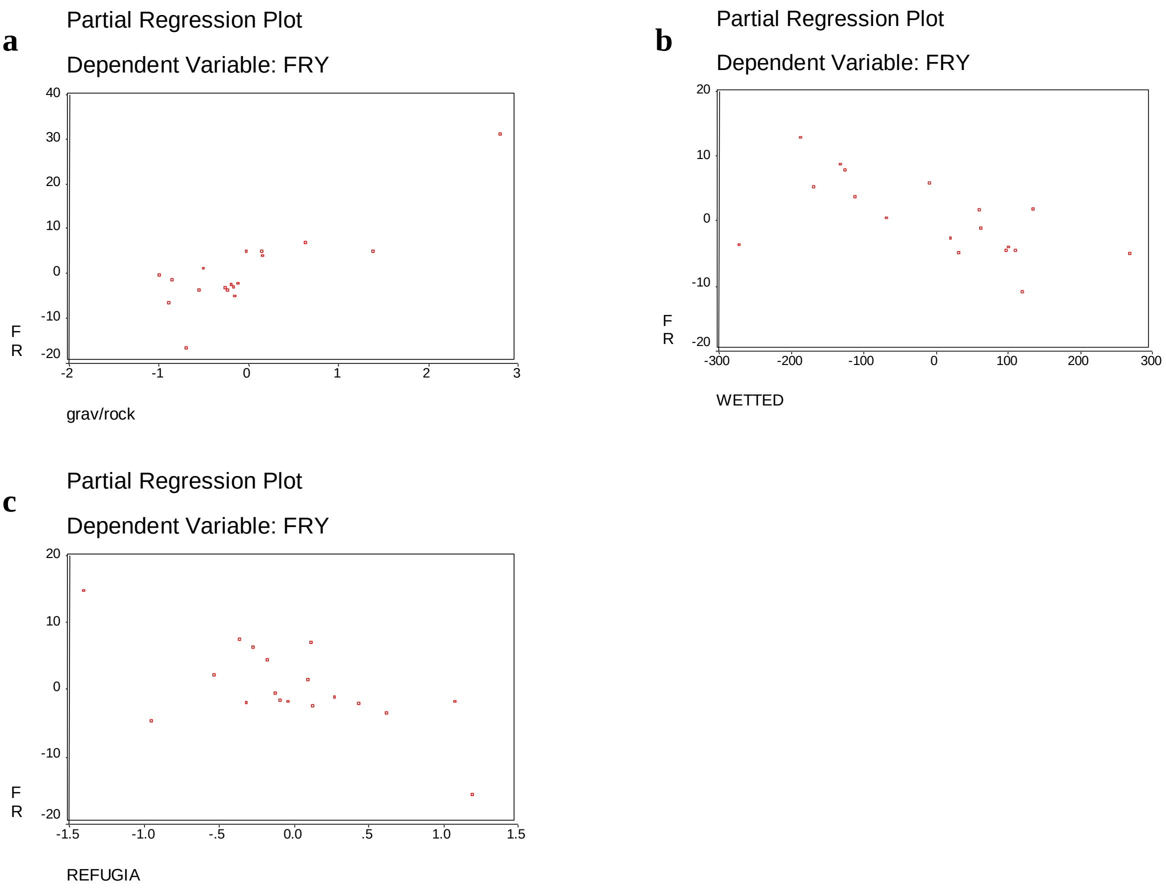
Equation 1. Fry = 8.86 *gravrock* – 6.593 *refugia* – 0.026 *wetted* + 20.26

This regression accounted for around three-quarters of the variance of the dataset ($R^2_{adj} =0.771$).

The overall fit of the regression was highly significant ($F_{3,17}$=20.07, p<0.001), with all three predictor variables having a significant effect:

gravrock	t=6.26, p<0.001
refugia	t=-3.24, p<0.01
wetted	t=-2.82, p<0.05

Figure 37 a, b and c. The partial regression plots for fry numbers against the significant physical variables: a) *gravrock*; b) *wetted*; c) *refugia*. (Partial regression plots are graphical representations of the relationship between the dependent variable and a single independent variable, with the effects of other independent variables held constant).



4.1.2 Par

4.1.2.1 Confirmatory analysis

The confirmatory model explained around 70% of the variance in the dataset (R^2_{adj} = 0.677), and produced an overall significant regression ($F_{10,17}$=4.56, p=0.028).

However, only the *refugia* term was a significant predictor (t=3.996, p=0.005) of par abundance in this model.

4.1.2.2 Stepwise regression

This approach revealed that significant predictive power could be gained by a model with just two independent variables:

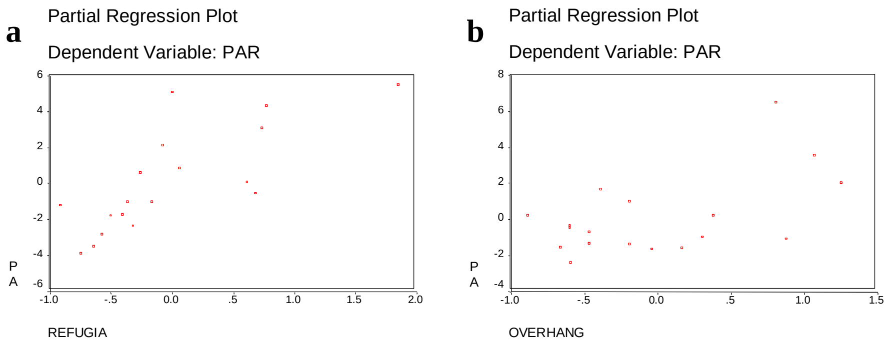
Equation 2. Par = 3.139 *refugia* + 1.811 *overhang* + 0.7795

This regression accounted for around 70% of the variance of the dataset (R^2_{adj} =0.701).

The overall fit of the regression was highly significant ($F_{2,17}$=20.93, p<0.001), with both predictor variables having a significant effect:

refugia	t=4.566, p<0.001
overhang	t=2.486, p<0.05

Figure 38 a and b. The partial regression plots for Par numbers against the significant physical variables: a) refugia. b) overhang



4.1.3 Adults

4.1.3.1 Confirmatory analysis

The confirmatory model had very high predictive power, explaining around 90% of the variance in the dataset (R^2_{adj} = 0.886), and produced an overall significant regression ($F_{10,17}$=14.149, p=0.001).

However, only the *woody* term was a significant predictor (t=3.319, p=0.013) of adult abundance in this model.

4.1.3.2 Stepwise regression

Significant predictive power could be gained by a model with just two independent variables:

Equation 3. Adults = 2.008 *woody* – 0.0014 *wetted* + 1.325

Again, this regression accounted for around 90% of the variance of the dataset (R^2_{adj} =0.905).

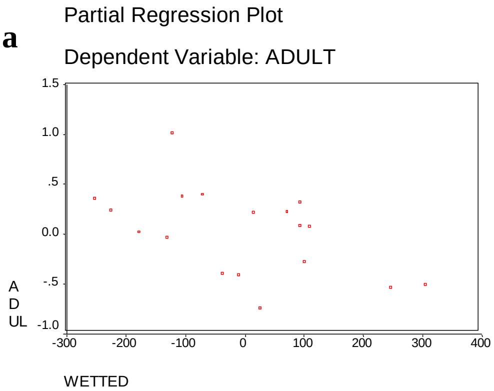
The overall fit of the regression was highly significant ($F_{2,17}$=81.726, p<0.001), with both predictor variables having a significant effect:

woody t=10.582, p<0.001

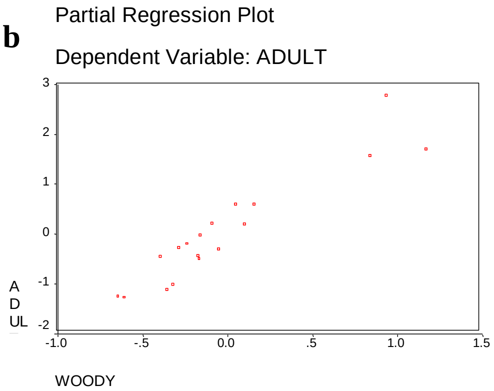
wetted t=-2.331, p<0.05

Figure 39 a and b. The partial regression plots for Adult fish numbers against the significant physical variables: a) *wetted* b) *woody*

a



b



4.2 Chemical variables

4.2.1 Fry

4.2.1.1 Confirmatory analysis

The confirmatory model had little predictive power,

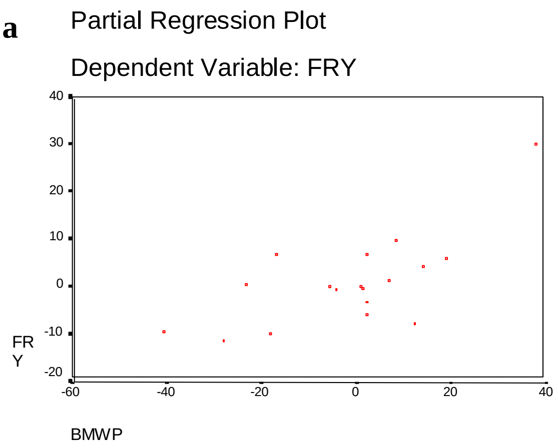
4.2.1.2 Stepwise regression

This regression accounts for around 30% of the variance of the dataset (R^2_{adj} =0.306). The overall fit of the regression was not significant ($F_{1,17}$=4.18, p<0.1).

NOTE: the residuals from fitting this model were non-normal, violating one of the assumptions of regression analysis. All common data transformations did nothing to alleviate this problem. Despite this, the results of these analyses, coupled with the results of the confirmatory model (which produced normal residuals) still suggest that *bmwp* is the strongest predictor of fry abundance. Because of this non-normality, we cannot be sure of the accuracy of the regression equation above.

Figure 40a. The partial regression plot for fry numbers against the chemical variable: *bmwp*.

a



4.2.2 Par

4.2.2.1 Confirmatory analysis

The confirmatory model had relatively low predictive power, explaining 25% of the variance in the dataset (R^2_{adj} = 0.261), and failed to produce a significant regression ($F_{6,17}$=2.0, p=0.151).

Ca2 was the only terms in the model to produce a significant effect (t=2.457, p=0.032).

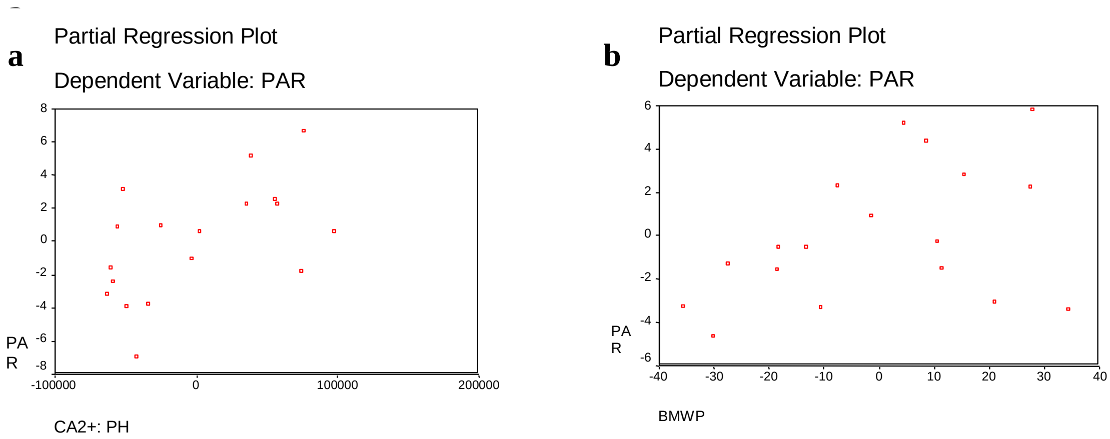
4.2.2.2 Stepwise regression analysis

The best predictive model from stepwise regression was:

Equation 5. Par = 3.41E-05*Ca2* + 6.26E-02*bwmp* – 6.464

However, this produced a low R^2 value (R^2_{adj} =0.289) and is therefore of limited predictive power.

Figure 41a and b The partial regression plot for par numbers against the significant chemical variable: a) *Ca2* b) *bmwp*



4.2.3 Adults

4.2.3.1 Confirmatory analysis

The confirmatory model had very low predictive power, explaining only 25% of the variance in the dataset (R^2_{adj} = 0.25), and failed to produce a significant regression ($F_{6,17}$=0.613, p=0.717).

No individual terms in the model were significant.

4.2.3.2 Stepwise regression analysis

According to the p-to-enter criteria used, no variables were entered into the regression analysis, again indicating that these variables have very little explanatory power.

4.3 Summary

It is clear from these data that the “physical” independent variables were far better predictors of fry, par and adult trout abundance (i.e. produced significant regressions with high R^2 values) than the “chemical” variables. In particular, *gravrock*, *refugia* and *wetted* had large effects of fry abundance, *refugia* and *overhang* affected par abundance, and *woody* and *wetted* influenced adult abundance. For chemical variables, the only conclusion was that there was a weak positive relationship between fry abundance and *bmwp* and juvenile abundance and *Ca2*.

5 Methods for Statistical Analysis of Salmon Abundance

The analysis described in the previous section was repeated for sixteen of the eighteen sites using salmon fry and juvenile numbers as the response variables instead of brown trout numbers. Two rivers were excluded from the analysis due to an absence of Salmon fry and juveniles, which may have been caused by poor river access and not related to local habitat features.

5.1 Physical Variables

5.1.1 Fry

5.1.1.1 Confirmatory analysis

The confirmatory model explained hardly any of the variance in the dataset ($R^2_{adj} \sim 0$), and produced no overall significant regression ($F_{10,5}=0.331$, $p=0.935$). Correspondingly, no terms in the model explained a significant amount of variance.

5.1.1.2 Stepwise regression

According to the p-to-enter criteria used, no variables were entered into the regression analysis, again indicating that these variables have very little explanatory power.

5.1.2 Par

5.1.2.1 Confirmatory analysis

As with fry, the confirmatory model explained virtually none of the variance in the dataset ($R^2_{adj} \sim 0$), and produced no significant regression ($F_{10,5}=0.767$, $p=0.664$). No individual terms in the model approached significance.

5.1.2.2 Stepwise regression

This approach revealed that significant predictive power could be gained by a model with just one independent variable:

$$\text{Par} = 16.76 - 0.0223\textit{wetted}$$

This regression had moderate predictive power, accounting for around 40% of the variance of the dataset (R^2_{adj} =0.390). The overall fit of the regression was highly significant ($F_{1,14}$=10.587, p=0.006).

5.2 Chemical variables

5.2.1 Fry

5.2.1.1 Confirmatory analysis

The confirmatory model had virtually no predictive power (R^2_{adj} ~ 0), and produced no overall significant regression ($F_{6,9}$=0.748, p=0.627). In this model, the residuals were not normally distributed (p=0.037), but this would be unlikely to have a large effect on the low predictive power of the model.

5.2.1.2 Stepwise Regression

According to the p-to-enter criteria used, no variables were entered into the regression analysis, again indicating that these variables have very little explanatory power.

5.2.2 Par

5.2.2.1 Confirmatory Regression Analysis

The confirmatory model had very low predictive power, explaining only 15% of the variance in the dataset (R^2_{adj} = 0.155), and failed to produce a significant regression ($F_{6,9}$=1.46, p=0.293).

5.2.2.2 Stepwise regression analysis

The best predictive model ($F_{1,14}$=9.315, p=0.1) from stepwise regression was:

$$\text{Par} = 0.148\,bwmp - 16.081$$

However, this produced a low R^2 value (R^2_{adj} =0.202) and is therefore of limited predictive power.

5.3 Summary

The physical and chemical variables measured appear to have no statistically discernible effect on the abundance of salmon fry. However, the variables *wetted* and *bwmp* do have some (albeit limited) predictive power regarding par abundance. The results are not discussed in detail in the next section due to the lack of significant correlations. The lack of correlation may result from the Salmon fry and juveniles being more cosmopolitan in their distribution and tolerance or the population may not be large enough to be subject to density dependent controls. Spawning Salmon are almost certainly not accessing all river sections with equal ease and frequency and therefore, up to a point, features far removed (in time and space) from the study section may be controlling salmon abundance; features such as access, distance from the sea and quantity of Salmon spawned in preceding years (initiating a positive feedback loop based on relative habitat quality in past years).

6 Results and Discussion of the Habitat Preference.

6.1 General summary

To summarize briefly, the habitat preference model indicates the following:

The preferred habitat of Dartmoor trout fry is:

Smaller streams with pristine water quality, lots of gravel around 2-4 cm in size and little cobble and boulder over 10cm in size. Trout fry are found less often in areas with large overhanging rocks in the stream. There is also a weak correlation with increasing trout fry numbers and increasing, instream-macrophyte vegetation. Trout fry were found in densities ranging from 0.53 fish / 100m^2 in the River Swincombe at Wydmeet, to 43.5 in the Upper Cherry Brook. The mean number of trout fry was 9.23 / fish 100m^2 and the standard deviation was 11.07 fish 100m^2.

The Juvenile trout appear in numbers in a wider variety of stream sizes and depths and there is more variation in the substrate composition of the riverbeds in which they are commonly found. There is a strong correlation with increasing juvenile trout numbers and the increasing area of potential cover within the stream and with increasing bank overhang. Increasing juvenile trout numbers are also strongly correlated with increasing amounts of woody material both in and overhanging the river. They also appear to prefer water with a combination of high calcium ion concentrations and high pH. The numbers of juvenile trout ranged from 13.53 fish / 100m^2 in the East Webburn at Wooder Manor to 0.52 fish / 100 m^2 in the Upper Cherry Brook. The mean number of juvenile trout was 5.59 fish / 100m^2 with a standard deviation of 3.61 fish / 100m^2.

Adult trout appear to prefer shady, smaller streams with woody material in the banks and appear reasonably robust to differences in other habitat features. There are positive correlations with river depth and bank overhang but they are not statistically significant (P=0.05). Trout falling into this size category were comparatively few. The maximum number of adult trout was 5.3 / 100 m^2 found in the Powder Mills site half a mile above the experimental section on the Upper Cherry Brook. The minimum number of adults was found 0.13 fish / 100m^2 at the site on The River Swincombe at Wydmeet. The mean number of adult fish from all of the sections examined was 1.43 fish / 100m^2 with a standard deviation of 1.29 fish / 100m^2.

These findings resemble those of other, similar studies on trout from different rivers (Bachman, 1984; Heggenes, 1989; Heggenes, 1996; Hesthagen, *et al*., 1997; La Voie & Hubert, 1997; Eklöv et al., 1998).

6.2 Macro scale factors

Walkover surveys of the eighteen sites were conducted to highlight macro-scale factors that may have been directly or indirectly influencing the fish population. The LEAPS were studied and local knowledge sought to identify extraneous influences. All sites conformed to their Target River Quality Objectives (REQs) for the chemicals tested. The target level was REQ1 in all the sites in the study. The Environment Agency using the BMWP system also biologically monitors the rivers of Dartmoor. The methodology and application of this system are discussed in the methods section of this study. The Environment Agency ascribes a river section a computer-model-generated target BMWP score using the RIVPACS III computer program. Their target score is generated using environmental and geographical features of the river section. The Environment Agency’s classification of the Upper Dart rivers was mostly Class a-Very good. Sites with significantly depressed scores were the West Webburn River and the Upper West Dart, at the site of the Leat offtake. The work in this study found the water quality to be high in both river sections when measured using the BMWP system.

All sites in this study appeared to be contiguous with reaches containing abundant habitat suitable for redd cutting and spawning by brown trout. There was however a distinct lack of spawning habitat for Salmon on the upper West Dart both above and below the Devonport leat intake. No salmon fry or par were found in these sections. Salmon fry and par have been found at the electrofishing site on the Upper West Dart at Crockern Tor about a mile down stream of the Devonport leat intake site. The two sites at the Devonport leat intake were on a steep gradient and were covered with large boulders. Pockets of gravel suitable for trout spawning were frequent but dispersed. The lack of salmon juveniles in the Devonport leat intake sections of the Upper East Dart could be due to problems with migratory fish access, although a fish impass was not found during our survey, or it could equally be due to the lack of suitable salmon spawning habitat observed.

A common feature highlighted during our walkover surveys was the presence of either ditches draining forestry or stock drinking points that were generating significant amounts of sand. The sand appeared to have been washed down stream and was discernable for several hundred metres below the point of generation. The sand appears to be generated as the stock or the water flowing in the ditch cuts through the friable peat layer overlying the sand layer. The sand homogenized the riverbed decreasing the diversity of flow regimes and cover suitable for many forms of invertebrates, fry and juvenile fish. The ditches draining the forestry plantations are also deeply incised with a two stage channel indicative of very high, erosive flows.

A further impact, evident throughout the catchment wherever stock had access to streams, was the over widening and shallowing of river channels through intensive riparian grazing. The sward, although tight, was very closely cropped and there was evidence that the river banks were being eroded during high flow events. This is a natural phenomenon leading to slumping and reprofiling of the banks and a narrowing and deepening of the channel profile. However, if a dense covering of vegetation is not present the slumped bank sections are unprotected and friable, they may be washed away when the river is in flood leading to over widening and shallowing.

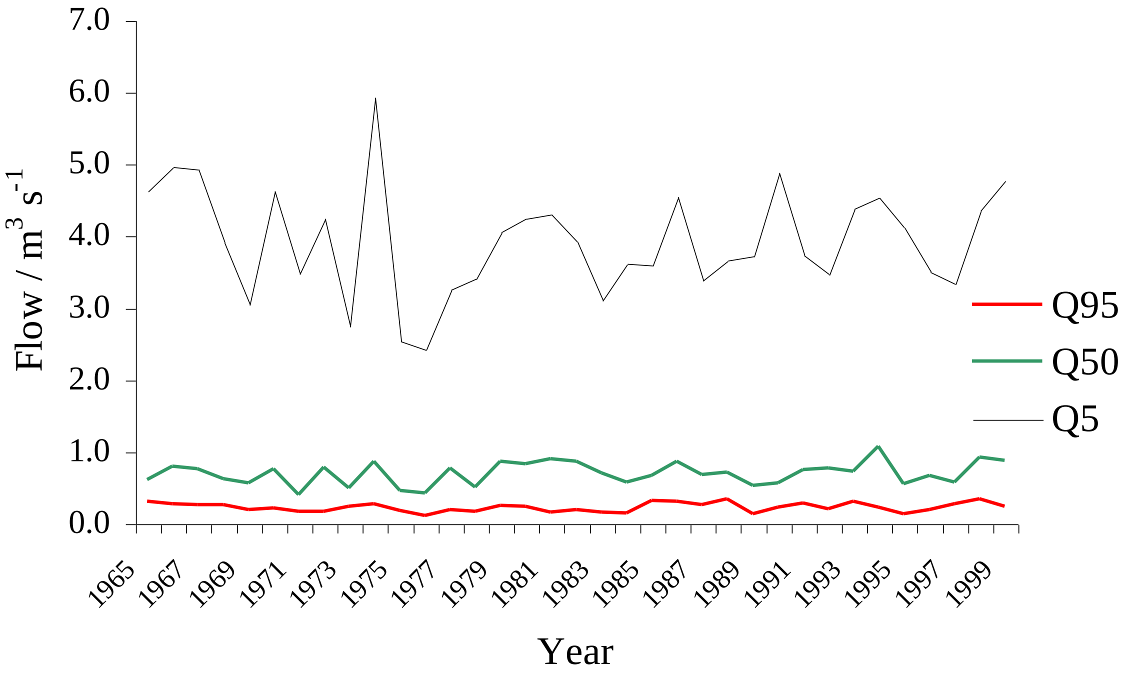
6.3 Flow analysis

The Environment Agency LEAP document subjects the recorded discharge rates for the Dart to a cursory examination. The LEAP gives no indication of trends in discharge or the separation of Discharges from the East and West Dart. The Discharge data from gauging stations on the upper Dart at Bellever (below Post bridge on the East Dart) and Dunnabridge (Just above the confluence with the Swincombe River on the West Dart) were examined in this study.

The mean daily discharge in the East Dart from 1965 to 1999 was calculated as 1.24 $m^3 s^{-1}$ with a standard deviation of 0.21 $m^3 s^{-1}$. The mean annual peak discharge was 14.30 $m^3 s^{-1}$ with a standard deviation of 4.60 $m^3 s^{-1}$. The highest discharge over the whole period was 29.06 $m^3 s^{-1}$ which occurred in the winter of 1979. The mean base discharge (mean of the lowest annual discharges) over the period was 0.19 $m^3 s^{-1}$ with a standard deviation of 0.051 $m^3 s^{-1}$. The mean annual Q95 (The flow exceeded for 95% of the time or for 347 days of the year) over the time period was 0.221 $m^3 s^{-1}$ with a standard deviation of 0.064 $m^3 s^{-1}$. If it is assumed that the Q 95 discharge is the base discharge of the river, *i.e.* that derived purely from storage within the catchment, then it can be compared to the mean daily flow to indicate the contribution of ground water to the overall discharge of the East Dart. The mean annual Q95 represents 17.8% of the mean daily flow indicating that there is a comparatively good supply of ground water in the catchment of the Upper East Dart.

The annual Q95, the Q50 (the discharge exceeded for 50% of the time) and the Q5 (the flow exceeded for 5% of the time) were analysed for trends over the period in which data had been gathered (1965 to 1999). No significant trends were found in the data. The data are graphically displayed in Figure 42.

Figure 42. Graph plotting the changes in the annual Q95, Q50 and the Q5 over the period 1966-1999 (Excluding 1976 due to an incomplete annual dataset).

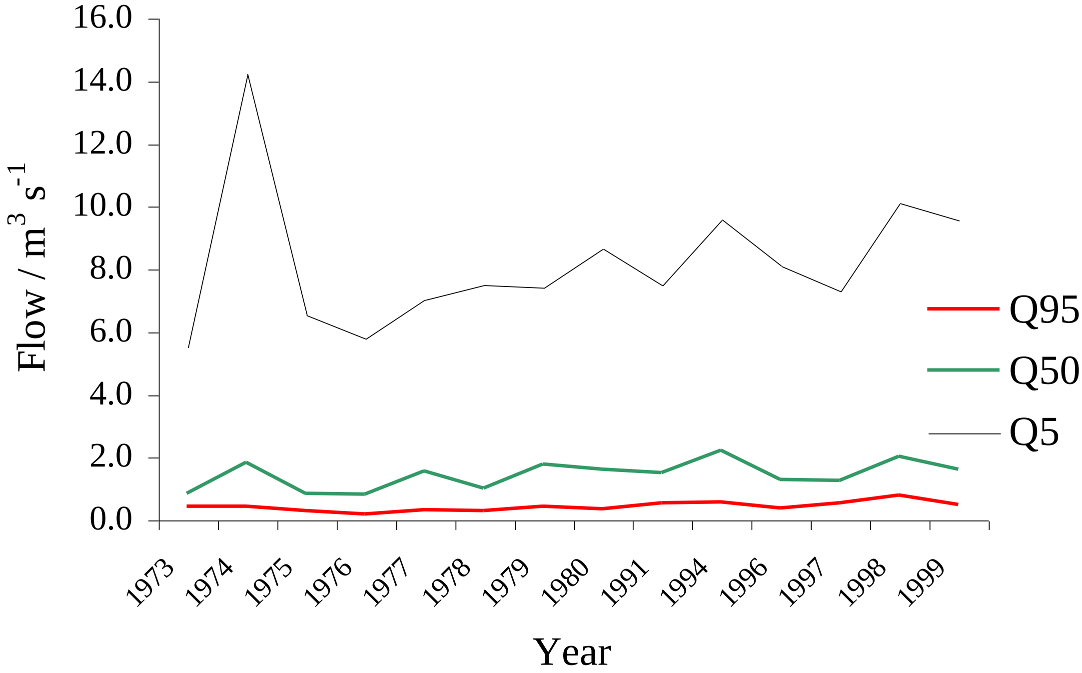


The mean daily discharge in the West Dart from 1973 to 1999 (excluding 1981-1990, 1992, 1993 and 1995 due to incomplete annual datasets) was calculated as 2.55 $m^3 s^{-1}$ with a standard deviation of 0.65 $m^3 s^{-1}$. The mean annual peak discharge was 28.69 $m^3 s^{-1}$ with a standard deviation of 11.28 $m^3 s^{-1}$. The highest discharge over the whole period was 53.71 $m^3 s^{-1}$ which occurred in the winter of 1979. The mean base discharge (mean of the lowest annual discharges) over the period was 0.35 $m^3 s^{-1}$

with a standard deviation of 0.12 $m^3 s^{-1}$. The mean annual Q95 (The flow exceeded for 95% of the time or for 347 days of the year) over the time period was 0.41 $m^3 s^{-1}$ with a standard deviation 0.15 $m^3 s^{-1}$. If it is assumed that the Q95 discharge is the base discharge of the river, *i.e.* that derived purely from storage within the catchment, then it can be compared to the mean daily flow to indicate the contribution of ground water to the overall discharge of the East Dart. The mean annual Q95 represents 16.2% of the mean daily base flow indicating that there is a comparatively good supply of ground water in the catchment of the Upper West Dart although less than the Upper East Dart. The annual Q95, the Q50 (the discharge exceeded for 50% of the time) and the Q5 (the flow exceeded for 50% of the time) were again analysed for trends over the period in which data had been gathered (1973 to 1999 with exclusions as mentioned). There was found to be a significant increase in the Q5 with time ($F_{1,12}$ =7.26, $P<0.05$) but the Q95 and the Q50 did not change significantly. The data are graphically displayed in Figure 43. The change in the discharge dynamics has important implications for the river both morphologically and biologically. The increasing Q5 indicates that flood discharge levels are increasing. Increasing discharge during floods will almost certainly lead to changes in the functional morphology of the river channel. The shape of the river channel is generally governed by the erosive capacity of the river during these high flow events. As a result the water may be more turbid in high flow events. Bed load transport may increase as the river bed substrate is sorted to suit the changing flood regime. There will almost certainly be an increase in salmonid egg mortality due to 'wash out' of the redds (Crisp, 1989) particularly those of smaller salmonids, such as brown trout, which tend to bury their eggs in shallower nests. There may be an increase in the number of fish directly displaced by the increased discharges.

The increase in the Q5 could result from a number of factors. On a global scale, changing rainfall patterns could be responsible. On a more local scale the increase could be due to improved land drainage or a general decrease in the infiltration capacity of the catchment due to soil compaction. These are common features in land that has been improved or further improved for agricultural use.

Figure 43. Graph plotting the changes in the annual Q95, Q50 and the Q5 over the period 1973-1999 (Excluding years as described).



6.4 Discussion of the possible influences of significant variables

It is clear from this study that the physical habitat availability strongly correlates with abundance of different aged trout. Hesthagen *et al*., (1999) studied chemical and physical variables using multiple regression models similar to those used in this study and found that chemical variables correlated with trout abundance strongly and that there was little effect from physical variables. Hesthagen's study was, like this study, performed in acidic softwater streams and so reinforces the need for the tailoring of models to specific circumstances. Hesthagen noted that only a single physical habitat variable seemed to correlate strongly with trout abundance at any one time and the identity of this variable changed with river systems and fish age. This again reinforces the need for a bespoke approach to habitat modeling in different river systems.

It is important to discuss the nature of some of the important variables and possible explanations for the observed correlation so that our management decisions can be as cost-effective, targeted and, of course, as successful as possible. The physical variables, broadly speaking, appear to control the population density, probably through density dependent mechanisms. Density independent factors, such as water chemistry, effect individuals of the population directly and may stop a population reaching the point at which density dependent factors dominate. For example, there is no point spending thousands of pounds creating suitable fish habitat if water chemistry limits the fish population size. The range of the chemical variables in this study was narrow on a national scale and all values of the chemical variables tested fell within the Environment Agency's highest bracket of water quality, indicating pristine water. It is therefore deemed legitimate to assume that the majority of the variation in the fish numbers was due to density dependent population control based on physical habitat suitability and biological interactions. A limited amount of data mining using combined physical and chemical data sets also showed that physical habitat variables had an overriding influence on fish abundance.

6.4.1 Important chemical variables

There are only limited correlations between trout numbers and water chemistry variables but these merit discussion. There was a weak correlation between BMWP score and trout fry abundance. As explained in the Methods Section, a

BMWP score is a integral score, based on the presence of different families of invertebrates and their relative tolerance to organic pollution (reviewed in Metcalf, 1989). If a family of invertebrates is intolerant to organic pollution, it has a higher BMWP score and if it is very tolerant of organic pollution, it has a low score. If, when you sample your river section, there are many different families of invertebrates present with a low tolerance level for pollution (and therefore a high individual BMWP score) the total BMWP score will be correspondingly high.

From the positive, but weak, correlation between the BMWP scores of Dart rivers and the density of trout fry in those rivers, one could infer that trout fry prefer water that is very low in organic pollution.

A possible reason for the lack of correlation with other chemical variables may be the lack of sensitivity of the testing or the composition of the suite of chemical variables recorded. Another factor may be that chemical tests are carried out on samples taken from the river at approximately monthly intervals. They therefore represent a snapshot of water chemistry. The BMWP score represents a time-integrated measure, which reflects the long-term quality of the water. One cannot however assume that there is a direct causal link between water quality and the abundance of trout fry. The correlation may be the result of differences in BMWP scores also encompassing differences in the preferred food species of different aged trout. For instance (Kreivi *et al*., 1999) found significant differences in prey selection between different sized brown trout. Aged 0+ trout preferred the mayfly *Ephemerella* nymphs (this nymph is very pollution intolerant and scores high on the BMWP scale). The 0+ feed on the cased caddis larvae *Micrasema* sp. later in the season. Aged 1+ trout fed selectively on caddis larve at all times of year, *Micrasema* sp. was selected for when available but in early summer in the absence of *Micrasema* sp larvae they selected non-cased caddis e.g. *Rhyacophila* sp. and *Hydropsychidae* spp. (these have intermediate scores on the BMWP scale). Areas with high BMWP could therefore be more preferable for younger trout because they have a wealth of their preferred food type and hence, the causal link is indirect. This is not presented as a conclusion but simply a cautionary example of how inferring causality could lead to mismanagement.

Horton (1961) also found significant differences in the food taken by different aged fish at different times of year in the Walla Brook on Dartmoor. He found that the numbers of terrestrial organisms taken (predominantly winged diptera) increased with the age of the fish. Food items of between 2 and 8mm were favored in all ages of fish. Generally, fish took more benthic fauna than terrestrial food.

The positive correlation between trout numbers and chemical variable *Ca2* (the ratio of Ca^{2+}:H^+ ions) is a result commonly found in studies of mildly acidified streams flowing off land with similar geology to Dartmoor (Harriman *et al*., 1987). The correlation may indicate the direct toxic action of decreasing pH in the absence of Calcium ions. For instance, the effect of Ca^{2+} ions in ameliorating the toxic effect on trout of H^+ ions on trout is well documented (Driscoll *et al*., 1980; Brown & Lynam, 1981; Hesthagen *et al*., 1999). Ca^{2+}: H^+ concentration has also been found to correlate positively with brown trout and Atlantic Salmon egg survival (Lacroix *et al*., 1985; Lacroix & Townsend, 1987). However, pH was not particularly low in any of the rivers. The lowest pH was 6.58 in the Cowsic River at Holming Beam. This is however the mean of one years monthly readings. When analysed in detail, the pH dipped as low as 5.3 in February 2000.

In water with low pH where pH is the sole contributing factor, the efficiency of the blood osmoregulatory process in trout is reduced at the gill/water interface (Evans, 1987). The threshold for toxic effects is approximately pH 5.0. Below this threshold, fish become stressed and, at a population level, mortality increases.

At low pH, Aluminum may be the cation preferentially exchanged for the surplus H^+ ions. This situation is prevalent in catchments where the soil has poor buffering capacity, such as peaty soils overlying granite bedrock where most of the base cations have been leeched away, comparable to the situation on Dartmoor. Aluminum has a similar toxic action on fish to H^+ ions, although toxic effects may occur at higher pH (5.0 to 6.0) (Baker & Schofield, 1980). The soil structure on Dartmoor often allows rapid passage of unbuffered water to the channel in storm events. Toxic acid-pulses are often a feature of rivers draining such catchments. Acid pulses are often accompanied by elevated concentrations of aluminum, which can be liberated from the streambed as well as from the soil (Norton *et al*., 1987). Constant low levels of pH can cause long term changes in the gill membranes of fish, which may result in decreased respiratory efficiency and growth rates.

Calcium may ameliorate the toxic effects of acidity in fish via the reduction of its displacement from gill membranes (McWilliams, 1983). The amount of calcium required to give a beneficial effect is in the region of 1-2 mg l^{-1}. The Swincombe, Cowsic and all sections of the Cherry Brook frequently dip below this level. The acidity of these rivers is also generally low, (*circa* 6.5 and dipping, as mentioned, to levels just above 5).

The effects of acidity upon fish populations may not be direct. The whole river ecosystem is affected by pH. Acidity may decrease the diversity of algae and macrophytes in the river (Grahn, 1977). In-stream vegetation is the primary source of energy to the river ecosystem in open moorland streams. Different invertebrates are also more or less tolerant to acid conditions. Invertebrates are more susceptible to the direct effects of pH rather than aluminum toxicity (Burton & Allan, 1986). Low pH often results in a loss of diversity of invertebrate taxa or a shift in the abundance of species. For instance, The organic pollution-intolerant nymphs of species of Stone flies (*Plecoptera*) are comparatively acid tolerant whereas invertebrates which are more robust towards organic pollution *i.e.* certain nymphs of species of Mayfly (*Ephemerptera*) and Caddis fly (*Trichoptera*) are acid sensitive. Horton (1961) and Horton *et al*. (1968) in two comprehensive studies of the bionomics of trout in Devon streams, tentatively suggested that production at the lower trophic levels in acid streams does appear to be limiting the growth rate of trout and the ultimate carrying capacity of the streams.

6.4.2 Important physical variables

Riparian and in-stream cover were found to correlate significantly with the abundance of fry and juvenile trout. Cover is considered to be an important factor in the spatial niche selection of brown trout by many authors (summarized by Heggenes *et al*.,1999). Brown trout are known to increase in number if cover is added to a section that initially has a dearth of it (Boussu, 1954; Hunt, 1977) and their numbers were found to decline if cover was removed from a stream bank that initially had a wealth of it (Boussu, 1954). Suitable fish cover takes many forms and in this study it was divided initially into four types, each of which overhung at least 10 cm of water, these were: bank characteristics; vegetative overhang; woody debris; in stream cover. The first two were combined for the statistical analysis as the variables showed strong colinearity. Fry showed a negative correlation with instream cover. Par showed a positive correlation with both bank overhang and instream cover and adults showed a strong positive correlation with the presence of woody debris cover.

The negative correlation between fry and instream cover is probably partly due to the hydrodynamics of the river sections in which the fry were found. Instream cover was usually in the form of overhang from large boulders in the river. Fry were preferentially found in streams with a high proportion of small gravel and low proportion of rock larger than 10 cm in diametre. The unembedded nature of the gravels in the Dartmoor streams surveyed would probably permit fry to hide among the gravels. This could be a much more convenient and preferred refuge for fry when available. Fry may also reside preferentially in these areas because other physical stream features suit their morphology and size. This is the province of microhabitat studies but the principals may be extrapolated to larger scales. For instance, fry feeding on drift need very slow water in close proximity to fast water. The rate of the exponential decline in water velocity with depth is difficult to measure in the field but is obviously more rapid in shallower sections with high surface water velocities. This rapid change in water velocity over a small distance means a fry will be able to sit in very slow water and feed in high velocity water, only a couple of body lengths away, optimizing the trade off between energy expended and energy intake (optimal foraging). Hence the fry's preferred fluvial situation at a microhabitat scale means that on a mesohabitat scale they are found to increase in abundance in homogeneous, sorted-gravel beds in comparatively shallow fast water (Leopold *et al*, 1964).

Fry are known to displace salmon fry and par where they are sympatric so their niche in the river is not greatly influenced by interspecific competition with salmon fry (Kennedy & Strange, 1986;Dewald & Wilzbach, 1992). Brown trout compete intraspecifically for habitat and size is almost exclusively the determining factor in the outcome of these competitive interactions, larger fish dominating smaller fish. Larger brown trout are also predatory on younger fish so the spatial segregation also lowers the risk of predation. A size-based dominance heirachy operates among trout, with smaller, subordinate fish taking up station in less profitable feeding areas (Gotceitas & Godin, 1992). You often see smaller fish arranged behind a larger fish of the same age class in a stream (S. Evans pers. com.). The larger fish takes the most profitable feeding position and the others fit in where they can without eliciting an aggressive reaction. The largest fish in a year class are often found in pools whilst their subordinates in the year class are still feeding in the shallow water. Näslund *et al*. (1998) demonstrate that sympatric brown trout have different life history strategies and their growth rate is decreased by their competitive exclusion from pools. In this study there was no apparent effect of sympatry on habitat selection and this variable was removed from the analysis at an early stage. There was no significant correlation between the abundance of fry and the abundance of other age classes of trout in the sections of the rivers tested.

Juvenile brown trout numbers were positively correlated with increasing in-stream cover and increasing bank overhang. Looking at the raw data much of the bank overhang was in the form of vegetation. The correlation between juvenile numbers and river sections with greater overhanging, vegetated bank area and larger in-stream structures providing cover may be a result of the need for juveniles to have access to cover whilst their body size prevents them from finding this within the gravel of the stream bed. Further to this argument, the increased body size and swim speed of the juveniles dictates that their position of optimal foraging will be in slightly deeper water where the separation between their slightly swifter holding current and swifter feeding current (compared to fry) is greater. Again, the fluvial dynamics of the required habitat for juveniles at a microhabitat scale may be responsible for the reported correlations between juvenile abundance and the prevalent river morphology in these areas at a mesohabitat scale. As mentioned Juveniles hold station further off the stream bed whilst feeding, which could effectively increase the range of their visual field and hence their territorial range. The correlation with increasing juvenile numbers and in-stream cover may therefore also be related to the increasing visual isolation a trout would experience in a stretch of river strewn with large boulders. Again, intraspecific competition may be influencing habitat selection. Juvenile trout were significantly negatively correlated with the presence of adult trout. This implies that, although the size difference between the two is minimal, (the modal size for the cluster of trout termed 'juveniles' in the electrofishing studies was 12 cm) there may be competition for habitat between them and the larger >15cm fish. In the absence of adult fish, juvenile fish are known to spread into habitat considered more suitable for adult fish.

Grazing pressure was estimated 50 m either side of the river sections examined to assist in discussions of potential causes of habitat changes. The grazing pressure was initially recorded on a nominal scale but was retrospectively converted to a grazing pressure index ranging from 1 to 10. A score of 1 indicated no grazing, as far as it was possible to tell, and a score of 10 indicated heavy grazing. It was hypothesized that grazing pressure was not correlated with vegetative overhang, bank overhang or woody debris in the river channel. The hypothesis was rejected at P= 0.05 in the case of woody debris. There was a significant negative correlation between the grazing pressure and the volume of woody debris in the banks and in the river. For vegetative and bank overhang the hypothesis was accepted in both cases ($P=0.05$ being the critical level) but could be rejected in both cases at the $P=0.1$ level. We can infer from these results that grazing has an important role to play in the architecture of the river-bank and hence grazing may also play an indirect role in altering the carrying capacity of a section of river for different size trout. Other changes in river channel morphology due to grazing are well documented (Smith, 1976; Thorn *et al*., 1996).

Adult brown trout abundance was strongly positively correlated with the presence of woody material in the bank and in the river. The preference of brown trout for areas with plenty of woody debris in the banks and in the channel is well documented (Gowan & Fausch, 1996). Sundbaum & Naslund, (1998) show definitively that woody debris serve to decrease intraspecific competition through providing visual isolation and that trout in channels with woody debris grow faster under otherwise similar conditions. Visual isolation is a critical factor in upland, moorland streams where pools are long, the maximum depth is about a metre and the water is clear. In many of the pools in the streams examined the bottom was covered in sand. This feature was prevalent in areas below stock watering points. The affected pools were often well grazed along the banks due to their proximity to areas of intense stock activity. The net effect of these impacts is to create a comparatively shallow pool habitat. The bottoms of such pools are generally featureless and interstities between bottom features are infilled with sand. Visual isolation within the stream is minimal and the cryptacity of trout when viewed from above is severely compromised. Few trout were seen in such pools but those that were, when they were disturbed, moved quickly around looking for cover before leaving the pool. Other features correlated with increasing adult trout abundance were increasing depth and decreasing river surface area. Larger streams are generally preferred by larger trout according to conventional wisdom. However, on Dartmoor larger trout were found in streams with smaller surface areas. This is again due to the fluvial dynamics of the streams. The discharge was similar in most of the streams analysed (mean = 0.50 m^3 s^{-1} standard deviation = 0.16 m^3 s^{-1}). The main difference in surface area was therefore due to changes in the flow type. Streams with small surface areas were narrow, deep and slow and usually had highly overgrown banks with gorse and small trees in sections. The best example of this is the section at Powdermills on the Cherry

Brook which held more adult fish than any other section analysed. The riverbanks on such streams were stable and due to the lack of grazing, vegetative succession had lead to the establishment of trees on some sections. Woody material in the river and woody root systems within the banks were a more common occurrence in such areas.

6.5 Modeling and impact assessment

With minimal effect from density independent population controls such as water chemistry, the physical habitat availability appeared to impose an upper limit on the density of fish supported in a river section. This habitat preference information can be used, via the equations in the statistical results section, to direct management of the streams to increase the numbers of a certain size-class of trout. For instance, if it was deemed that a section of a Dart tributary, was an important area for fry we could use Equation 1 from the previous section to calculate present and potential fry carrying capacity of the stretch.

Equation 1. Fry = 8.86 *gravrock* – 6.593 *refugia* – 0.026 *wetted* + 20.26.

To get a prediction of the existing fry carrying capacity of the section we first need values for the three important physical variables for fry used in Equation 1 *i.e.* *gravrock*; *refugia* and *wetted*. These should be recorded using the same methods as outlined in Table 1 in Methods section and then combined if necessary, as outlined in Table 20. Hypothetical values for the variables (highlighted in red) are substituted into Equation 1 in the example below to demonstrate the point

$$\text{Fry} / \text{m}^2 = (8.86\times1.2)–(6.593 \times0.85\ \text{m}^2) – (0.026\times420\ \text{m}^2) + 20.26,$$

to give

$$\text{Fry} / \text{m}^2 = 14.3.$$

The density of trout fry in the hypothetical stream is 14.3 /m^2. To enhance the fry carrying capacity of this hypothetical section we could increase the value of the variable *gravrock* through management. *Gravrock* is the ratio of riverbed covered with gravel (less than 4cm), to the area covered with larger stones. If this ratio were increased through management to 5 the fry density would theoretically increase to 48/m^2. Fry abundance might also by enhanced by removing shade and cover and allowing the river to widen and shallow effectively decreasing the value of the *refugia* variable. Macrophyte vegetation would also be encouraged by the increasing light penetration. The statistical analysis showed a weak positive correlation with increasing macrophyte cover and trout fry numbers.

There was no strong correlation between water chemistry and fish abundance in this study but as mentioned, the range of the chemical variables was narrow. Other Dart streams must also be assessed for water chemistry so that if values of chemical variables fall outside the range investigated in this study they can be assessed independently as a potential limiting factors. It is probable that the correlation between fry numbers and the BMWP score is due to the improved habitat for epibenthic invertebrates (highly represented in the BMWP tallies) in sections of river suitable for fry. Horton (1961) tentatively suggested that the population of trout in the Walla Brook was limited by the abundance of epibenthic fauna (although he was unable to accurately quantify the abundance of eroded drifting invertebrates). This correlation requires further investigation. The effects on fish numbers of the Calcium ion to Hydrogen ion ratio are a common finding. In rivers with low pH and low Calcium, these problems must be addressed to get maximal effect from any physical habitat manipulations. Also, as stressed throughout this study, physical management of instream habitat must be carried out with knowledge of the spatial scales of the trout population. This is especially important in sensitive upland areas, which possibly contain the majority of the spawning and juvenile habitat of the Dart brown trout and Salmon. The relevance of this is discussed later.

7 Growth

Scales from approximately 50 Cherry Brook, brown trout were collected by the Environment Agency in 1998. Scales from each fish were stored separately and the length of each donor fish recorded. The Westcountry Rivers Trust scientific team, as part of this study, aged the scales using standard methods.

The weight (W) of fish generally alters in proportion to the length (L) roughly in accordance with the cube law. Horton (1961) found that, for Dartmoor brown trout, the relationship between weight and length could be described by the following equation:

$$W=0.01439.L^{2.904}.$$

This relationship does not deviate far from the cube law. This equation was used to calculate the weight of the brown trout collected for this study from the Cherry Brook. The weight and age data for were used to calculate the growth rate as follows.

The annual growth rate (k) of the trout in the Cherry Brook was assumed to be exponential so that $W = Ae^{kt}$ (Brody, 1945), where e is the base of natural logarithm, A is the natural log of W when t = 0, W is the weight at t_1, and k is the instantaneous growth rate. Hence $k = (\log e W_2 - \log e W_1) / (t_2 - t_1)$.

The calculated growth rate of brown trout from the Upper Cherry Brook in 1998 was 0.534 yr^{-1}. The growth rate of Dartmoor brown trout from the Walla Brook in the late 1950s was calculated by the same process from the data recorded by Horton (1961). The mean growth rate over three years from Horton's data was 1.08 yr^{-1}. This is higher than the growth rate recorded from the Cherry Brook in this study. The difference may result from the fact that growth rates calculated from Horton's data are based on the sizes and weights of younger fish ranging over three years from 0+ to 2+. Growth rates in this study were calculated from older fish ranging in age from 2+ up to 5+. The growth rates were calculated for each year and the values were considerably smaller in successive years. There is a known to be a decrease in growth rate with age in brown trout. The growth rate of 2+ to 3+ trout from Cherry Brook in 1998 was 0.67 yr^{-1} and the growth rate of 1+ to 2+ trout from Horton's study was calculated as 0.79 yr^{-1}. This was the closest comparison of growth rates possible between the studies and the two values are much nearer. The data set is not extensive enough to make confident comparisons but if we assume that both growth rates represent Dart trout generally, it is apparent that there has been no dramatic change in the size at age or growth rate of brown trout in the Dart since the late 1950s.

However, as Demonstrated in Horton *et al*. (1968), the growth rate of these moorland populations is much slower when compared with other more alkaline rivers such as the River Yarty and the River Kennet. Even when temperature differences are taken into consideration there is still a disparity in the growth rates. This may be a direct effect of acidity on fish growth but as concluded in the aforementioned study by Horton *et al*, it appears to be food availability that is limiting fish growth in rivers which are otherwise highly suited to salmonid reproduction. The large numbers of fry and juveniles in the Walla Brook compete strongly for available food and the net result is numerous small fish with slow growth rates. This may, in part explain correlations between BMWP and pH scores and numbers of young fish. The increasing diversity of food available in streams with high BMWP scores may increase fry and juvenile carrying capacity and growth rates.

Horton's data on the Biometrics of Dartmoor trout can also be used in conjunction with the data from this study to generate a 'cohort life table' (see Table 2) for the brown trout from the Upper Cherry Brook if the following assumptions and measurements are accepted (Horton, 1961):

- Female Dart trout are sexually mature in their 4th year (Horton, 1961);
- Male Dart trout are sexually mature in their 3rd year (Horton, 1961);
- 64% of the Dart breeding population are male fish (Horton, 1961);
- There are on average, 372 eggs per redd with 10-15% mortality prior to hatching (Horton, 1961);
- We use the compound exponential formulae of Ricker (1954) to predict egg survival to yearlings using the constants discussed in Horton (1961).

Table 2. A cohort life table for trout in the Upper Cherry Brook.

Life stage	Number at start of each stage a	Proportion of original cohort surviving at each life stage l	Proportion of original cohort dying at each life stage d	Mortality rate q	$\text{Log}_{10}\,a$	$\log_{10} l$	Killing power k	Eggs produced in each stage F	Eggs produced per surviving individual at each stage m	Eggs produced per original individual in each stage lm
eggs	1218	1	0.9004	0.9004	3.086	0	1.002			
0+	121	0.0996	0.0569	0.5717	2.084	-1.0018	0.368			
1+	52	0.0427	0.0312	0.7307	1.716	-1.36973	0.570			
2+	14	0.0115	0.0049	0.4285	1.146	-1.9396	0.243			
3+	8	0.0066	0.0057	0.875	0.903	-2.18264	0.903	1083	135	0.8865
4+	1	0.0008	0.0000	0	0.000	-3.08573	0.000	135	135	0.1108
5+	1	0.0008			0.000	-3.08573	0.000	135	135	0.1108
									$\Sigma 1m$ or R_o	**1.1081**

The mechanics of the table are secondary in importance in this instance but the figure relevant to this study is the figure in bold at the bottom right. This figure is R_o or the reproductive rate. The R_o value, is the number of offspring (of the first stage in the life cycle-in this case fertilized eggs) produced per original egg by the end of the cohort. It therefore indicates, in species that reproduce annually, the overall extent by which the population has increased or decreased over that generation. The trout population in the above table has a R_o value of 1.108. This would indicate that if all assumptions hold constant, the population should increase by about a tenth every generation until limited by density dependent processes and self-thinning (*sensu* Elliot, 1993). The numbers of the fish were taken from a section the Upper Cherry Brook stretching from the road-bridge down to the corner of the Bellever plantation and measuring approximately 350 metres. If this were a discrete breeding population there would be no reason to worry for the health of the population. However, If this were the case and one more fish of breeding age were removed from the stretch each year, the population would have a R_o of less than 1 and would be in decline. This situation is hypothetical but highlights the importance of informed stock management. The missing factor is an understanding of the spatial limits of the population and movements within it. Were this known, it would be possible to use models such as the one developed in this study or HABSCORE to calculate the expected numbers of brown trout throughout the range of the population and then use the information to develop dynamic cohort life tables. Changes in dynamic variables such as recruitment and mortality resulting through stochastic events (weather, pollution etc.) could be made via reactive monitoring or using the data from the routine monitoring of the Environment Agency. Bag limits could be set annually using this information and the habitat managed to improve the surplus yield from the population without approaching a critical level and without having to stock fish.

8 The Dartmoor Brown Trout Tagging Study

As mentioned throughout this study, to effectively manage the habitat of a population of mobile animals, such as brown trout it is essential that the spatial limits of a reproductively distinct population be defined. The habitat within the area defined can then be managed to enhance and stabilize the population as a whole. Otherwise, by altering habitat in one area to relieve a perceived local bottleneck in the trout numbers one could be instigating limitations on the breeding population as a whole at another level. Not only must the potential watershed scale of habitat dispersal be acknowledged to successfully manage a population of brown trout (Näslund *et al.*, 1993) but the range of reproductively isolated subpopulations within the catchment must also be understood. To get an initial idea of the range of brown trout dispersal from natal streams, a study was initiated involving the marking and recapture of brown trout from the Cherry Brook. The Environment Agency fisheries team electrofished a 400m stretch of the upper Cherry Brook and a 400m stretch of the lower Cherry Brook for brown trout.

Over 150 trout were caught and passed to the bank where they were anesthetized and marked. The fish were marked by injecting a fluorescent orange elastomer compound (Northwest Marine Technology, Inc.) under a transparent area of skin (see Figure 43). The elastomer compound although malleable to begin with, hardens into a rubbery solid that stays in-situ for several years if correctly injected (pers. Comm. Dr D. J. Solomon). Fish of different sizes from the two reaches were given distinguishing marks as depicted in Figure 44. From previous studies it is apparent that fish below 15cm long are relatively abundant but there are a dearth of fish over 20 cm long, in the Cherry Brook.

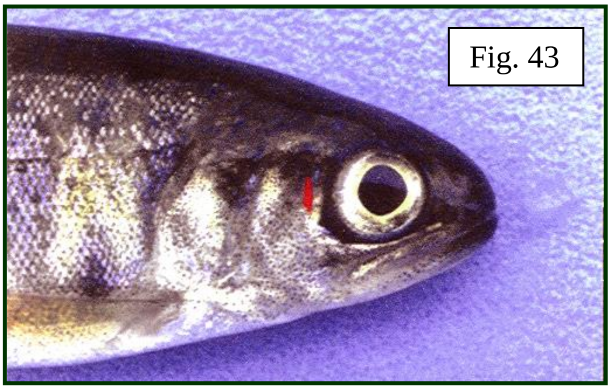
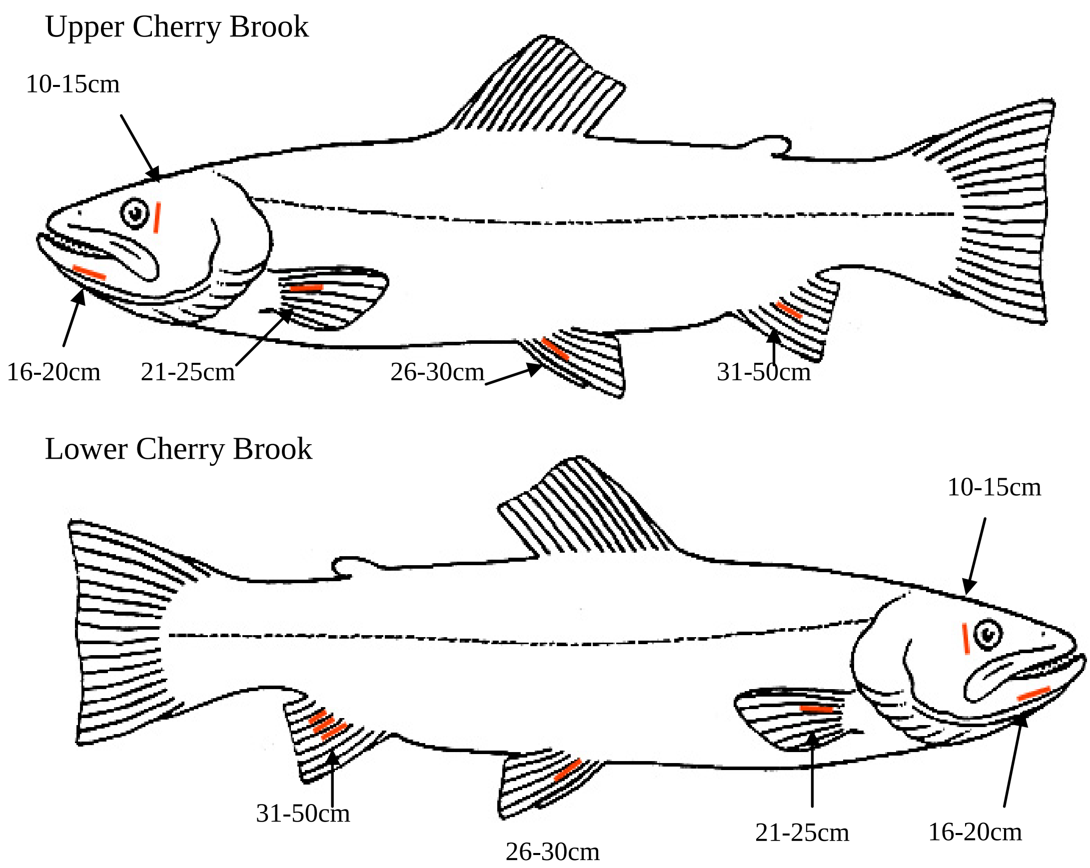


Fig. 43

The size range marked in this study (10 to 50 cm) bridges this rapid population drop-off. The aim of the study is to locate the marked fish through angling and future electrofishing surveys and to build up an idea of the range of the brown trout spawned in the Cherry Brook. Anglers and the Environment Agency Fisheries Department, during their regular electrofishing of the Cherry Brook, will record the location, size and marking of recaptured fish. To this end, a catch return form with a pre-paid and addressed envelope has been has been included with every Duchy fishing permit to be sold during the next season (See Fig 45 in Appendix III).



There are several possible explanations for the sudden decline in trout larger than 15 cm long: they may smolt and become sea trout due to a lack of suitable habitat locally as they grow; larger resident fish and birds may predate them (many anglers have reported the presence of several juvenile fish in the digestive tract of larger fish caught on the moors); they may move within the streams to stretches, which have a larger proportion of habitat suitable for fish of their size. Whatever the explanation, the information is vital to the successful management of the species and there is a dearth of long term studies documenting ontogenetic migrations of riverine brown trout. To further our knowledge in this field the Westcountry Rivers Trust is discussing, with Exeter University and the Wild Trout Society, the possibility of a study examining the population genetics of Dartmoor brown trout.

9 Conclusions and Recommendations

This study was initially targeted at addressing the dearth of adult brown trout in the Upper Cherry brook. We have identified several possible causes for the perceived decrease in numbers of adult brown trout in Dartmoor rivers. We have also sounded several cautionary notes about habitat management and gaps in knowledge that need to be addressed. With these in mind what follows is a list of recommendations for physical work on the aforementioned section of the Upper Cherry Brook. The process of limiting factor identification could also be applied to other stretches of Dart; for instance, the Lower Swincombe and the upper West Dart which both have few trout. Also included are recommendations for future research and development studies, which we consider essential to the management on trout populations.

With habitat restoration the first rule is to do no harm to the species under management, or to other species using the same resources, such as salmon, eels, bullheads, otters etc. These recommendations take into account the habitat requirements of these species.

- Improve degraded adult trout habitat. *e.g.* areas not suitable for juveniles or fry of brown trout or Salmon. There are several pools on the Upper Cherry Brook which are clearly degraded adult trout habitat. We recommend the exclusion of stock from the immediate vicinity of these areas and their exclusion from the river channel above these sections. This would serve to increase most of the factors correlated with the adult brown trout abundance in this study. The mechanism for this and the implications will be decided in discussions with Dartmoor National Park ecologists, which are already planned. Fencing is the obvious solution but more subtle methods may work. *e.g.* Off stream drinking with incentives such as salt licks. Once riparian vegetation has reached a certain level of succession it will form its own barrier.

- Buffer the flows in ditches draining forestry plantations and maybe treat them for acidity using low-tech, flow-responsive methods as outlined in Arnold *et al*. (1988). This may increase energy flux into the ecosystem by increasing primary productivity.

- Add features to runs to improve the visual isolation of juvenile trout and increase the carrying capacity of a section. This can be achieved using carefully placed brush or boulders following the procedures outlined in the Environment Agency guidance manual 'Restoration of Riverine Trout Habitat' (Summers *et al*.,1996). The statistical models can be used to assess the amount of instream cover required in a section and tailor works accordingly.

- Promote the catch and release of all breeding aged trout caught on Dartmoor streams. Dartmoor trout are thought to be sexually mature at 3+. In the Upper Cherry brook the mean size of 3+ trout is 19.7cm and range 16 to 22cm. Therefore, trout of approximately 16 cm and above should not be killed.

- Create a protocol for recording angling effort and catch so results are nationally comparable. This may be an increasingly important tool for fisheries management in the future given the possibility of reductions in the Environment Agency's budget for fisheries. This also serves to promote the role of angling in conservation.

- An intensive study of river chemistry (such as that undertaken by Cornwall EA on the Small Brook) to investigate pH fluctuations in Dart tributaries with and without connections to forestry plantations.

- Further trout tagging in conjunction with the planned genetic study of Dartmoor brown trout to increase our knowledge of the spatial extent and the level of reproductive isolation of trout populations. With this quantified, habitat can be managed over the full range of the population using models such as the one detailed in this study and HABSCORE to stabilize and manage the population. Life tables and other dynamic models can be used to keep yields high and safe guard the population.

- Examine and include further sections of Dartmoor rivers in the models outlined in this study to increase their predictive capabilities and the range of their application.

- Controlling stock access to spawning reaches especially when eggs are green and vulnerable to vibration.

- Further investigate changes in flow on the in the upper East Dart.

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11 Appendix Section