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MODELLING RELATIONSHIPS BETWEEN HABITAT AND DYNAMICS OF A WILD BROWN TROUT (*Salmo trutta* L.) POPULATION IN THE RIVER PIDDLE, DORSET, U.K.

A thesis submitted to Middlesex
University in partial fulfilment of the
requirements for the degree of

Doctor of Philosophy

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ABSTRACT

The status of "wild" brown trout (*Salmo trutta,* L. 1758) populations in the UK is increasingly giving cause for concern (Giles, 1989; Crisp; 1993). Declines in freshwater stocks are often associated with anthropogenic influences destructive to river channel structure and ecosystem function which are contributing to widespread loss of salmonid habitats (Crisp, 1989; White, 2002). Chalk streams are subject to considerable habitat degradation such that rehabilitation requires management actions which better integrate habitat and ecological processes operating to influence fish populations. The influence of local meso-scale habitats upon brown trout population dynamics in two contrasting sectors of the River Piddle, Dorset, UK was quantified using the Physical Habitat Simulation Model (PHABSIM). Sectors examined represented 'typical' semi-natural chalk-stream conditions in the Piddle/Frome catchment area. Spatial availability and temporal variations in habitat quality (WUA) were modelled and tested for correlation against age-specific trout densities obtained from eight years quantitative electro-fishing data. Analyses indicated; **(1)** availability of marginal habitats associated with abundant bank-side cover was critical to adult over-winter survival and was a key factor determining local carrying capacity, **(2)** abundance of juvenile trout was strongly related to critical periods for spawning and rearing habitats, **(3)** low habitat durations during the first summer acted as a bottleneck at the juvenile life stage and **(4)** a variety of different meso-habitat types was important to juvenile recruitment dynamics. The implications of these findings are explored in the context of management of chalk rivers with respect to;- **(i)** habitat factors limiting trout recruitment dynamics **(ii)** utility of PHABSIM as a management tool for identifying population bottlenecks and **(iii)** potential for river rehabilitation strategies to effectively manipulate natural mechanisms regulating brown trout populations in chalk streams.

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Finally, a word for Dr Colin Adams who recognised sufficient value in this work to appoint me as Biologist for LLFT in 2005 and thus gave this effort and sacrifice some degree of meaning which otherwise it would never have had!

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CHAPTER 1: INTRODUCTION

1.1. BROWN TROUT LIFE CYCLE

Brown trout (*Salmo trutta,* Linnaeus 1758) is a polymorphic native European fish species whose range is defined by the Mediterranean and Atlantic coasts in the south and west and Iceland and northern Scandinavia in the north, although it's eastern limits are more difficult to define (Frost and Brown, 1967). Successful introductions have taken place in at least twenty four countries outside Europe, from North America to Australia and New Zealand (Elliott, 1989). The fish communities of the British Isles are relatively "young" in geological and evolutionary terms and brown trout are believed to have recolonised freshwaters about 12000 years ago at the end of the Pleistocene.

Various authors have described the trout life cycle (Frost and Brown, 1967; Maisse and Bagliniere, 1999). Brown trout spawn in late autumn or winter, usually between November and January according to stimuli of water temperature and flow. Fertilised eggs are buried in a nest known as a "redd" constructed in gravel substrate and develop at a rate dictated by ambient temperatures. When the alevins hatch they disperse through the gravel interstices until their yolk-sacs are exhausted at which point they emerge in the river as "fry" (Allan and Ritter, 1977). The fry develop the ability for station holding in open water approximately 10-12 days after emergence in preparation for the establishment of territories (Heland, 1971a). Later they develop into trout parr but subsequent development is split into two separate life history strategies; anadromous (migratory) sea trout which mature in the sea returning to freshwater to spawn and resident brown trout which complete their life cycles entirely in freshwater (Elliott, 1994). Brown trout which remain resident in streams are strongly territorial and exist within a social dominance hierarchy (Fausch and White, 1981). They may migrate vast distances within a river system or complete their life cycles entirely within the confines of a small stream (Elliott, 1994). Consequently, growth, maturation rates and longevity vary greatly depending on the life history strategies adopted.

1.2. BROWN TROUT HABITAT AND THE STREAM ENVIRONMENT

The physical and biological structure of the stream environment is the product of interactions between a myriad of complex processes. These processes are controlled by catchment wide macro-scale variables, such as climate and geology which govern channel morphology and thus physical habitat structure (Newbury and Gaboury, 1993; Summers *et al.,* 1996). Consequently, the term "habitat" covers a range of spatial scales which fit within a hierarchical classification (Fig.1.1) where each smaller scale habitat develops within the constraints set by the larger scale habitat of which it is a part (Frissell *et al.,* 1986).

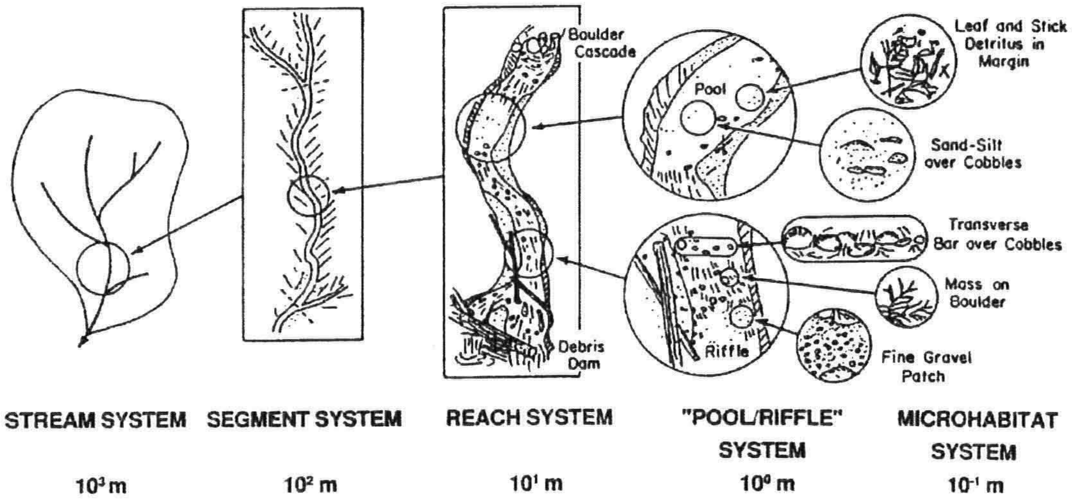

Fig. 1.1. Hierarchical organisation of a stream system and its habitat sub-systems (after Frissell *et al.,* 1986)

The trout zone of a stream (Huet, 1949) is typified by fast flowing, well oxygenated water with low annual temperatures. It is found mainly in upland headwater areas of rain-fed rivers, but also in strongly flowing chalk streams of relatively shallow depth. Four physical factors distinguish the trout zone; width (<1m to 100m), slope (>4.5/1000m or 1.4/1000m in calcareous regions), mean monthly summer temperature (<20-22°C) and stream order (1 or 2).

Brown trout require environments with high habitat diversity. This is because different life stages of brown trout require different habitats with specific characteristics suited to that particular life stage. Trout fry are vulnerable to predation and require habitats in shallow protected stream margins where velocities are relatively low. Water depth and cover are increasingly important habitat components for older trout which tend to occupy deeper water with increasing size (Bohlin, 1977). This means that the nature of available habitats can fundamentally influence the numbers of trout of a given age that can be supported within a stream. Thus habitat can determine trout population structure and act as a limiting factor on abundance (Armstrong *et al.,* 2003).

1.3. CONSERVATION STATUS OF BROWN TROUT

Substantial declines in populations of Atlantic salmon *(Salmo salar)* throughout its natural range since the 1960s (Jonsson *et al.,* 2003) have led to it being designated for protection by the European Union (EU) under the *Directive on the conservation of natural and semi-natural habitats and of wild fauna and flora (92/43 EEC) (Habitats Directive 1992)* (Anon., 1992a). Brown trout *(Salmo trutta)* have not been afforded similar conservation status despite similar declines in many anadromous stocks such as the West coast of Scotland (MacLean and Walker, 2002). Furthermore, reviews of the status of "wild" brown trout populations in the UK have indicated widespread concern about declines in freshwater stocks and considerable evidence of on-going decline (Giles, 1989; Crisp; 1993).

The presence of wild brown trout in a river is an excellent indicator of a healthy aquatic ecosystem (Elliott, 1994; Bagliniere and Maisse, 1999). However, high sensitivity to water quality and very specific habitat requirements (Crisp, 1993) make brown trout a potentially vulnerable species as conditions necessary for their survival are coming increasingly under threat (Hansen and Loeschcke, 1994). Although general water quality standards have undergone considerable improvements in the UK in the last 15 years, anthropogenic influences destructive to river channel structure and ecosystem function are contributing to widespread loss of salmonid habitats (Crisp, 1989; White, 2002).

1.4. CAUSES OF WILD BROWN TROUT DECLINE

Habitat degradation represents a major threat to wild brown trout (Winstone *et al.* 1993; Summers *et al.* 1996; Fisheries Review Group, 2000). In recent decades, intensive development of floodplains has increased the need for "hard" river engineering to improve flood defence resulting in widespread habitat loss and flow regime modifications (Brookes and Shields, 1996). Agricultural land use practises associated with intensification under the EU Common Agricultural Policy (CAP) continues to contribute to widespread and on-going degradation of lotic environments. Large scale arterial drainage schemes in the 1950's and 1960's to bring fertile floodplain land into production resulted in straightening and deepening of river channels reducing habitat diversity and removing important spawning gravels. Soil erosion from ploughed arable land increases sediment supply to rivers and has led to siltation of spawning gravels. Eutrophication from intensive use of fertilisers has caused water quality problems and led to de-oxygenation. Overgrazing of riparian land by sheep and dairy cattle has caused accelerated bank erosion which has exacerbated siltation problems and impacted river channel structure.

Population growth, particularly in the south of England, has increased pressure on groundwater resources. Groundwater abstraction has created problems associated with low flows which have been particularly marked in southern England (Johnson *et al,* 1995: Strevens, 1999). In addition to causing severe reductions in physical habitat, low flows also reduce dilution of pollutants exacerbating problems of eutrophication and siltation.

Problems of acidification have occurred where long term acid rain combines with base poor geology of low buffering capacity. Afforestation of upland catchments with coniferous stands has exacerbated acidification which has caused extensive damage to headwaters. Cumbria and north Wales are regions where upland salmonid nursery streams have been affected by acidic waters toxic to trout eggs and alevins. Forestry practices have also affected discharge regimes and overshadowing of nursery streams reduces primary production and temperatures thus reducing trout production (see Giles, 1992; Crisp, 1993 for reviews).

Furthermore, decades of increasing angling pressure, with cropping of trout exceeding natural replacement capacity of rivers, has led to widespread artificial stocking of streams with hatchery reared fish to maintain the socio - economic value of fisheries (Hartzler, 1988; Giles, 1992). Restocking has historically been perceived as a remedy for declining salmonid stocks but has been shown to represent a significant threat to conservation through genetic interactions between native and hatchery-reared trout (Hansen and Loeschcke, 1994). Salmonids from a "foreign" stock may be less well adapted to the river environment and inter-breeding between these fish and native stock can result in modification of phenotypic characteristics of natural populations (Guyomard, 1989). Use of genetic tagging to monitor the influence of stocked trout in tributaries of Lower Lough Erne, Northern Ireland, demonstrated the genetic contribution of stock fish in some tributaries to be up to 90% (Ferguson and Taggart, 1991). Consequently, there is concern that interbreeding between wild and non-native individuals can alter locally adapted gene pools which may confer reduced adaptiveness and resilience to environmental stresses upon their offspring, with potentially long term evolutionary consequences (Ferguson, 1989). Introductions of hatchery trout can also result in increased stress to wild fish and displacement from preferred feeding stations. These problems are exacerbated where large trout are stocked into nursery areas increasing predation on and displacement of native juveniles (Bachman, 1984).

1.5. RATIONALE FOR MANAGEMENT OF WILD BROWN TROUT

In addition to the intrinsic conservation value of wild salmonid populations, sport fishing for trout and salmon is a major recreational activity and the socio-economic value of fisheries is substantial. In Wales freshwater fisheries presently contribute around £35m per annum to rural economies (Fisheries Review Group, 2000). In England and Wales the value of trout fishing rights exceeds £500 million and expenditure by game angling license holders is estimated to be around £300 million per annum (Radford *et al.,* 2001). Restoration of game fisheries therefore has significant socio - economic value. Restoring the River Eden, Cumbria has been estimated to be worth £1.8 m annually to local rural economies (Eden Rivers Trust, *unpublished*). Angling tourism generates substantial transfer of resources from urban to rural areas. In Ireland overseas anglers are estimated to spend £80 million a year, most of which is spent in rural areas (Fisheries Review Group, 2000). The Irish government have recognised the contribution of angling to the national economy by actively promoting freshwater fisheries and angling tourism through the securing of EU Objective 1 Funds which have focused primarily on habitat improvements for salmon and sea trout fisheries.

The "Salmon and Freshwater Fisheries Review" (Fisheries Review Group, MAFF, 2000) recommended that fisheries should be supported by urgent research into factors affecting long-term sustainability and "the potential for habitat restoration to restore salmonid populations." The National Trout and Grayling Fisheries Strategy (Environment Agency, 2003) resulting from the Review is grounded in the concepts of sustainable fisheries development and provides the conceptual framework for the present study. This recognises that an integrated management strategy for wild brown trout should conserve wild populations of high genetic diversity and protect important habitats but that this needs to be balanced by maintenance of an exploitable fish resource to meet the demand from recreational fisheries (Hansen and Loeschcke, 1994). Thus, fisheries habitat enhancement is placed at the core of conservation actions to address declines in self sustaining wild salmonid populations, while allowing appropriate "supportive" stocking to maximise socio – economic benefits from angling.

In lowland rivers of southern England where there has been a long history of stocking trout, populations have not remained genetically isolated. Thus, for the purposes of this study, the definition of a "wild" trout is ***"an indigenous brown trout that has not been introduced by artificial means, and is native to a stream in which the population is sustained by the natural adult spawning stock."*** This definition is broad enough to encompass populations that have not remained genetically pure but where in all other respects trout are effectively wild. Thus, the term *"native"* refers to stream-bred rather than necessarily genetically indigenous trout.

1.6. TROUT STREAM HABITAT RESTORATION AND MANAGEMENT

The "restoration" of rivers is a relatively new discipline predominately derived from North American experience (White, 2002). Habitat improvements in the UK were largely undertaken piece-meal prior to the 1990's, often as adjuncts to flood protection or land drainage schemes (Mann and Winfield, 1992) and experience from the USA has been slow to filter through. Where natural ecosystems have been lost or degraded, restoration implies a return to a "natural" pre-disturbance condition where structure and function are restored as closely as possible to the conditions under which they evolved (Kauffman *et al.,* 1997). This "ecological restoration" can only be effective at a catchment scale and socio-political pressures make such approaches problematic in practice. In lowland rivers in particular, centuries of anthropogenic influence have meant it is often impossible to define a pre-disturbance "reference" condition to guide such management interventions (Holmes, 2002).

Consequently, the term "river restoration" has fallen from favour in recent years being replaced by "rehabilitation." This term refers to measures which *assist* river systems to recover following anthropogenic disturbances to as natural a state as possible. River rehabilitation proliferated in the UK during the 1990's (Petts, 1996). The River Restoration Project demonstration sites on the River Cole and River Skerne (River Restoration Project, 1993) were the first fully documented projects to undertake rehabilitation of ecological and geomorphic integrity, albeit on a local scale.

The narrower concept of "enhancement" refers to any improvement of a structural or functional attribute for a species or habitat. In fisheries management, enhancement measures are often focused specifically on a single species (trout and/or salmon) and a specific ecosystem component (physical habitat). These have tended to be small scale in stream "improvements" such as pool creation but many such projects have remained poorly documented with limited information about impacts on populations (Summers *et al.* 1996). Local enhancement of salmonid streams in the UK is increasingly being undertaken by Rivers and Fisheries Trusts. These environmental charities are successfully attracting grants and external funding for habitat improvements, such as those increasingly available under agri-environment and biodiversity preservation initiatives such as the Countryside Stewardship Scheme.

Implementation of the Water Framework Directive for EU member states will have important implications for fisheries management and should facilitate a more holistic "catchment" approach allowing macro-scale problems to be more effectively addressed by river rehabilitation (Kondolf and Downs, 1996). Salmonid habitat enhancement initiatives such as the Conservation of Atlantic Salmon project in Scotland are already starting to address habitat issues at larger catchment scales as part of the EU LIFE programme.

1.7. KEY RESEARCH THEMES

Modelling relationships between habitat and trout abundance is important to improve understanding of mechanisms regulating populations. The Physical Habitat Simulation Model (PHABSIM) (Bovee, 1982) comprises a suite of programmes that manipulate hydraulic and biological parameters to predict habitat gains and losses for stream dwelling salmonids over a range of river discharges. There has been a rapid increase in operational use of PHABSIM in the UK (Dunbar *et al.,* 2001) and the model has typically been employed to evaluate impacts of abstraction and to define in-stream flow requirements (Petts and Bickerton, 1993; Johnson *et al,* 1995; Strevens, 1999). However, use of the model to assess physical habitat in relation to channel alterations/enhancements or fish population dynamics in the UK has been limited. These have become important new areas of research in recent years in response to changing attitudes to river management, strengthened environmental legislation and the concomitant requirements to quantify environmental impacts on aquatic species (Maddock, 1999). Research by the Centre for Ecology and Hydrology (CEH) identified an urgent need for further validation of links between PHABSIM derived habitat predictions and salmonid abundance (Dunbar *et al.,* 2001). This is the context within which the goals of the present study are set. Studies that match physical and hydraulic characteristics of streams with population dynamics have the potential to elucidate the role played by habitat limiting factors and can contribute to improving the viability of habitat enhancement as a management tool for maximising self-sustaining salmonid populations.

1.8. AIMS AND OBJECTIVES

This thesis seeks to address aspects of the recommendations from the CEH/EA report Ecologically Acceptable Flows – phase 3 (Dunbar *et al.,* 2001). The primary goal is to model relationships between habitat variability and population dynamics of brown trout in a small chalk-stream to address the following aims;-

1.8.1. Aims

1. Model seasonal fluctuations in habitat availability and quality for different brown trout life stages.
2. Examine relationships between habitat and annual variations in trout abundance.
3. Test and validate PHABSIM derived habitat predictions in relation to trout population dynamics and evaluate the model as a tool for fine scale habitat modelling in chalk streams.

1.8.2. Objectives

Objective 1: Analyse the dynamics of the brown trout population in the River Piddle

Objective 2: Quantify habitat quality in contrasting reaches of the River Piddle for juvenile and adult brown trout during summer and winter.

Objective 3: Examine effects of temporal changes in habitat on trout abundance and identify aspects of habitat that may be acting as population limiting factors.

Objective 4: Assess the importance of spawning and rearing habitats in relation to juvenile recruitment in the River Piddle.

CHAPTER 2: REVIEW OF CURRENT KNOWLEDGE

2.1. LIMITATIONS ON PRODUCTION OF SALMONID POPULATIONS IN STREAMS

Wild salmonid populations are regulated by a combination of density - dependent and density - independent mortality. Density – dependent causes of mortality occur when changes in population density affect competition for space and food (Elliott, 1985, 1994: Kennedy and Strange, 1982; 1986a; 1986b). Density - independent mortality occurs as a result of abiotic factors and is mainly environmental in origin (e.g. temperature, discharge and habitat). These latter can have large effects on survival and act to determine abundance whereas underlying density – dependent mechanisms act to regulate abundance (Milner *et al,* 2003).

2.1.1. Density – Independent Regulating (Abiotic) Factors

Complex interactions between abiotic factors affect trout populations and are shown in Figure 2.1. Water quality factors will tend to affect presence or absence of the species. Other factors may determine local distribution patterns or set boundary conditions which determine abundance.

Water quality

The most important water quality parameters affecting brown trout are temperature, dissolved oxygen (DO) and pH. Water temperature is the most important controlling factor affecting salmonid ecology (Haury *et al.,* 1999), whereas DO and pH will be more likely to determine presence/absence of salmonids. Preferred temperature ranges between 7 ^{0}C and 17 ^{0}C with optimum growth rates occurring at 13-14 ^{0}C (Crisp, 1993). Respiratory metabolism increases with temperature and above 19 ^{0}C feeding ceases. The upper thermal limit is 21-25 ^{0}C (Alabaster and Lloyd, 1987; Crisp, 1993). Egg development rates, embryo oxygen uptake and survival are also influenced by temperature. Egg survival exceeds 95% at temperatures of 0-10 ^{0}C but declines to less than 50% above 12 ^{0}C (Crisp, 1993).

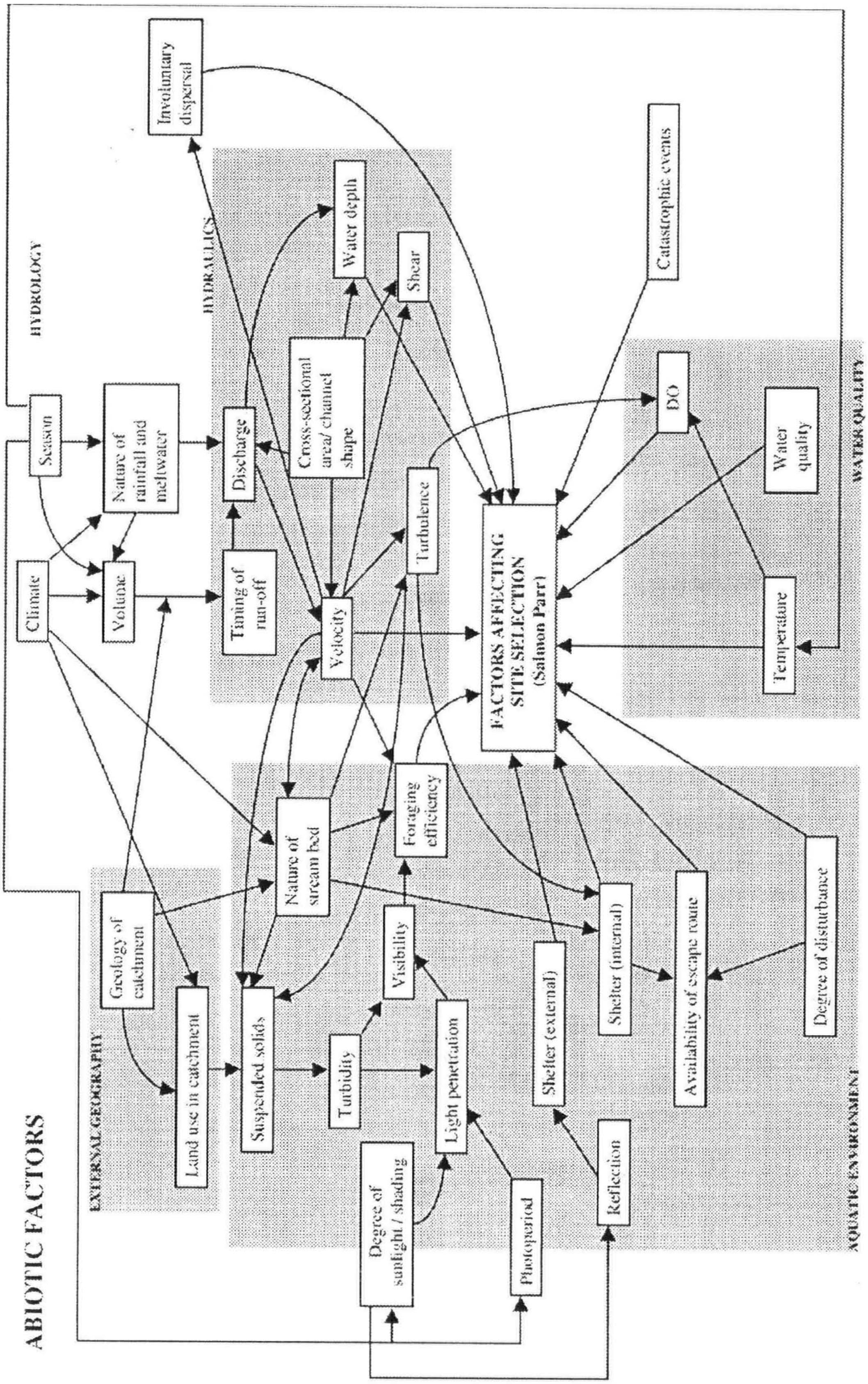

Fig. 2.1. Interactions between abiotic factors affecting stream dwelling salmonids *(reproduced with permission of J.D.Armstrong)*

Water temperature is also a behavioural regulator acting as a stimulus for migration and spawning (Haury *et al.,* 1999) and indirectly modifies other parameters such as dissolved oxygen and primary and secondary productivity (Westlake *et al.,* 1972; Haury *et al.,* 1999), which together ultimately affect trout biomass (Mann *et al.,* 1989).

Minimum oxygen concentrations are 5.0-5.5 mgl^{-1} but should ideally be above 80% air saturation. Dissolved oxygen requirements are inversely related to water temperature declining with increasing temperatures. At 80% saturation oxygen concentrations reduce from 10.2 mgl^{-1} at 5 ^{0}C to 7.3 mgl^{-1} at 20 ^{0}C (Crisp, 1993). Water pH below 4.5 or above 9.0 is lethal to salmonid eggs (Crisp, 1989). Low pH values can also lead to indirect toxicity due to dissolving of aluminium ions in solution or reduction of nitrogenous nitrogen to ammoniacal nitrogen (Crisp, 1993; Haury *et al.,* 1999).

Physical structure of the trout's environment

The trout stream environment is conditioned by river channel morphology which is a product of the interrelationships between discharge, gradient and sediment supply. These, in turn are governed by macro-scale variables such as climate and geology (Frissell *et al.,* 1986; Newbury and Gaboury, 1993).

The morphology of natural alluvial streams provides a greater diversity of habitat features for salmonids than steep, upland streams. In low gradient "alluvial" streams where depositional processes tend to dominate, the distribution of local bed scour and aggradation associated with converging and diverging flows produces characteristic morphological features of pools, riffles and meanders (Gregory *et al.,* 1994). These features are closely interrelated as locations of riffle crests determine distribution of stream energy as different alignments of successive riffles disperse flow alternately to opposite banks reinforcing the pattern of converging and diverging flow (Gregory *et al.,* 1994). Where one bank is undercut more readily meander formation is initiated. Pools typically develop on the outside of bends with riffles located at inflection points between bends. The spacing between riffles and pools and thus meander wavelengths are correlated with channel width, which in turn is a function of stream power and erodibility and cohesion of bed and bank materials (Schumm and Khan, 1972). Thus, variations in bed and bank materials will result in variations in stream width which will affect the spacing between riffles and pools. The form of pool and riffle sequences are also influenced by sediment supply as coarse, angular gravels will lock together creating "armour" against bed erosion to form stable riffle bars.

These features provide the physical structure of trout habitat (Summers *et al.*,1996) and are positively correlated with high mean standing stock of trout (Kozel *et al.*, 1989). Lower gradient streams tend to be correlated with higher trout abundance because they tend to produce a greater diversity of habitat features than upland rivers (e.g. Kennedy and Strange, 1982; Hermansen and Krog, 1984). In addition, lowland rivers are generally more fertile and riparian and in-stream vegetation has a more important influence on stream structure and trout habitat than in upland rivers (Bird *et al.*, 1995). In chalk-streams, vegetation plays a fundamental geomorphological role, affecting bank/bed stability, sediment transfer and hydraulic behaviour, as well as providing important physical habitat in the form of cover for trout.

Habitat diversity and bottlenecks

Habitat diversity is of fundamental importance to self sustaining populations of brown trout in lotic environments because availability of suitable habitats determines the numbers of fish that a stream can support. This is known as the carrying capacity. Different life stages of trout require specific habitat conditions such that amounts and types of different microhabitats can act to limit trout abundance and influence population structure (Allen, 1969; Milner *et al.*, 1978). Thus, absence of a critical habitat type for a particular life stage will act as a population limiting factor at that stage of the life cycle. This is the concept of the "habitat bottleneck" (Fig.2.2). Identifying where habitat bottlenecks are occurring is critical to conservation and management of wild trout populations but the amounts and types of habitat needed to maximise carrying capacity are difficult to define and poorly understood (Hunter *et al.*, 1991).

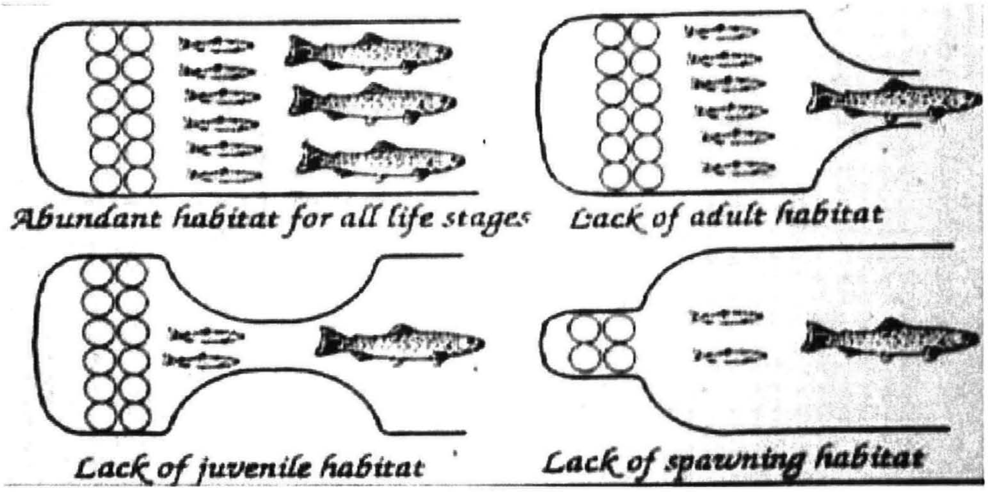

Fig. 2.2. The concept of trout populations being constrained by habitat bottlenecks (Adapted from Garcia de Jalon, 1995).

2.1.2. Density – Dependent Regulating (Biotic) Factors

Early studies of salmonid population dynamics show the determining role of behavioural factors, notably competition for space and food, in limiting natural populations (Allen, 1969). This is especially marked in brown trout due to a highly developed sense of territoriality which develops at a very early age (Kalleberg, 1958; Bachman, 1984; Elliott, 1990). Heland (1971a) showed that territorial behaviour and establishment of defensible territories by fry occurs between two and three weeks after emergence from the gravel.

Bachman (1984) showed that brown trout territories in a Pennsylvanian spring creek changed little over a period of years and that trout occupied the same well defined locations within a home range comprising a number of holding stations where maximum food value could be achieved with minimum energy expenditure. Fausch (1984) established that trout hold positions which maximise net energy gain and that position choice was highly correlated with growth rates. Fish which obtain the most energy efficient territories become the largest and a social hierarchy develops in which the dominant trout defend the best territories (Fausch and White, 1981). This hierarchical structure results in subordinate individuals becoming marginalised and forced to either migrate or die (Kalleberg, 1958; Elliott, 1990).

Consequently, territorial behaviour is responsible for regulating trout densities at the juvenile stage effectively imposing a limit on stream carrying capacity which then determines the future adult population of the stream (Le Cren, 1973; Elliott, 1984, 1994). At low spawning densities competition is limited and therefore reproduction is efficient and numbers of juveniles produced are closely proportional to spawning levels. As spawning numbers increase so does competition between fry and density – dependent factors serve to restrict the population as carrying capacity is approached. Thus, survival (from eggs to older life stages) usually decreases with increasing spawner density, changing most rapidly as carrying capacity is approached. The curve that expresses the form of this population regulation was defined by Ricker (1954) as typically dome shaped and is known as a stock – recruitment relationship.

Density – dependent regulation of abundance governs the general form of stock – recruitment relationships for trout (Elliott, 1994) and there is substantial evidence to show that the main regulating processes act during the very early stages of the salmonid life cycle (Egglishaw and Shackley, 1977; Gardiner and Shackley, 1991; Kennedy and Strange, 1986). In a long term study of sea trout in Black Brows Beck, Cumbria, England, Elliott (1993a) showed that regulation of population size was achieved through density – dependent mortality operating over a short critical period (30 – 70 days) when fry dispersed from the spawning gravels. Subsequent survival was shown to be proportionate and influenced by density independent factors. Gee *et al,* (1978) found maximum salmon smolt production (equated to juveniles age 2+) in the River Wye, Wales was attained at a fry density of 0.75 per m^2 on the 1^{st} June and that at densities above and below this level, production decreased following a similar dome shaped Ricker model.

The biological productivity of a stream will put a ceiling on trout production. However, the energy equivalence hypothesis states that the maximum biomass does not limit trout numbers *per se* because it can be composed of many small fish or a few large ones (Le Cren, 1969). As individuals grow the resources they require increase such that, assuming food and space remain constant, the number of fish can be expected to decrease as mean weight increases in response to competition by a process known as "self – thinning."

2.1.3. Relationships between Habitat, Carrying Capacity and Density Dependent Regulation

Habitat availability and quality have special importance as controlling factors of salmonid abundance in streams. As a critical resource (space) can limit populations at habitat bottlenecks. Carrying capacity, as determined by physical habitat, is independent of density but creates a bottleneck that increases competition thus stimulating density-dependence to operate (Milner *et al,* 2003). Such bottlenecks have been demonstrated to occur at the early post emergent fry stage and at spawning where spawning gravels are limited. The rate of self thinning is likely to vary depending on whether food or space is limiting (Grant and Kramer, 1990) and further variation would be expected to occur as suitability of habitats vary with fish size (Armstrong *et al*, 2003). Thus, self-thinning is most likely to occur when trout are growing through bottlenecks (Elliott, 1990) and as such a self thinning gradient may effectively define carrying capacity for different sizes of fish within a stock (Armstrong, 2005). Therefore, trout populations are limited by both biotic and abiotic factors which operate simultaneously and vary spatially and temporally in their degree of importance.

2.2. PHYSICAL HABITAT USE BY BROWN TROUT IN STREAMS

Stream resident salmonids habitually restrict their activities to localised subsets of the environment which best satisfy their immediate requirements (Jenkins, 1969) and distribution and abundance are strongly influenced by habitat especially during population bottlenecks (Elliott, 1994; Armstrong *et al,* 2003). Several abiotic factors are thought to be of particular importance in setting boundary conditions affecting carrying capacity and hence production of trout. These include temperature and annual stream flow variation (Binns and Eiserman, 1979). In addition, the importance of water depth, flow velocity, substrate particle size and cover have been well documented (Heggenes (1988b; 1990) and numerous studies have shown one or more of these variables to be correlated with distribution and/or abundance of brown trout in a wide range of stream types (e.g. Boussu, 1954; Fausch and White, 1981; Kennedy and Strange, 1982; Shirvell and Dungey, 1983; Cunjak and Power, 1986). Thus, broad ranges of acceptable conditions for these habitat attributes have been defined according to their suitability for different life stages of trout and salmon (see Armstrong *et al,* 2003 for a full review). Habitat Suitability Index (HSI) curves which express preferred ranges for depth, velocity, substrate and cover have been developed for use in habitat models (e.g. Raleigh *et al.,* 1986) and comprise the biological component of the Physical Habitat Simulation Model (PHABSIM) used in this study. Consequently, the importance of these four habitats attributes to stream dwelling brown trout will now be reviewed.

2.2.1. Water depth

Total water depth is important in determining habitat suitability, especially in small streams and for larger fish. Several authors have reported that brown trout tend to show increasingly strong preference for deeper stream areas with increasing size and age (Heggenes, 1988a). Solomon and Templeton (1976) found that individually marked brown trout in a small English chalk stream tended to occupy water with a progressively greater mean depth at age 1+ than age 0+. Kennedy and Strange (1982) found that salmon and brown trout fry were significantly more abundant in shallow water (<20cm) in two small Irish streams, while adults (2+ and older) were mainly present in deeper areas (>20cm). Bohlin (1977) reported a correlation between length of juvenile anadromous brown trout and depth of habitat utilised. Egglishaw and Shackley (1982) found a positive correlation in small Scottish streams, between densities of 0+ and 1+ brown trout and variations in area of water depth exceeding 10cm. This correlation became progressively stronger for older trout at depths greater than 15, 20 and 25cm respectively. Heggenes (1988b) showed that 0+ brown trout in a small Norwegian stream preferred a depth range of 10-20 cm while larger 1+ trout were more often found in deeper pools (30-40 cm).

2.2.2. Water velocity

Local variations in velocities create sheltering and feeding lies for all life stages of brown trout, the suitability of which are closely related to availability of low velocity niches (Bachman, 1984; Fausch, 1984). The quantity of drifting invertebrates, and therefore food availability, which pass a given spot is related to current speed (Elliott, 1967). Optimum feeding stations are those where energy expenditure is lowest relative to energy gain (Fausch, 1984). Shirvell and Dungey (1983) reported snout velocity to be the most important factor determining position choice by large brown trout in New Zealand streams which they attributed to energy cost-minimisation.

Water velocity may be a limiting factor for young salmonid fry, which are susceptible to downstream displacement at comparatively low velocities (>0.15 ms^{-1}) within eight weeks of emergence (Heggenes and Traaen, 1988a). Thus fry are unable to occupy habitats combining smooth substrates with even relatively low water velocities, placing immediate constraints on habitat availability.

It is clear that brown trout utilise deeper areas of stream more frequently with increasing size/age, placing 0+ fish at a competitive disadvantage, but this is less clear in respect of water velocity. Brown trout preferentially select low snout velocities but there is considerable variation as to preferred velocity ranges (Heggenes, 1988; Heggenes and Saltveit, 1990). In an Ontario river, Cunjak and Power (1986) observed considerable differences in snout velocities selected at two different river sites by older (>age 1+) brown trout (mean snout velocity 5.7 ms^{-1} compared to 16 ms^{-1}). These fish generally held positions in both faster and deeper water than 0+ trout, whereas several authors have reported that brown trout use slow-deep pool like areas with increasing size (Bohlin, 1977; Egglishaw and Shackley, 1982; Heggenes, 1988a, b). Such discrepancies are likely to be a result of the wide variety of streams observed but could also suggest that depth has greater importance in habitat selection than velocity.

There is considerable evidence for seasonal variation in velocity preference (Cunjak and Power, 1986). Brown trout seek out habitats characterised by slower velocities during winter, probably partly as a response to reduced nutritional requirements and energy conservation. Traditional summer feeding stations are typically in proximity to fast flowing water where maximum energy efficiency can be derived from drift feeding.

2.2.3. Stream substratum

Substrate conditions provide shelter from high water velocities and from predators (Heggenes, 1988). Stream-dwelling brown trout specifically select feeding stations where rocks or coarse particles deflect currents creating low velocity niches (Bachman, 1984) and concentrate currents into specific zones improving feeding niches which maximise energy efficiency (Fausch, 1984). Consequently, brown trout tend to avoid areas of fine substrate, such as silt and sand, preferring coarse gravel and cobble (Bohlin, 1977; Heggenes, 1988a, b) and spend much of their time close to the stream bed rather than in mid water or at the surface (Jenkins, 1969; Shirvell and Dungey, 1983; Heggenes and Saltveit, 1990).

The relatively uniform nature of gravel substrates in chalk-streams may reduce its importance for adult trout (Gosse and Helm, 1982) but brown trout fry prefer coarse cobble substrates to finer pebbles and gravels (Heggenes, 1988c). Trout fry have limited swimming ability and are susceptible to downstream displacement (Heggenes and Traaen, 1988a; Heland, 1999). Interstitial spaces between substrate particles create low velocity niches and sheltering lies in which fry can take cover (Bachman, 1984; Heggenes, 1988c). In addition, substrate size can determine the degree of visual isolation between young fry during initial establishment of territories (Heland, 1999). Where visual isolation is greater, average territory size is smaller resulting in increased carrying capacity at this life stage (Kalleberg, 1958).

Substrate type is also a critical factor determining quality of spawning habitat and choice of redd sites (Ottaway *et al.,* 1981). Substrates are unsuitable for spawning if particles are too large or tightly packed. Reported particle sizes range from coarse sand to larger cobbles (2-100mm) but medium gravel is generally considered to be preferred (Armstrong *et al.,* 2003). Shirvell and Dungey (1983) reported a mean particle size at spawning redds of 14mm and Crisp and Carling (1989) a median grain size of 10-20mm. Successful egg incubation depends on intra-gravel flow which is reduced where substrates contain fine sediments resulting in low embryonic survival (Maret *et al.,* 1993). Alexander and Hansen (1983) reported a 40% increase in numbers of young brown and rainbow trout when sandy bed load sediment in a stream was reduced by 86%.

2.2.4. Cover

Cover is especially important for brown trout and provides sanctuary from predators, protection from the current and visual isolation (Heggenes, 1988b). Juvenile and adult brown trout normally maintain station close to a shelter (Boussu, 1954) but adult trout will feed at greater distances from cover than juveniles (Lambert and Hanson, 1989) but tend to spend more day light hours under cover (Bachman, 1984).

Defining and quantifying cover presents considerable difficulties in comparison to the other main physical habitat variables. "Cover" can take many different forms, including brush, overhanging vegetation, undercut banks, boulders, water depth, turbulence and shade (Lewis, 1969; Fausch and White, 1981; Cunjak and Power, 1986; Wesche *et al.,* 1987). However, cover can be divided into two basic types; "overhead" cover and "in-stream" cover.

Overhead cover

Bank-side and marginal river vegetation plays a direct role as shelter (Boussu, 1954; Egglishaw and Shackley, 1977). Summers *et al.,* (1997) demonstrated a six fold increase for brown trout in a small chalk-stream tributary of the river Piddle following fencing and re-establishment of riparian vegetation. Lewis (1969) reported overhead cover to be the single most important factor affecting brown trout distribution in a stream. Overhead cover provides shading which has been noted to be of importance to adult trout which become increasingly negatively phototropic with age and develop progressively stronger shelter seeking behaviour (Butler and Hawthorne, 1968; Bagliniere and Maisse, 1999). Bachman (1984) showed that use by brown trout of stations with overhead cover increased with age. In two Norwegian streams, brown trout (>130mm) showed a clear preference for habitats providing a high degree of overhead cover (Heggenes, 1988a, b). Cunjak and Power (1986) demonstrated brown trout to have a strong preference for positions beneath overhead cover and that association to cover was significantly greater in winter than summer.

In-stream cover

Woody debris, stumps and root wads constitute important sheltering and "velocity" cover within a stream (Lewis, 1969; Milner *et al.,* 1978). Fausch and White (1981) showed that presence of submerged cover played important role in determining preferred resting positions between brook and brown trout, the latter being dominant competitors for positions beneath cover. Cunjak and Power (1987) tested the relative importance of above-stream and submerged covers and found that brook trout and brown trout both utilised submerged cover significantly more frequently than above water cover. Hunt (1982) observed a six fold increase in abundance of brown trout (>254mm fork length) following the addition of half-log covers to a Wyoming stream where cover was scarce.

In chalk-streams, submerged macrophytes are important both as shelter and in the structure of habitat by providing visual isolation (Jenkins, 1969; Bagliniere and Maisse, 1999) and modifying flows creating velocity niches (Dawson, 1978). Hermansen and Krog (1984) reported that macrophyte cover together with the amount of undercut bank were significantly correlated with densities of brown trout (>150mm) in a small Danish lowland stream.

Cover is particularly important because by providing hiding and foraging locations cover availability and diversity can increase the number of territories that can be established thus increasing stream carrying capacity (Wesche, 1980).

2.2.5. Summary

The relative importance of the four main habitat variables is difficult to assess and interactions between physical habitat variables appear to be more important than the suitability of individual variables (Heggenes, 1988). Shirvell and Dungey (1983) reported that velocity appeared to be the most critical factor affecting position choice, but that brown trout more readily chose positions with optimum combinations of depth and velocity rather than positions with more preferred values of either factor alone. Cunjak and Power (1986) observed that larger trout (age 1+) consistently occupied positions in faster and deeper water than age 0+ trout. Trout also utilise shallower water more readily in summer where cover is present (Boussu, 1954; Bachman, 1984). However, competition for space and food may modify habitat use (Heggenes, 1988a; Heggenes and Saltveit, 1990). Strong intraspecific competition characterises brown trout social behaviour with smaller trout tending to be restricted to sub-optimal habitats (Jenkins, 1969; Bachman, 1984; Heggenes, 1988a).

There is considerable evidence that where resources are sufficient resident brown trout complete their life cycles within a relatively "local" area of stream (Jenkins, 1969; Solomon and Templeton, 1976; Bachman, 1984). This "home range" consists of a variety of specific stations used by trout at different times for different purposes. Habitat use tends to be activity-specific with different characteristics for feeding, refuge and spawning habitats. Shirvell and Dungey (1983) showed that large adult brown trout (mean fork length 420mm) in New Zealand rivers preferred a mean depth of 31.7 cm for spawning sites but 65 cm for feeding positions. Competition for stations within overlapping home ranges means that availability and juxtaposition of suitable micro-habitats can regulate population size even in streams where food supply is abundant (Jenkins, 1969; Shirvell and Dungey, 1983; Hunter, 1991).

Therefore, where populations are habitat limited, greater habitat diversity will increase the likelihood of a self sustaining population being maintained by local adult stock. Consequently, where anthropogenic effects on streams have led to habitat degradation wild trout stocks can be improved by management actions which enhance physical habitat diversity. The effects of some of these measures on trout populations will now be reviewed.

2.3. ENHANCEMENT OF WILD TROUT HABITATS

Kauffman *et al.,* (1997) distinguish between two fundamental approaches to restoration; passive and active. Passive or natural restoration refers to the halting of activities causing ecosystem degradation. Active restorations are needed when the inherent capacity of ecosystems to recover naturally has been lost. Summers *et al.* (1996) emphasise that habitat management is fundamentally an ecological task and that "engineering" should adopt a "soft" approach wherever possible based on encouraging natural processes to create the desired in-stream habitat, rather than a "hard" approach which involves a degree of channel "straight-jacketing." Many studies document common methods used to enhance habitat diversity in salmonid streams (Gore, 1985; Hunt, 1988; 1993; Hunter, 1991; Summers *et al.* 1996). Some techniques which have been applied to lowland rivers in southern England are considered below.

2.3.1. Creation of within Channel Diversity

The importance of habitat diversity for the carrying capacity of a trout stream has been well documented and consequently much in-channel enhancement work has focussed on improving channel diversity. Deflectors work well in low gradient streams and can function as point bars, narrowing the stream and re-directing flows creating deeper, faster water (White and Brynildson, 1967; Hunt, 1993). Deflecting currents away from nearside banks allows fine sediment deposition in the lee assisting bank consolidation and paired deflectors can narrow the channel creating deep scour pools from which eroded gravel is deposited downstream to provide spawning habitat. Low profile weirs are used to create diversity by concentrating currents. An upstream pointing "V" weir with a low centre steers currents towards the centre of the stream creating scour pools and can also assist gravel accumulations above weirs and on pool tail-outs. In an evaluation of trout population response to habitat enhancement in six Colorado streams, Riley and Fausch (1995) showed that K-dams increased pool volume by an order of magnitude in two years, with adult brook trout numbers increasing in one stream by 231 %. Uses of different combinations of these in-stream structures for narrowing and deepening channels and increasing pool - riffle frequencies have been widespread in the USA. Hunt (1969, 1971, 1976, 1988) demonstrated their effectiveness for enhancing habitat diversity in Lawrence's Creek, Wisconsin where brook trout numbers over 15cm fork length were increased from 562 (pre-restoration 3 year mean) to 1638 (post-restoration 3 year mean).

2.3.2. Improvement of Spawning Habitat

Chalk and limestone streams suffer particular problems of lime concretion and high fine sediment loadings. Solomon and Templeton (1976) showed that trout fry densities in a Hampshire chalk stream were highest where the bed was harrowed annually and concluded that harrowing alleviated gravel compaction and concretion. Summers and Giles (1995) showed that riffle "cleaning" with high pressure water jetters to de-silt spawning gravels increased both egg survival and numbers of spawning fish in the Hampshire Avon where egg survival rates as low as 10 % increased up to 90 %.

Suitable spawning gravels are often limited in low energy chalk streams which have been impacted by dredging and gravel planting can be used to increase spawning areas. O'Grady *et al.* (1991) created riffles in the River Boyne, a drained lowland stream in Ireland, by placing rubble mats in deep slow reaches which successfully increased the number of salmonids. Solomon (1983) cites a study in Wyoming where pools were excavated and the gravel used to plant a riffle downstream of each pool. Numbers of spawning cutthroat trout increased from six to 250 over ten years. Where gravel substrate is highly mobile downstream pointing "v" gabion weirs can be used to dissipate the flow and acts as gravel traps (Hunter, 1991).

2.3.3. Channel Narrowing

Chalk streams in southern England have suffered from problems associated with low flows particularly since the late 1980s and channel narrowing (partial infilling of the channel behind an erosion resistant face of logs, rip-rap or geotextiles) has been employed to produce deeper, faster flowing water where higher velocities scour gravels clean of sediments. In the River Dun, a small Berkshire chalk stream, narrowing to 40 % to accommodate normal summer base flows induced a self cleansing regime and allowed flora and fauna to re-establish (RSPB, 1994).

2.3.4. Prevention of Stream-Bank Erosion

Livestock grazing is a major cause of erosion by trampling and vegetation removal and is considered the most prevalent cause of stream ecosystem degradation in the western USA. Cessation of grazing in riparian zones is often the single most effective approach to restoring salmonid habitats allowing re-establishment of riparian vegetation (Beschta *et al.,* 1991; Kauffman *et al.,* 1993). Dahlem (1979) found that stock exclusion increased the amount of stable bank by 20 % resulting in an increase of between 52 - 70 % in spawning gravels as a result of reduced sediment inputs. Summers *et al.* (1997) demonstrated a ten fold increase in juvenile trout numbers in the two year period following fencing in the Devil's Brook, a tributary of the River Piddle, Dorset.

2.3.5. Creation of Marginal Cover

Cover is an extremely important aspect of habitat for all life stages of stream dwelling salmonids. Boussu (1954) found a direct relationship between increases and decreases in trout numbers and removal and replacement of cover. Marginal cover can be divided into (i) above water overhead cover and (ii) submerged cover. Overhead cover is afforded by grasses, bushes or trees, the cover value for trout being dependent on width of overhang, height above the water surface and depth of water beneath. Submerged cover can be provided by structures designed to simulate undercut banks such as cantilevered “skyhook" covers which overhang into deeper water from a shallow shelf and are backfilled with soil material to form a new bank line. These were first used in Wisconsin streams for the dual purposes of narrowing over wide streams and providing cover in a simulated undercut (Hunt, 1993).

2.3.6. Creation of In-Stream Cover

Boulder placement can enhance stream carrying capacity by increasing hydraulic sheltering lies and visual isolation. O'Grady *et al.* (1991) used boulders on the River Boyne, Ireland to reinstate bed "roughness" which resulted in substantial increases in numbers of salmon and trout parr. Maughan *et al.* (1978) found that trout occupied lies in close proximity to boulders. Hunt (1988) reported increases in both wild brook trout and brown trout associated with boulders on the Hunting River, Wisconsin.

Tree trunks, branches and logs provide excellent cover for fry and juvenile trout as they are more effective than boulders at producing low velocity niches under spate conditions. Such large woody debris can also act to create local scour increasing channel diversity. Submerged shelters such as half-log cover platforms also provide hydraulic shelter and visual isolation. Hunt (1982) placed 142 submerged structures in a 750m length of a Wisconsin stream with little cover and found a 533 % increase in numbers of trout > 300mm fork length.

2.3.7. Summary

The nature of the stream environment will govern the suitability of different habitat enhancement measures and their effectiveness can vary considerably (Rosgen, 1996). Hunt (1988) evaluated 45 trout habitat restorations carried out between 1953 and 1985 in Wisconsin streams and concluded that current deflectors and bank-side covers were the most successful devices overall especially when used in combination. However, many studies reporting increases in trout numbers may be partly due to local re-distribution of fish rather than increases in abundance which are more difficult to detect at a population level. Salmonids occupy their habitat fully only at certain times of the year and habitat may only be limiting during such critical periods (Milner *et al,* 2003). To enhance habitat effectively, it is necessary to identify these critical periods and focus management interventions in the first instance on these stages (Armstrong *et al,* 2003).

2.4 MODELLING RELATIONSHIPS BETWEEN HABITAT AND TROUT POPULATIONS

The potential for habitat bottlenecks to stimulate density dependent mortality in juvenile salmonids and thus for physical habitat to act as a population limiting factor, is well established (Nehring and Anderson, 1993; Elliott 1994; Milner *et al.,* 2003). Measurement of in-stream habitat is therefore critical for estimating potential carrying capacity of streams. In addition, understanding links between habitat and population dynamics is essential where fisheries management interventions involving habitat enhancement and river rehabilitation are to successfully improve salmonid production.

In theory, a dependence of stream salmonid abundance on habitat implies that it should be possible to derive predictive relationships between abundance and habitat features. There have been many attempts to develop empirical models as management tools to provide indices of habitat quality, predict fish abundance or predict consequences of habitat manipulation (Milner *et al.,* 1998). A plethora of multiple regression based models have been developed which relate habitat measurements to observed numbers of trout in order that expected numbers can be predicted in similar streams. Reviews of commonly used North American and European models have shown that many such models can account for significant proportions of variance in measured salmonid abundance (Fausch *et al.* 1988; Barnard and Wyatt, 1995).

One of the most successful modelling systems has been HABSCORE (Milner *et al.*, 1993) which uses a combination of site variables measured by transect survey and map-based variables, reflecting each sites location within the catchment. Models developed for four categories of salmonid: trout YOY (age 0+); trout PYOY (>0+); salmon YOY (age 0+) and salmon PYOY (>0+) output predictions of expected numbers per 100 m^2 (assuming that recruitment is not limited and habitat condition is pristine). A Habitat Quality Score (HQS) gives a measure of difference between expected and observed trout densities. This is not to be confused with carrying capacity which may rarely be reached in areas of natural recruitment because density – independent effects keep the population at lower levels (Milner *et al.*, 1998).

2.4.1. Predictive Models: Some Limitations and the Importance of Scale

The likelihood that many sites used in habitat modelling have population densities below their carrying capacity is one of the principle constraints on the performance of habitat models (Armstrong, 2005). Predictive models have been found to lack geographical transferability and rarely perform well in stream types other than those in which they were developed (e.g. Binns and Eiserman, 1979).

Those models combining both local site features (e.g. width, depth, substrate, cover) and catchment scale variables (e.g. altitude, geology, and discharge regime) tend to perform best. This is because "spatial nesting" of riverine habitats means that local stream influences often originate at larger spatial scales (Frissell *et al.*, 1986). The interdependence of stream channel structure with fluvial dynamics and geology means that catchment variables are both independent factors in their own right and act as surrogates for site specific variables such as substrate and flow type. Thus, the relative importance of habitat factors to fish distribution and abundance may depend upon the scale at which habitat is examined (Rabeni and Sowa, 1996). This is because overall variability in salmonid populations, when measured over time and many different sites, is composed of both spatial and temporal variance. Spatial variance is determined by factors associated with the physical features of each site (local habitat) and is thus the variance component that most habitat models attempt to explain. Many habitat models developed on short term data sets explain up to 75% of population variance (Fausch *et al.* 1988). However, these results can be misleading because they ignore temporal variation which can cause spatial variance to be comparatively low (Armstrong *et al.*, 2003).

Wiley *et al.* (1997) examined sources of variation in brown and brook trout abundance in Michigan streams to evaluate relative influence of variations in space and time. Variances were partitioned into catchment-scale spatial factors (soil type, geology, land cover, gradient), and regional and local temporal factors. These latter considered annual variations in abundance resulting either from factors operating simultaneously across all spatial scales (e.g. climatic or hydrological) or from site specific factors operating locally (e.g. anthropogenic disturbances or predation and competition). The relative magnitudes of these three components of variance were used to assess the importance of ecological processes operating at different scales. Regional scale temporal variance was found to explain 50% of variation in brook trout abundance whereas spatial variance accounted for 50% of variation in brown trout abundance suggesting that site-specific habitat requirements were more important influences on population dynamics of brown than brook trout.

HABSCORE models based on data sets for the River Conwy, north Wales where time series were available showed that a relatively high proportion of total variation in YOY and PYOY trout and salmon was accounted for by spatial variance (46 – 62%) when considered at the river catchment scale. Temporal variance for the same age classes was low (4 – 12%). However, when variance was estimated at the within – tributary scale mean spatial variance (22 – 42%) was of a similar order of magnitude to temporal variance (24 – 39%) (Milner *et al.*, 1995). These results demonstrate the importance of scale in that at the smaller tributary scale of analysis, factors other than local site habitat were having an equally strong and synchronous influence on abundance.

Multi-scale approaches are therefore more effective in identifying limiting mechanisms regulating populations. Rabeni and Sowa (1996) used a hierarchical approach employing three spatial scales to look at relations between habitat and smallmouth bass in Missouri streams. Scale was found to be important in distinguishing habitat factors responsible for presence and abundance from those affecting within stream distribution.

Habitat – fish relationships are extremely complex and dynamic and models linking habitat variables to production of salmonid fishes are inevitably simplifications of complex ecological processes. Therefore, caution should be applied when using them to predict effects of altering specific habitat components to guide habitat improvement schemes.

2.4.2. The Physical Habitat Simulation Model

A model which has been applied widely in North America for quantifying ecological effects of flow regulation and predicting habitat gains associated with stream enhancement) is the Physical Habitat Simulation Model (Bovee *et al.,* 1998). PHABSIM is a suite of hydraulic and hydro-ecological models developed by the US Fish and Wildlife Service as part of the In-stream Flow Incremental Methodology (IFIM; Bovee, 1982) and is based on the assumption that species life cycles and distribution are responses to hydraulic conditions.

The biological component of the model comprises habitat suitability curves which express target species preferences for depth, velocity and substrate/cover as a numerical value between 0 – 1 (Habitat Suitability Index or HSI). Salmonids are particularly suited to the methodology because they exhibit habitat preferences within a range of tolerable conditions that are specifically defined in terms of depth and velocity. The suitability of habitat as defined by these preference curves is combined with hydraulic data to produce an index of habitat quality expressed as Weighted Useable Area (WUA). Thus, the area of stream providing suitable habitat conditions for different life stages can be quantified as a function of discharge (Johnson *et al.* 1995). In common with other predictive models, PHABSIM makes an implicit assumption that population dynamics are related to habitat availability in streams but does not predict changes in fish communities or abundance in response to habitat. Nevertheless, numerous studies on salmonid streams in the Western USA have successfully demonstrated good correlations between PHABSIM derived habitat predictions and biomass or density of trout (e.g. Stalnaker, 1979; Nehring and Anderson, 1983; 1993). Nehring and Anderson

(1993) found that WUA was significantly correlated with trout densities in 10 out of 11 Colorado streams studied.

However, other studies failed to validate links between habitat predictions and salmonid abundance which led some authors to question the robustness of PHABSIM as a predictive tool (Mathur, *et al.,* 1985; Rimmer, 1985; Irvine *et al.,* 1987; Scott and Shirvell, 1987; Orth, 1987). Many of these studies lacked sufficient methodological rigour and ignored the fundamental assumption that physical habitat must be the primary population-limiting factor (Shuler and Nehring, 1994). In some earlier studies other factors such as food abundance were shown to have been more important population regulating mechanisms than physical habitat (e.g. Rimmer, 1985; Irvine *et al.,* 1987).

The most contentious aspect of PHABSIM concerns definition of habitat preference curves because habitat predictions (WUA) are sensitive to the types of curves used (Bovee *et al.,* 1998: Vismara *et al.,* 2001). Recent work has shown that curves are also sensitive to density (Greenberg, 1994) and vary with discharge (Holm *et al.,* 2001). There is an on-going debate in the literature as to the applicability of "generalised" versus "site-specific" suitability curves which can result in considerable differences in predicted WUA (Dunbar *et al,* 2001). This is because site and season can have a strong influence on salmonid habitat use due to habitat availability varying spatially between sites and temporally within sites. Thus, shapes of HSI curves can be conditioned by when and where the habitat use data was collected and constrained by habitat availability in the sampled stream. Some authors argue that site specific curves always represents the best choice but transferability of HSI curves to river "types" other than those in which they were developed has been found to be poor and has been criticised as scientifically unrigorous (Johnson *et al.*, 1993; Williams *et al.,* 1999). However, Shuler and Nehring (1994) compared site specific curves developed for juvenile and adult brown trout in the Rio Grande River with curves previously developed in a similar river (South Platte) to test effects on WUA predictions. They found that both sets of curves accurately predicted the relative magnitude and direction of responses of brown trout to changes in habitat. Vismara *et al.,* (2001) found that HSI curves developed for brown trout in the River Adda, Italy were highly correlated for velocity and depth suitability with those developed by other authors in a variety of river types.

2.4.3. Application of PHABSIM in Studies Linking Habitat to Fish Populations

However, PHABSIM continues to be an evolving methodology based on a sound premise that population size at any given time is determined by past habitat conditions rather than those prevailing at the time of sampling (Bovee *et al,* 1998). Despite the models inherent limitations, one of its great strengths for modelling dynamic systems is thus its ability to account for the effects of temporal as well as spatial variations in habitat (Capra *et al,* 1995). Knowledge of critical habitat limiting periods is one of the primary needs in understanding fish population dynamics (Bjorn and Reiser, 1991) and PHABSIM can be applied to elucidate bottlenecks to production. Capra *et al* (1995) found that magnitude and durations of critical periods (when WUA was below a pre-determined threshold) were related to trout population structure in two wild brown trout rivers of different morphology in France. The relationship between spawning habitat conditions and relative density of 0+ trout the following year suggested a continuous duration of more than 20 days with spawning WUA below 80% of optimum acted as a temporal bottleneck to recruitment. This study demonstrates the efficacy of PHABSIM outputs for interpreting population limiting events, especially given that WUA is likely to be more closely correlated with fish abundance during critical periods than at other times (Orth, 1987; Milner *et al.,* 2003).

In a study of population dynamics of bass in the Huron River, Michigan (Bovee *et al.* 1994) used PHABSIM to determine habitat - population relationships. Habitat effects were shown to be most critical to early life stages and timing of extreme events was as important as magnitude. Population related habitat limitations were found to be associated with high flows and lowest habitat amounts were not necessarily the most biologically significant events affecting population dynamics.

Shuler and Nehring (1994) used PHABSIM to assess trout population response to habitat enhancement (boulder placement) on the Rio Grande River, Colorado. GIS maps of predicted changes in habitat quality resulting from different habitat enhancement demonstrated that trout showed preferences for mid-channel boulder groupings and wing dams at low to moderate flows, and marginal boulders and wing dams at high flows. Shallow areas (depth <1m) had higher habitat quality where boulder structures were present. Overall, boulder placement led to a direct increase in density and biomass of trout exceeding 35cm fork length.

PHABSIM has also been applied to assess habitat improvement schemes in the UK (Elliott *et al.,* 1996). However, the main driving force behind development of PHABSIM in the UK has been for use in assessing effects of abstraction on salmonid habitat availability (Dunbar *et al.,* 2001). A research and development project "Ecologically Acceptable Flows" (R&D Project 282-EAF) was established to support application of PHABSIM to UK rivers (Johnson *et al.,* 1993). Johnson *et al.* (1995) assessed impacts of groundwater abstraction on brown trout populations of the River Allen, Dorset in order to define a minimum ecologically acceptable flow regime as part of EAF phase 1. Habitat time series were developed for the period 1970-1991 for four life stages of brown trout based on historical flows. A groundwater model was used to develop a time series of "naturalised" flows with the historical effect of abstraction removed which allowed impacts of abstraction on habitat to be assessed. Results indicated that habitat was most impacted in summer and reductions were in direct proportion to the abstraction effect. Juvenile habitat was most significantly impacted and was critically limited for 50 % of the time.

2.4.4. Summary

PHABSIM undoubtedly has considerable application as a management tool for quantifying availability and quality of physical habitat in a variety of contexts. It has been used successfully to predict salmonid abundance based on WUA and has been rigorously validated by numerous studies during the last twenty years. The potential to identify population limiting bottlenecks either as temporal events or spatially limited habitat can improve understanding of factors effecting carrying capacity in salmonid streams. The present study attempts to explore this potential in a UK chalk stream where habitat appears to be the primary limiting factor, by examination and validation of relationships between habitat (WUA) and variations in abundance within a population of wild brown trout.

CHAPTER.3. THE RIVER PIDDLE: PHYSICAL DESCRIPTION AND BACKGROUND TO THE STUDY AREA

The River Piddle, Dorset, England is renowned for its native brown trout populations which merit a high level of protection and consist primarily of resident trout with a small anadromous component (Environment Agency, 1999). The trout population in the area of Tolpuddle was monitored annually from 1993-2001 by the Game Conservancy Trust using electro-fishing and comprised the study area for this project. The physical characteristics of the catchment are described below.

3.1. CATCHMENT AND GEOLOGY

The River Piddle is a third order stream draining a catchment of approximately 183 km^2 in area. It rises at four major springs near the village of Alton Pancras and flows approximately 40 km south and east to form a common estuary with the River Frome, before discharging into the English Channel via Poole Harbour (Fig. 3.1).

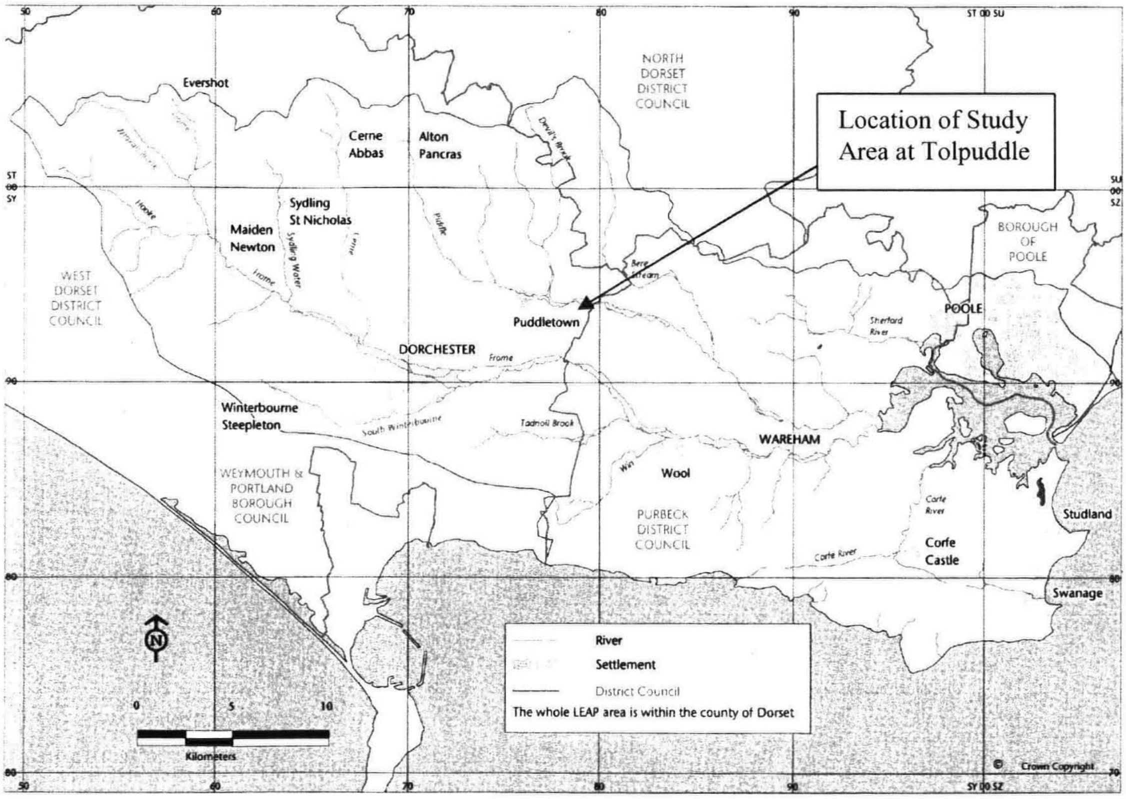

Fig. 3.1. Map showing the River Piddle catchment and location of study area

The Devil's Brook and Cheselbourne stream join the Piddle east of Puddletown, and the Bere Stream meets at Warren. In the upper reaches the river is mainly a winterbourne. The middle reaches comprise a braided network of water meadow and flood relief channels. The major aquifer is Upper Cretaceous Chalk, but further south there is also more recent geology of Reading Bed sands and gravels. The lower part of the catchment comprises more acidic, sandy soils characteristic of Dorset heath land. Land use on the more fertile floodplain is predominantly permanent pasture and arable land. Grassland and arable land constitute approximately 70-80% of the land use in the Piddle and Frome Local Environment Area Plan (LEAP) region (Environment Agency, 1999).

3.2. CLIMATE AND HYDROLOGICAL REGIME

Rainfall distribution over the catchment is highest at the western (upper) end of the catchment and lowest in the east around Poole Harbour. Annual average rainfall totals (1969-1990) range from 948 mm at Puddletown to 776 mm in Poole (Environment Agency, 1999). The high porosity of chalk ensures that the Piddle derives the majority of its flow from groundwater aquifers and relatively little from run-off. The buffering effect of the aquifer produces a stable flow regime with an absence of extreme low flows and sudden spates. Winter high flows rarely exceed bankfull stage and summer base flows are maintained by groundwater (Mann *et al.*, 1989). Long term mean monthly flows at Tolpuddle (1965-2000) range from approximately 0.18 m^3s^{-1} in August/September to 2.4 m^3s^{-1} in February. Median flow (Q50) 1965 – 2000 is approximately 0.54 m^3s^{-1} (appendix.3).

3.3. ECOLOGY AND FRESHWATER FISHERIES

The Piddle is a typical lowland chalk-stream possessing a range of distinctive characteristics common to this unique ecotype. Groundwater rises at a relatively constant 9-10 ^{0}C throughout the year maintaining stable seasonal and diel temperature regimes. The filtering effect of chalk screens out impurities and produces base rich alkaline waters containing calcium carbonate in quantities greater than 200 mgl^{-1} giving the water a translucent clarity (Mann *et al.*, 1989). Water quality throughout the majority of the catchment achieves a RE1 (chemical) compliance with River Quality Objectives (River Ecosystem Classification) – *water of very good quality suitable for all fish* *species.* Those limited areas not achieving this standard, notably the Bere Stream, are affected by discharges from watercress beds and fish farms.

The Piddle supports high primary and secondary production dominated by large aquatic macrophytes, mainly *Ranunculus* spp. (Westlake *et al.,* 1972). The high levels of primary production result in high macro-invertebrate productivity (Wright *et al.,* 1994) that forms the basis of trout diet (Maitland and Campbell, 1992). Dominant fish species are resident and anadromous brown trout *(Salmo trutta*) and *Salmo salar* (Atlantic salmon), *Phoxinus phoxinus* (minnow), *Cottus gobio* (bullhead), *Noemacheilus barbatulus* (stone loach), *Esox lucius* (pike) and *Anguilla anguilla* (eel) (Bird *et al.* 1995). Trout productivity and growth rates are high in chalk streams (Mann *et al.,* 1989; Giles, 1994). Brown trout at Tolpuddle attain a modal length of 200mm at age 1+ with asymptotic lengths in excess of 400mm.

The Piddle is designated a *priority habitat* (chalk river habitats) under the UK Biodiversity Action Plan (UK BAP) because of a number of important species of conservation concern most notably, native white-clawed crayfish (*Austropotamobius pallipes*).

3.4. GEOMORPHOLOGY, VEGETATION AND HABITAT

The products of chalk weathering produce coarse flint gravel beds but soft, easily eroded banks (Summers *et al.,* 1996). The dampening effect of the aquifer combined with a low mean gradient (2.18m/km) results in stable flows and relatively low stream powers. Thus, channel morphology tends to be less diverse than lowland streams flowing over mixed geology and the most common morphological features are relatively uniform "glides" (Raven *et al.,* 1998). However, in-stream and riparian vegetation is relatively more important than in other river types (Holmes, 2002). Fertile alkaline soils produce a lush littoral margin, dominated by tall herbs and emergent reeds such as *Glyceria maxima* and *Phalaris arundinacea* which trap sediment at the margins and stabilise bank materials through moisture reduction and the binding effects of roots (Gurnell, 1995). In stream macrophytes bind gravel substrates together reducing bed scour resulting in less highly developed pool - riffle sequences (Dawson and Kern-

Hanson, 1979). Vegetation plays a fundamental geomorphological role, effecting bank/bed stability, sediment transfers and hydraulic behaviour, as well as providing important physical habitat in the form of cover for trout.

3.5. PROBLEMS OF HABITAT DEGRADATION

The chalk streams of southern England have been historically subjected to major alterations especially associated with deepening and straightening to improve land drainage for agriculture with a consequent reduction in natural physical diversity (Petts, 1984). Water mills and weirs transformed these streams from a sinuous pattern of shallow, anastomosed channels with pool and riffle sequences, often into highly engineered impoundments of uniform width and depth. The River Piddle has been subject to channelisation and dredging which has removed much of the original diversity and stream power has been insufficient to restore this natural habitat diversity (Brookes and Shields, 1996). Physical channel structure has been severely impacted by overgrazing of livestock in unfenced riparian zones. The Piddle has the most severe bank erosion problems of all the Wessex streams with an estimated 25km of river exposed to cattle grazing (Game Conservancy Trust, *undated*). This has resulted in heavily trampled banks, loss of riparian vegetation and severe channel over-widening in some reaches. This occurs because the binding effect of bank-side vegetation is lost but macrophyte roots bind substrate gravels which limit bed scouring such that lateral displacement predominates and the banks are more easily eroded (Summers *et al.*, 1996). This is a major problem leading to trout habitat loss. Over-wide streams become increasingly shallow as the channel spreads laterally resulting in loss of pools and deeper water as flow concentrates at the banks, lowering bed levels at the margins, while the "channel" becomes colonised by terrestrial vegetation resulting in complete elimination of trout habitat.

In common with other chalk streams in southern England, the river Piddle suffers from problems resulting from ground water abstraction for potable supplies. A series of twenty-eight boreholes in the catchment take groundwater for a variety of public and private uses including agriculture, industry and domestic supply. Since the mid-1980s there has been increasing concern about the ecological effects of abstraction exacerbating problems of low flows. Abstractions at Alton Pancras, Briantspuddle and

Dewlish have been shown to significantly reduce flows and over 10km of river have been identified as experiencing significant impacts on ecology and fish habitats (Hill and Langford, 1992: Environment Agency, 1996a). The Piddle suffers particular problems of siltation and eutrophication. Run-off from agricultural land has caused siltation problems detrimental to salmonid spawning (Crisp, 1993) and elevated nitrate levels have led to nutrient enrichment resulting in widespread algal colonisation of substrates. These problems have been exacerbated by low flows which have reduced the magnitude and frequency of flushing flows.

3.6. MEASURES TO ALLEVIATE HABITAT DEGRADATION

A programme of physical habitat restoration was initiated by the Game Conservancy Trust on three chalk river systems in 1994 including the river Piddle. The main aims were to restore channel diversity and improve spawning habitat and refugia for larger wild brown trout (Summers *et al.,* 1996; Summers *et al.,* 1997; Giles, 1997a, b; Cowx and Welcomme, 1998). The most commonly used techniques on the Piddle were fencing in conjunction with substrate redistribution methods (Game Conservancy Trust, *undated*; Langford *et al.,* 2001). Fencing was introduced "on a wide scale" to restrict cattle access to short sections or to cattle drinks. Current deflectors and weirs were used to re-distribute substrate by enhancing scour and creating pools. Staked log covers and floating cover boards were added to some pools to provide refugia and increase potential cover for trout. Some limited substrate augmentation was undertaken in certain reaches where gravel riffles were introduced. Gravel jetting using high pressure hoses was also employed to de-silt gravels and increase effective spawning areas. Impoundments were alleviated where possible by removal of obstructions, hatches and sluices to allow free flow of water. To address ecological problems associated with low flows a stream flow augmentation scheme was introduced by the Environment Agency in 1998 based on a pre-determined ecologically acceptable minimum flow threshold at Briantspuddle (Strevens, 1999).

3.7. THE STUDY AREA

The River Piddle study area is shown in figure 3.2. The Upper river sector (Cobbs Wood) consists of approximately 0.5 km of main stem from the confluence with the

Devils Brook before it bifurcates, converging into a single channel again approximately 1 km downstream. The Lower river sector (Tolpuddle) begins at this junction and flows for approximately 400m to a set of former hatches which marks the downstream boundary of the study site.

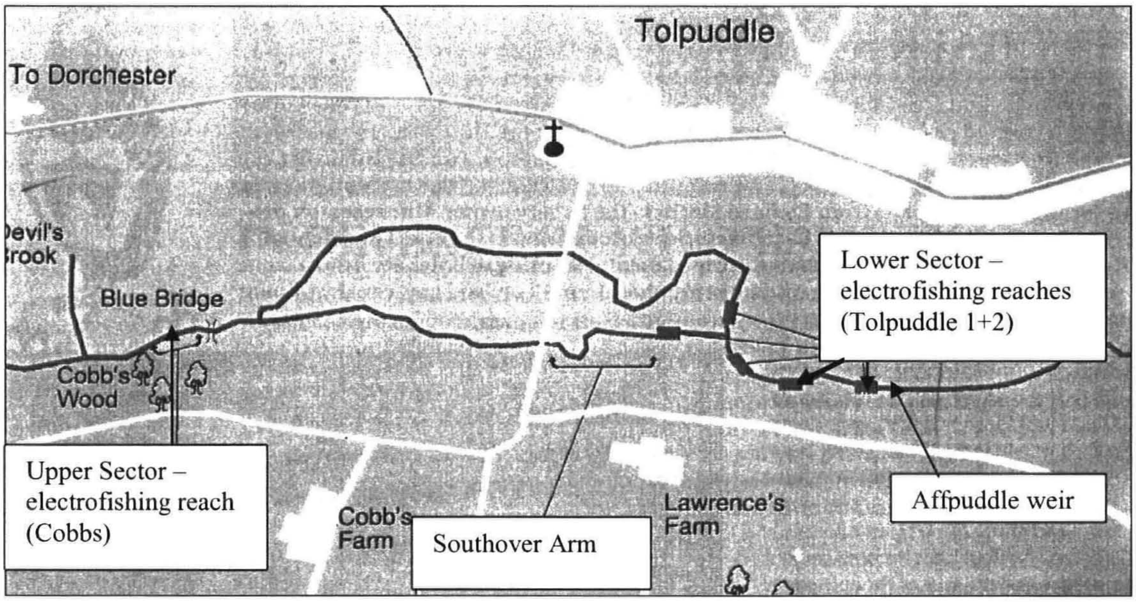

Fig. 3.2. Map showing the locations of the Upper and Lower river sectors at Tolpuddle.

The lower sector comprises grazed pasture on the left bank but is permanently fenced providing a mature riparian zone with some over shading from trees. The upper sector predominantly traverses an "open" riparian zone of improved pasture. This reach was fenced in 1994 to alleviate effects of cattle poaching which was severe in places. This facilitated rapid recovery of dense littoral margins in this reach. The river Piddle in this area is an important brown trout fishery and was selected because it has been managed for twenty years on a "catch and release" basis to conserve wild stocks. Therefore, the trout population is not subject to cropping by angler harvest and there is no stocking of hatchery trout. Pike *(Esox lucius)* were removed as part of the Game Conservancy project and their numbers routinely controlled during the study period to alleviate the effects of piscivorous predation. Thus, physical habitat could reasonably be assumed to be the most important limiting factor which provided an opportunity for the present study to examine wild brown trout population response to habitat effects in a chalk-stream.

CHAPTER.4. FIELD METHODS AND MATERIALS

The Physical Habitat Simulation Model (PHABSIM) quantifies stream area providing suitable habitat for salmonids under differing flow conditions and was used in this study to model the effects of habitat on the population of brown trout in the river Piddle. In order to calibrate the model data were collected following standard use of transects to characterise stream conditions as outlined in Bovee *et al.,* (1998). Fieldwork comprised three distinct phases;

1. habitat mapping and selection of study reaches
2. surveying of transects for sampling habitat within selected reaches
3. sampling of habitat conditions at transects for input to PHABSIM

4.1. HABITAT MAPPING

The study area was divided into three discrete sectors for the purposes of habitat mapping: upper main stem, lower main stem and middle, where the river divided into two arms. A walk-over survey was conducted in spring 1999 to determine habitat types present and the relative proportions of each type in each sector. This approach consisted of mesohabitat typing as a basis for selection of PHABSIM reaches, and followed procedures outlined in Maddock (1996). Simple morphological habitat units were identified based on local channel geometry and the flow types classification used in the River Habitat Survey (Raven *et al,* 1998). These were classified visually as follows;

- Pool
- Flat
- Deep glide (max depth >0.5m)
- Shallow glide (max depth <0.5m)
- Riffle
- Rapids/cascade

A measuring tape was pegged out along the bank to form a longitudinal datum against which to draw an accurate sketch map of each sector. Maps were plotted on a grid section data sheet at a scale of 1:500 and were used to assess proportions of different meso-habitats present in each river sector. This assisted selection of representative reaches and placement of transects by ensuring habitats were sampled in proportion to their occurrence (Bovee *et al.,* 1998).

4.2. REACH SELECTION

Reaches selected for application of PHABSIM were based on assessment of morphological diversity from habitat mapping and pre-defined electro – fishing sections used by the Game Conservancy Trust. Main stem river sectors comprised four contiguous electro-fishing sections varying in length from 65m to 185m. Contrasting reaches of similar length with differing habitat characteristics and population dynamics were selected; one from the upper main stem (Cobbs Wood) and two from the lower main stem (Tolpuddle). The following criteria were used for selecting the study reaches:-

- Morphological diversity (proportion of riffles, pools and glides)
- Sinuosity
- Bank-side land use (e.g. grazed pasture or water meadow)
- Overhead cover (e.g. over-shading from bank-side trees)
- Fencing (whether this had been erected post baseline fish data)
- Brown trout population structure
- Locations of electro-fishing sections
- Locations of hydraulic controls

A simple diversity index was applied to score each reach out of 100 based on the proportions of different meso-habitats present in each electro-fishing section (appendix.1). For the Upper sector a reach of above average habitat diversity was selected that flowed through fenced open pasture with a trout population dominated by adults. For the Lower sector more uniform reaches of below average diversity, partly over-shaded by trees were selected which consisted principally of age 0+ and 1+ trout. Both reaches were coincident with electro-fishing sections. The Lower sector consisted of two shorter electro-fishing sections adjacent to each other which were modelled as a single reach for habitat purposes. This allowed for increased spatial resolution in examining population response to habitat. Selection of study reaches was also constrained by methodological requirements of PHABSIM hydraulic models insofar as the most downstream transect in each reach had to be located at a hydraulic control that governed water surface slope upstream (Elliott *et al.,* 1996). It was also necessary for this to correspond with the position of the downstream stop net for the electro-fishing section. In both selected reaches there was close correspondence ensuring a match up between habitat modelling and population data. At the downstream end of the Lower sector an old set of hatches acted as the hydraulic control which greatly assisted hydraulic calibration enabling the two contiguous downstream reaches to be amalgamated for hydraulic modelling purposes.

4.3. TRANSECT PLACEMENT AND SURVEYING

PHABSIM utilises a transect based approach in order to characterise channel form. A paired measurement of distances and bed elevations across transects defined channel width and cross sectional geometry. Micro-habitat variables were point sampled over a channel cross section, the points defining a series of grid cells into which the river bed was divided. Longitudinal distances between transects defined cell dimensions (Fig.4.1). Transects representing particular meso-habitats were located roughly centrally in a cell, having due regard for presence of various micro-habitat features and different cover types (Bovee *et al.,* 1998). Transect end positions (headpins) were marked on both banks using either wooden stakes or fence posts as permanent headpin markers.

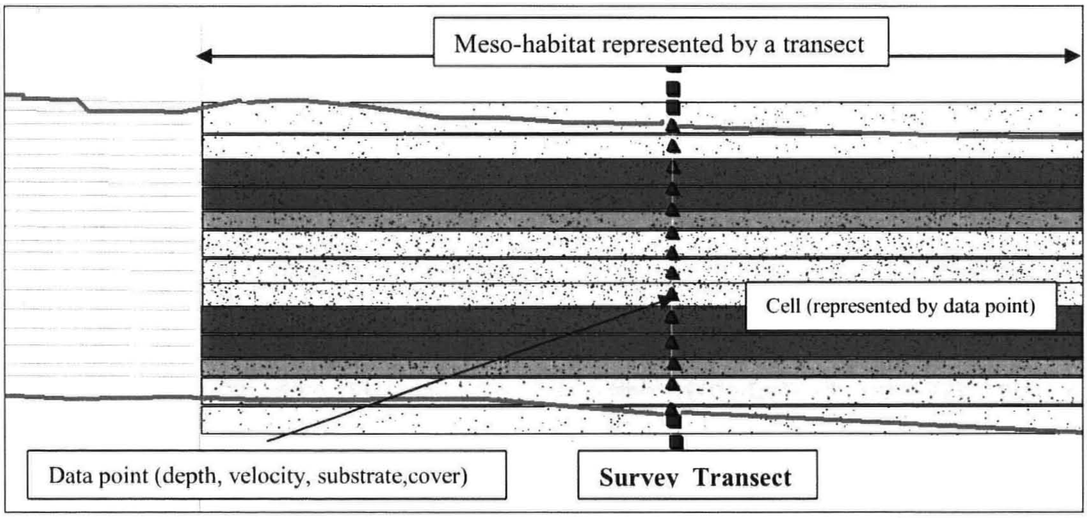

Fig. 4.1. Matrix of habitat cells used in a PHABSIM study.

Transects were placed to represent all mesohabitat types present in selected reaches in approximate proportion to the total amount of each habitat type occurring in that river sector. For example, habitat mapping showed that 60-65% of the upstream sector consisted of shallow glide such that additional transects were located in shallow glides to approximate the proportion of this habitat type. A greater number of transects were used in reaches with high habitat diversity than those with low diversity. This approach ensured that both habitat availability and continuity were accurately sampled. Transects were placed perpendicular to the flow direction with the most downstream transect located at a hydraulic control. To maximise accuracy of hydraulic simulations transects were placed at all other hydraulic controls in a reach and a minimum of two transects were located in positions where a reliable discharge estimate could be obtained in accordance with standard practice (Elliott *et al.,* 1996).

Transects were surveyed using a Leica T1010 EDM total-station theodolite (Leica AG, Heerbrugg, Switzerland) accurate to the nearest five seconds of arc, to accurately obtain headpin positions, elevations and channel cross sections (Bovee, 1982; Elliott *et al.,* 1996). Use of a total-station had a number of advantages over other stream surveying methods such as dumpy level and range finder. An electronic distance measuring device (EDM) eliminated the need for manual measurements with a tape. These measurements are considerably more accurate than other methods which tend to be subject to a greater degree of operator bias and errors during data collection (Kellie, 1994). The use of a total station eliminated these problems, and was also faster than other methods capable of producing comparable data. Distance and location of survey points relative to station (EDM) position were recorded automatically to a PCIMCA data card which was downloaded to a spreadsheet. The use of a hand held Garmin Global Positioning System (GPS) to locate station position provided a reference point for geocoding survey points within a Geographical Information System (GIS).

Channel cross sections were surveyed between July and November 1999 from marked headpins. Headpins marking transect end points were located as far as possible at or above bankfull discharge and used to establish a point of known elevation relative to adjacent headpins shot from the same station position. Shots were taken at points selected to coincide with breaks of slope and changes in substrate and cover conditions in order to accurately describe channel profile. The EDM was positioned to maximise the number of headpin shots that could be made from the same location reducing the number of times the station had to be moved. Where visibility along a reach was good, it was possible to survey as many as three transects from one station position, but it was usually only possible to survey 1 or 2 transects at a time as bank-side trees interrupted shots and some reaches required numerous station positions. Headpin positions were plotted on scaled planimetric reach maps to establish relative positions and elevations of transects. Station re-positioning required a standard survey foresight to be taken to a fixed datum followed by a back sight to the same datum taken from the new position to establish difference in elevation (Keim *et al.*, 1999; Elliot *et al.*, 1996). This enabled headpin elevations shot from the new position to be adjusted relative to previous elevations.

Cross section horizontal distances (x- coordinates) were taken as zero at the headpin marker peg and measured from this datum according to standard convention (Bovee *et al.*, 1998). Elevations (y-coordinates) at each point were measured relative to headpin datums. Sufficient survey shots were made to provide reliable estimates of discharge through transects such that not more than ten percent of total discharge at low flows passed between two adjacent points (Elliott *et al.*, 1996). As far as possible a minimum of twelve cells were located in the flow at low summer stage to maximise the accuracy of hydraulic modelling (Bovee, 1982). This resulted in survey shots within the channel itself being taken at intervals between 0.3 - 0.6 m.

4.4. SAMPLING OF HABITAT CONDITIONS

Measurements of depth, velocity, substrate and cover were taken in order to calibrate seasonal differences in habitat suitability for four life stages of brown trout: spawning, young of year (YOY), post young of year (PYOY) and adults. Data were collected between summer 1999 and summer 2000 to enable habitat conditions to be modelled over an annual cycle. Data collection periods were determined by appropriateness to the life stages being modelled and the need to meet the hydraulic requirements of PHABSIM for a wide range of calibration flows. The timing of data collection was as follows;-

June - September 1999 (calibration low flow - moderate macrophyte biomass)

Summer habitat:
YOY, PYOY and adults

December 1999 – February 2000 (calibration high flow - low macrophyte biomass)

Winter habitat:
PYOY and adults
Spawning/incubation conditions

May 2000 (calibration spring flow for maximum macrophyte biomass)

Spring habitat:
Early post emergent YOY

4.4.1. Hydraulic Measurements

PHABSIM hydraulic models derive depths and velocities for ungauged flows from those measured at the calibration flows. This required a stage - discharge relationship to be established in each study reach. For this purpose water surface elevations were measured at each transect for a minimum of three different discharges according to standard procedures (Bovee *et al.*, 1998). Velocities were also measured for the high (winter) and low (summer) calibration flows.

Water Surface Elevations

Water surface elevations were measured at all transects for a minimum three calibration flows; low summer flow (July-September), high winter flow (January-February) and intermediate spring flow (April-May) to determine water depth (stage). The EDM was used as a standard level to read elevations directly from a graduated surveying staff. This was easier to hold precisely on the water surface by forming a meniscus round the base of the staff and discrepancies between readings were immediately evident and could be repeated were necessary. Readings were taken to within +/ - 5 mm.

PHABSIM assumes the water surface across transects to be uniform, although local water slopes can be quite marked under certain conditions, such as bends at high flow. Therefore an average water surface elevation was taken at each transect. Elevations were taken at 2-3 points across transects and repeated twice at each point to minimise error and produce a mean water surface elevation in accordance with standard practice (Elliott *et al.,* 1996). Water surface elevations were measured relative to the headpin marker which provided a fixed datum. Subtracting bed elevations from water surface elevations provided an accurate measure of water depth.

Maximising the range between highest and lowest calibration flows reduced the risk of prediction errors becoming magnified for simulated flows extrapolated above the highest calibration flow (Elliott *et al.,* 1996). The highest calibration flow followed a winter flood event and was the largest discharge that could be safely gauged by wading. It was not possible to gauge bankfull discharge for safety reasons and over-bank flows were not modelled. Surveying of water surface elevation was always conducted on the same day to minimise effects of flow fluctuations. Where separate but contiguous reaches were calibrated at different times, under different flow conditions, water surface levels were re-surveyed at the hydraulic control marking the top and bottom of adjoining reaches to enable adjustment for the difference. The presence of stage boards at the downstream transects of both study reaches increased the accuracy of the stage-discharge relationships and assisted the process of adjusting water surface elevations for different study reaches under different calibration flow conditions.

Velocity measurements

Mean column velocities were measured at all points on each transect for a minimum of two calibration discharges; summer low flow (July-September) and winter peak flow (Jan-Feb). Velocities were measured over as small a time interval as practical during which there was no rainfall to minimise effects of flow fluctuations. Velocity metering was carried out on the same day as water surface elevations for each reach. Where adjoining reaches comprised one long contiguous sector where a full velocity set had to be measured over a longer time interval, water surface elevations were retaken at a previously measured hydraulic control so that any variation over time could be recorded. Velocity distributions under uniform flow conditions vary depending on cross-sectional channel shape (Chow, 1959). Where flow was distributed relatively uniformly mean column velocity was estimated at 0.4 of the total depth in accordance with standard procedures. Where flow was irregular due to presence of weed beds or in meanders, readings were taken at 0.2x and 0.8x depth and averaged to give a more accurate representation of mean velocity (Newbury and Gaboury, 1993).

A Valeport Braystoke BFM002 miniature current flow meter with 50 mm impeller was used to measure velocity. When a second operative was available another meter of identical type was employed to maximise the number of transects metered in one day. Group calibrations conducted by the manufacturers using a sample batch of identical meters indicated average performance of the entire family to vary by less than 2.2% ($p = 0.05$) for flows above 0.5 ms^{-1}. Only at very low current speeds below 0.15 ms^{-1} was there likely to be significant variation in performance between meters. This was considered acceptable for estimation of mean column velocities.

Discharge measurements

Discharge was measured for all calibration flows at the downstream hydraulic control and at least one other transect in each reach to provide the most reliable estimate (best estimate *Q*) (Bovee, 1982). These were usually located in glides with steady flow parallel to the banks and a fairly uniform depth of water not less than about 0.5 m (Elliott *et al.,* 1996). Discharge was estimated using the continuity equation;

$$Q = V \times A$$

where Q is discharge (m^3s^{-1})
V is velocity (ms^{-1})
A is cross-sectional area of the flow (m^2)

To increase accuracy discharge was calculated for individual cells, and summated to give total discharge across the transect (Newbury and Gaboury, 1993; Elliott *et al.,* 1996). Mean column velocity was measured in each cell using a current meter as described above. The cross sectional area was calculated for individual cells using the average depth between two adjacent survey points and multiplying by cell width.

Plotting channel cross section profiles together with water surface elevations in a drawing software package enabled accuracy of the cross sectional areas to be double checked.

4.4.2. Habitat Measurements

Flow dependent habitat variables water depth and column velocities were derived from hydraulic data as described above. However, PHABSIM utilises at least one flow independent habitat variable (Channel Index) which requires measurements of substrate and/or cover.

Substrate

Mean particle size of material comprising the dominant substrate type in each cell was measured using nested sieves. A visual assessment was made to select a cell representative of dominant substrate for a particular transect and a "kick" sample was wet sieved on site to determine dominant size category.

TABLE. 1. Substrate code classification scheme

SUBSTRATE TYPE	PARTICLE SIZE	SUBSTRATE CODE
Plant detritus/ organic material		**0**
Silt/ clay	<0.0625mm	**1**
Sand	0.0625 - 2.0mm	**2**
Fine gravel	2.0 - 18.0mm	**3**
Coarse gravel	18.0 - 40.0mm	**4**
Pebble	40.0 - 64.0mm	**5**
Fine cobble	64.0 - 100.0mm	**6**
Coarse cobble	100.0 - 256.0mm	**7**
Boulder	>256 mm	**8**
Bedrock		**9**
Terrestrial vegetation		**10**
Man made material		**11**

(Plant detritus and organic material refers to dead and rotting vegetation covering the stream bed. Terrestrial vegetation refers to grasses, nettles or trees which may be found within cells. Man made material refers to concrete or other artificial materials used to modify the channel.)

A sample of materials collected during sieving was measured to determine mean particle size. The x, y, and z-axes of a selection of particles were measured with callipers and averaged. Substrate codes for use in habitat modelling were based on the bed material size classification adapted from White and Brynildson (1967) (Table.1). In cases where two size categories comprised roughly equal proportions both substrate codes were recorded. Substrate surveys were carried out for summer and winter.

Cover

Seasonal assessments of cover were undertaken in August / September and January/ February. Exposed root wads, woody debris and vegetation provide complex cover habitats for trout (Hunter, 1991). These were difficult to categorise due to the range and diversity of factors which constitute cover in a stream (Wesche, 1980). The following definitions were developed for categorising cover:-

- ***object cover*** -submerged or partially submerged objects (eg. branches, roots and logs) which deflect the flow and provide velocity shelter.
- ***overhead cover*** - objects or terrestrial vegetation external to the stream, or emergent marginal vegetation, which overhang the stream either on or above the surface and which have "clear water" beneath of a depth not less than 0.25 m.
- ***undercut bank*** - provide protected lies where the bank toe slope has been eroded such as the outside of a bend.
- ***instream vegetation*** - floating and submerged macrophytes which provide shelter for trout

Protocols were developed for characterising commonly occurring cover types. For example, roots or trailing branches often provide object cover at the margins which collect significant quantities of drifting weed and debris. Where these form substantial rafts on the surface they afford a combination of object cover and overhanging cover providing both velocity shelter and overhead protection. Floating cover boards installed at the channel margins were considered to have a cover value equivalent to undercut banks. In-stream vegetation was categorised as submerged (1) or floating (2), and did not include emergent marginals, which were classified as overhanging cover where appropriate. Submerged vegetation referred to aquatic macrophytes such as *Ranunculus spp.* Floating vegetation referred to vegetation growing on the bed or banks forming floating "mats" on the water surface (Elliott *et al.,* 1996). The dominant vegetation and total percentage vegetation cover within a cell were estimated by visual observation.

Surveys were carried out visually by wading across transects and assigning a cover value code at each vertical. A ranging pole was used to make approximate measurements of widths of overhanging vegetation and degree of bank undercutting within a 2m distance upstream and downstream of the transect. All observations were carried out by the author to ensure consistency. The numerical cover code assigned to each cell was derived from a cover classification scheme adapted from Trihey and Wegner (1981). This scheme groups cover types into "cover value categories" according to their importance to brown trout (appendix.2). Single object cover rated lowest in value (rating A); overhead cover rated (B) and undercut bank (C). Combinations of cover types were given a higher cover value (D). A score was assigned to each cell based on the percentage of that cell affected by a given cover category. EXAMPLE: a combination of object cover and overhead cover present in 60% of a cell rated D3 resulting in a cover index of 11 (see appendix.2).

4.5. ASSIGNING UPSTREAM WEIGHTING FACTORS (UWF).

Standard PHABSIM protocols required meso-habitats represented by each transect to be estimated as a proportion of stream to the next upstream transect (Bovee *et al.,* 1998). Thus, a transect placed in a riffle which extends half way to the next upstream transect is assigned a weighting factor of 0.5. This defines a series of cells over which habitat values at that transect are assumed to apply. Upstream weighting factors were estimated by making a visual judgement as to the point at which the upstream transect became more representative of stream conditions than the downstream transect. This point was marked on the bank and a 50m tape used to measure distances to adjacent upstream and downstream headpins.

4.6. BROWN TROUT POPULATION SAMPLING

Population estimates for brown trout were made from raw electro-fishing data collected by the Game Conservancy Trust between 1993 and 2000. Quantitative three pass electric fishing was conducted annually in spring (April) and autumn (September), using a 240 volt generator driven pulsed D.C machine towed behind the operators in a 2m GRP boat. A crew of 4 workers operated two hand held anodes and two nets on the main river sections. Upstream and downstream limits of individual reaches were screened using 13-mm mesh hardware cloth stretched across the stream and supported by fence posts to ensure population closure. After capture, trout were held in fine mesh keep-nets before being anaesthetised in a solution of ethyl 4-aminobenzoate (benzocaine) ($0.1 gl^{-1}$). Fork lengths were measured to the nearest millimetre and larger trout were weighed to the nearest 10g before being revived and returned. Population estimates were determined from the autumn electro-fishing data. This was more representative of population structure because it included young-of-the-year (trout aged 0+) and high depletion rates were obtained during low flow conditions with high efficiency of capture commonly in the order of 95%.

4.7. RECORDING OF FIELD DATA

The EDM automatically recorded all data (distance, elevation, easting and northing) for each survey shot. Data were also recorded manually as a back up. Distances across transects were recorded in metres to define cells. Headpin heights and bed elevations were recorded relative to a fixed datum to the nearest millimetre. Water surface elevations were recorded to the nearest 5mm. Dates and times of water surface elevations and velocity readings were also recorded. All repeat visits to measure velocity, substrate and cover were recorded on audio tape using a Dictaphone which enabled additional descriptive information about sites to be included, such as presence of weed beds.

CHAPTER. 5. PHYSICAL HABITAT SIMULATION MODELLING AND ANALYSIS

PHABSIM employs a range of modelling techniques in order to derive a functional relationship between habitat (expressed as Weighted Useable Area) and discharge which allows the area of stream providing suitable habitat conditions to be quantified. There are three basic stages in the modelling approach:

1. Input of raw data to PHABSIM
2. Hydraulic modelling to determine depths and velocities in relation to discharge
3. Habitat modelling to derive habitat – discharge relationships

5.1. INPUT OF RAW DATA TO PHABSIM

Water surface elevations were measured relative to transect headpins which were surveyed from different station locations. This required measured elevations of transect headpins and water surface levels to be standardised to ensure accuracy during modelling. A headpin was selected in each reach and assigned an arbitrary value of 100 to serve as a datum. Elevations of all other headpins were then adjusted relative to +/- 100 so that all transects were hydraulically linked and water surface elevations were referenced to the same datum elevation (100). Errors as small as +/- 5mm can have disproportionate effects on water surface slope under certain conditions (Elliott *et al.*, 1996; Anon, 2001). Reducing to a single datum minimised amplification of measurement errors between headpins when shot from different station positions and when re-measuring changes in water surface levels at a later date. Average water surface elevations at each cross section were input and quality checked by plotting a longitudinal scatter-graph to ensure that the water surface sloped in a downstream direction.

5.2. HYDRAULIC MODELLING TO DETERMINE DEPTHS IN RELATION TO DISCHARGE

5.2.1 Defining the Stage – Discharge Relationship

Hydraulic models used to establish water surface elevations at ungauged (simulation) discharges required calibration from stage-discharge relationships developed from measured (calibration) discharges at downstream hydraulic controls (appendix.3). Stage-discharge relationships were developed as follows. In the lower sector a sluice gate (T.0) provided the best discharge estimate and acted as stage of zero flow (SZF) for all upstream transects. Transect 1 (where a stage-board was located) produced a more reliable stage measurement due to the impounding effect of the sluice which controlled water surface slope upstream. The stage – discharge relationship at transect 1 was used for hydraulic calibration. This achieved the most accurate discharge, water surface level and SZF combinations. A similar approach was adopted for the upper sector where a transect was located at a stage board immediately downstream of the hydraulic control to provide a best estimate of discharge.

Water surface level (WSL) elevations were used to establish depths across each transect by subtracting bed elevations. Different hydraulic modelling approaches (see p.155 for model descriptions) were used to predict water surface levels at ungauged flows (simulation discharges) as follows:-

1. The stage-discharge model (STGQ) performs a log-linear regression between observed stage and discharge for three measured (calibration) flows to determine a stage – discharge relationship. The resulting equation predicts stage at unmeasured (simulation) flows.

2. The MANSQ model utilises Manning's equation to define relationships between discharge and hydraulic parameters of each independent cross section. Slope represents the difference in WSL between adjacent transects and a correction coefficient (beta) is used to minimise differences between observed and expected WSL at each transect.

3. The Water Surface Profile (WSP) model uses a standard step-backwater technique to predict WSL. WSP requires all transects are hydraulically linked to a downstream hydraulic control where there is known stage-discharge relationship. An energy balance model is used to project WSL to each subsequent upstream transect.

5.2.2 Water Surface Model Selection

Different in-stream situations require different techniques to model hydraulic conditions accurately and appropriate model selection was necessary to avoid potentially problematic effects during habitat modelling. Hydraulic calibration was conducted using both the WSP and STGQ models independently. WSP was used for simulating high winter flows because it is the most reliable model for extrapolation beyond the highest calibration discharge (Bovee *et al.,* 1998). Use of roughness modifiers to vary Mannings *n* also provided scope to compensate for the hydraulic effects of seasonal vegetation growth which were significant. The WSP model generally works best in complex situations such as chalk streams with substantial backwater effects whereas STGQ performs better in hydraulically "simple" applications such as high gradient streams (Elliott *et al.* 1996). However, STGQ was found to perform well at middle and lower parts of the flow range where effects of channel irregularities and breaks of slope became more marked. Therefore, final water surface calibration employed a "mixed" modelling approach with the model that produced the best fit between observed and predicted stage at a cross section being used in the final production run.

5.2.3. Calibration of the Stage-Discharge Model (STGQ)

Empirical data from measurements of water surface elevations at three different calibration flows gave the stage – discharge regression;

$$Q = a\,(WSL - SZF)^{b}$$

Where;

Q = discharge
WSL = water surface level
SZF = stage of zero flow

a = constant derived from measured values of discharge and stage

b = constant derived from measured values of discharge and stage

Stage-discharge regressions used a single best estimate discharge for all transects in a reach. This was because variations in channel geometry meant that cross section discharges often differed from best estimate discharge which was common when measurements were taken in habitat types that were poor in terms of obtaining good discharge estimates. Accuracy of water surface simulations depended on relative differences in regression line slopes at adjacent transects. Under some conditions cross section discharge provided a better fit to observed water surface elevations than best estimate discharge at individual transects but in general produced poor relationships.

Determination of stage of zero flow

The STGQ model utilises stage of zero flow (SZF) in the stage-discharge computations, which was determined by a longitudinal plot of thalweg elevations at each transect in an upstream direction. The lowest bed elevation (thalweg) at the downstream hydraulic control is the water surface elevation at which flow will cease (SZF). This controls water surface slope for a series of transects upstream until thalweg elevation at a transect exceeds that at the hydraulic control. This forms SZF for the next upstream series of transects.

Assigning calibration sets and running the model

A minimum of three (and up to four) measured discharges were used to calibrate the model as follows;

- Cal 1: summer base flow (lowest *Q*)
- Cal 2: winter low flow
- Cal 3: winter peak flow (highest *Q*)
- Cal 4: spring flow

This covered as wide a range of flows as possible in order to increase reliability of predictions. A number of model runs utilising different calibration sets were employed to achieve the best fit between observed and predicted WSL at each transect. This maximised flexibility of model calibration making it possible to take seasonal effects into account. For example, for intermediate flows occurring in winter and spring, using Cal 2, 3 and 4 calibrated the model for the period covering minimum plant biomass to maximum biomass. For intermediate or low flows in summer and winter Cal 1, 2 and 3 calibrated the model for the period of declining plant biomass to minimum biomass. In some cases using all four calibration sets produced the best fit between observed and predicted WSL, but fewer calibration sets were more commonly used because effects of macrophyte growth in spring resulted in a higher stage and a non-linear relationship with discharge. As the model can only handle linear relationships, the curved nature of this four-point relationship meant selection of fewer calibration sets had a significant impact on results. For example, selecting Cal 2, 3 and 4 resulted in higher predicted stage at medium and low discharges than using Cal 1, 2 and 3, the differences becoming greater with declining discharge.

The shape of this relationship meant STGQ proved less reliable than WSP for calibrating spring flows. In most other cases a three-point regression (Cal. 1, 2 and 3) was used for calibration purposes. Model accuracy was sometimes improved, particularly at low flows, by using a two-point regression in the model. Where stage was over estimated using a three-point relationship, use of Cal 1 and 2 reduced predicted stage. Alternatively, selecting Cal 2 and 3 increased predicted stage where it was under estimated.

5.2.4. Calibration of the Water Surface Profile Step-Backwater Model (WSP)

The WSP model is a standard step-backwater technique which uses the concepts of mass balance (continuity) and energy balance to compute flows in a step-wise sequence upstream for adjacent pairs of transects. The continuity equation calculates a flow balance and velocity. The energy balance represents differences in total energy between adjacent transects as water moves downstream. The Benoulli equation (Chow, 1959) calculated total stream energy at a cross section as follows;

$$H = z + d + v^2/2g$$

Where;

H= total energy at a transect

z = bed elevation

d = depth

$v^2/2g$ = velocity head (energy component due to velocity)

v = mean column velocity

g = acceleration due to gravity

Differences in total energy divided by distance between two cross-sections gives the slope of the energy grade line. Thus,

$$Se \;=\; H\;1 \;-\; \frac{H\;\;2}{Dist}$$

This equation represents energy balance between two adjacent transects (bed slope, hydraulic slope and energy slope are considered to be equal under uniform flow conditions $S_o = S_h = S_e$). The model cross checks flow and energy balances by comparing this energy slope with that derived using Manning's equation as follows;

$$Se = \{\frac{Q}{R}\}0.66 \times A\{\frac{n}{1.49}\}2$$

Where,

Q = discharge

R = hydraulic radius

A = cross-sectional area

n = roughness

S_e = energy slope

Setting initial hydraulic conditions

WSP required a water surface elevation at the downstream hydraulic control as a starting point for computing energy slope upstream. Initial water surface elevations were provided using the stage-discharge relationships at hydraulic controls. Where a mixed modelling approach (using STGQ and WSP models) was employed, initial conditions required re-initialising for WSP because use of a stage-discharge model at a particular transect broke the upstream energy balance computation. The WSP/STGQ option acted as a re-initialiser where the stage-discharge relationship at the next upstream transects provided new conditions for projection of water surface levels upstream.

Standard calibration procedure for WSP was adopted using the high (winter) discharge to calibrate the model. This was best practise because high calibration flows provided more reliable water surface predictions above the highest measured discharge and residual errors became increasingly compressed when simulating down to lower discharges (Anon., 2001). The high calibration flow also provided the largest range of observed Manning's *n* values which was critical to WSP model performance.

Calibrating initial discharge using Manning's *n*

Before model simulations could be undertaken values for Manning's *n* which achieved the "least error fit" between observed and predicted longitudinal water surface profiles needed to be derived for the high calibration discharge. A global Manning's *n* was applied at all transects and varied by trial and error until the best agreement between measured and simulated water surface profiles was obtained (Bovee *et al.*, 1998). Increasing transect roughness (raising *n*) increased resistance to flow and reduced mean velocity through the cross section resulting in an increase in water surface height. Lowering *n* achieved a reduction in water surface height. Careful consideration of in-channel conditions was necessary in making adjustments to Manning's *n* because unrealistic variations can affect reliability of extrapolations to higher or lower discharges (Anon., 2001). Recommendations for alluvial streams suggest that variations between transects should be limited to 5% - 15% given no major topographic or geologic influence. Local adjustments to *n* were made at paired transects in a step-wise direction upstream because water surface height is a function of channel roughness at a cross section and the adjacent cross section downstream.

Setting Manning's *n* at the downstream hydraulic control determined starting height of the water surface upstream. Manning's *n* at transect 0 was set sufficiently high that a low value at transect 1 produced the required water surface slope upstream. This is a commonly used practice which reduces the need for substantial changes in *n* at subsequent transects (Anon, 2001). This approach was particularly useful at the downstream hydraulic control in the lower sector where an offset sluice caused the flow to hit a blank wall before spilling over the sill at the side. The wall effectively acted as an impoundment (especially at higher flows) controlling water surface height upstream, the effect of which was simulated using a very high roughness value at Transect 0.

Applying roughness modifiers at lower calibration flows

Following initial model calibration to the highest discharge, additional calibration flow data were utilised to empirically derive relationships between roughness and discharge for use in hydraulic simulations. In open channel hydraulics resistance to flow increases with decreasing discharge. This inverse relationship between roughness and discharge meant that *n* values obtained in the initial calibration had to be modified in order to accurately reproduce longitudinal water surface profiles at lower calibration discharges. A roughness modifier *(rMOD)* was applied to adjust the magnitude of *n* in relation to discharge. A trial and error approach was repeated to select *rMOD's* that minimised error between observed and predicted water surface profiles at the remaining calibration discharges. A coefficient of 1.0 was applied at the initial (high) discharge to calibrated Manning's *n* values, which were modified by an appropriate factor greater than 1.0 to increase roughness at lower calibration discharges. A target "agreement" between observed and predicted WSL was taken as +/- 5mm because smooth flowing lowland chalk streams typically have few hydraulic fluctuations which allowed more accurate calibrations.

Estimating roughness modifiers for simulation discharges

Once initial Manning's *n* values and roughness modifiers were established for all calibration flows, relationships between roughness and discharge at unmeasured (simulation) flows were determined empirically from the roughness values used in calibration of WSP. A log-linear regression was developed from which roughness modifiers for ungauged simulation discharges were derived.

Accounting for seasonal effects of vegetation using WSP

Abundant growth of submerged macrophytes (especially *Ranunculus.spp*), emergent marginal plants and other riparian vegetation produced marked seasonal hydraulic effects which substantially influenced hydraulic modelling accuracy. In spring (April/May) peak macrophyte biomass caused large roughness increases resulting in high water surface levels and a non-linear stage-discharge relationship where stage increased as discharge fell. Stage-discharge models cannot work in situations where there is a reversal in normal depth – discharge relationships. Therefore, a separate hydraulic calibration was undertaken for the measured spring flow using WSP. This method is the most physically based approach available within PHABSIM (Bovee *et al.*, 1998) and provides the ability to include both spatial changes in roughness and temporal variations resulting from changes in discharge. Manning's *n* values from the initial calibration were retained and appropriate roughness modifiers established by trial and error. A log-linear regression using spring (Cal.4), summer (Cal.1) and low winter (Cal.2) calibration flows enabled a roughness adjuster to be empirically determined and applied to simulation flows in spring during the period of maximum biomass. Modelling for later in the year had to take account of declining macrophyte biomass but increasing marginal vegetation. In particular, large "rafts" of watercress *(Rorippa spp.)* typically resulted in substantial channel narrowing in summer maintaining thalweg depths. This altered velocity profiles as marginal roughness increased, creating a velocity "spike" as flow was pushed towards the channel centre. This was accounted for during calibration of the VelSIM model by adjusting Manning's *n* (see 5.3.1). Water surface level predictions modelled using WSP were altered as a result of this change in roughness and required re-calibrating to enable a better fit with the observed velocity profile.

5.2.5. Evaluating Water Surface Model Performance

Minor surveying errors of a few millimetres can have disproportionate effects on water surface level calibration. Longitudinal plots of water surface slope were used as diagnostic tools for evaluating agreement between predicted and observed water surface levels at calibration discharges (Fig.5.1). These revealed situations where hydraulic models broke down and produced irrational results (e.g. water surface between two transects sloping uphill).

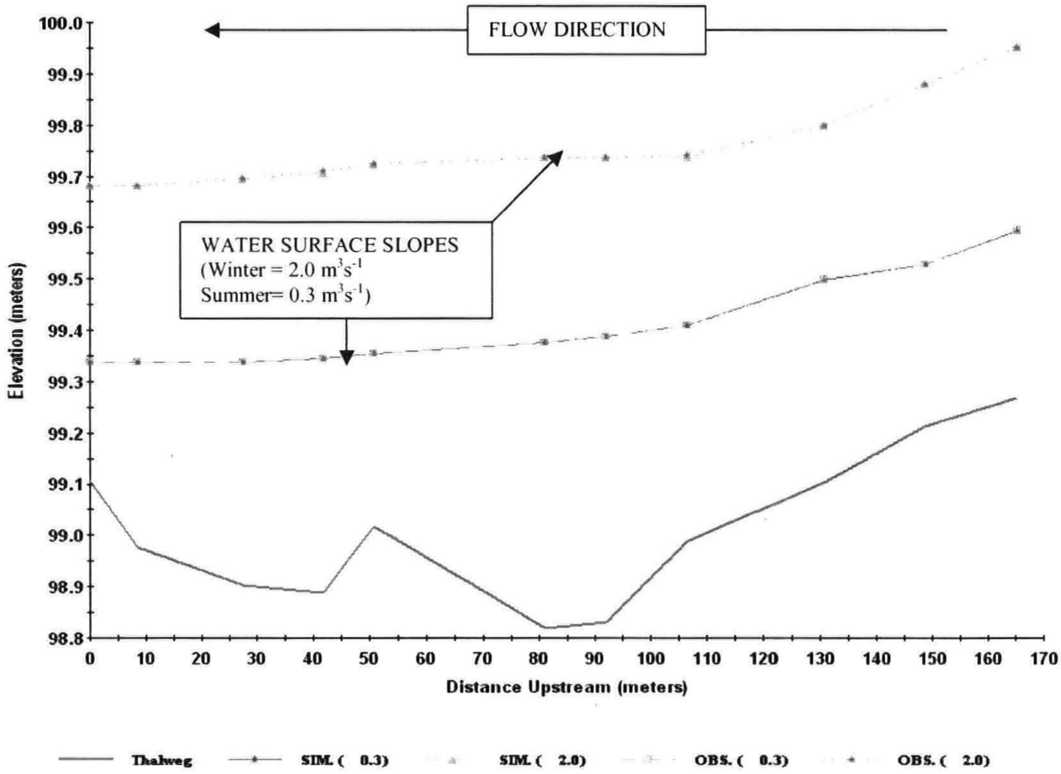

Fig. 5.1. Longitudinal water surface slope for summer and winter calibration discharges

This was a common problem for stage-discharge models when the regression lines of two transects cut across each other, especially when extrapolating for discharges outside the calibrated range. For step-backwater models extrapolation was less problematic as simulation errors became compressed at lower discharges. These plots were useful in determining validity of simulations as they enabled a visual assessment to be made of smoothness of transition of water surface slopes between low flows with marked irregularities and higher flows with a more gradual slope. Cross section profiles were also examined to identify individual transects with disagreements between observed and predicted WSL.

5.3. HYDRAULIC MODELLING TO DETERMINE VELOCITIES IN RELATION TO DISCHARGE

The second step in the hydraulic modelling process involves simulating velocity profiles at each cross section. VelSIM is an empirical model for determining velocity distributions at each transect independently. The programme uses measured velocities as a template for predicting velocities at ungauged (simulation) discharges and calculates Manning's *n* for each cell based on water surface level, slope and velocity provided as part of the calibration data. Individual cell velocities can then be computed for any discharge from Manning's equation using the initial *n* value derived from the calibration velocity set:

$$Vi = \{\frac{1.486}{ni}\} \times di_{0.66} \times Se_{0.5}$$

where,

n_i = estimated Mannings *n* at cell i.

Se = energy slope for transect

d_i = depth at vertical i (substituted as a surrogate for hydraulic radius)

V_i = measured velocity at vertical i

5.3.1. Calibration of VelSIM

VelSIM model calibration was undertaken following standard procedure using a multiple velocity data-set for a minimum of two (and up to 3) measured velocity profiles. Closeness of fit between observed and predicted velocity patterns at calibration discharges was used to assess simulation accuracy and validate calibration of VelSIM (Fig.5.2). A number of manipulations were required to address the following problems and achieve satisfactory velocity simulations:

1. errors occurred due to differences between "best estimate" discharges for a reach (on which predicted velocities were based) and cross section discharge based on measured velocities at an individual transect. In order to maintain mass balancing VelSIM applies a velocity adjustment factor (VAF) to predicted velocities which is a correction coefficient, the magnitude of which reflects the difference between best estimate discharge and cross section discharge.

2. At high flows above the highest calibration discharge, cells at stream margins that were previously dry required predicted velocities but had no values for Manning's *n*. VelSIM automatically applies *n* values from adjacent cells or attributes a default value of 0.06. This led to errors between observed and predicted velocities particularly in marginal cells where computed *n* was too low resulting in predicted velocities higher than observed velocities.

It is a common problem for VelSIM to over-predict velocities at stream margins (Anon, 2001). This occurred due to *n* being under estimated because of the high roughness caused by marginal vegetation. Where predicted velocities were too high this also caused mid channel velocities to be under estimated due to application of VAFs by the programme in order to maintain mass balance through a cross section. Since these "edge" habitats were particularly important to all life stages of trout careful examination of the computational process was necessary during model calibration.

In order to improve the match between observed and predicted velocity patterns at the calibration discharges, estimated values of Mannings *n* were adjusted, either for individual cells or globally for all cross sections in a reach. Setting minimum *n* values (NMIN) increased roughness in mid channel where *n* was generally lowest which reduced predicted velocities but resulted in simulated velocities being almost universally under-predicted. Setting maximum *n* values (NMAX) reduced roughness at the highest values and increased predicted velocities but also had the effect of increasing marginal velocities where reductions were usually required due to high roughness.

Most velocity profiles were under-predicted at the low calibration flow (summer) because seasonal growth in marginal vegetation resulted in substantial increases in roughness which had an acute effect on velocity predictions because *n* values at channel edges were too low to account for this. However, the fit between observed and predicted velocities was found to be generally good at the high calibration flow (winter). Therefore, two discreet velocity files were created within PHABSIM to model summer and winter profiles separately. Increased *n* values were input for cells at stream margins to compensate for increased roughness which depressed "edge" velocities but increased them in mid channel. Selection of *n* values had to take into account distribution of *n* at the high calibration flow as selected values applied uniformly for all discharges at individual cross sections. However, because computed *n* values at the margins were generally much higher for winter flow, it was possible to substantially increase *n* for marginal cells in summer without adversely affecting winter velocity profiles.

5.3.2. Selection of Calibration Velocity sets

Selection of calibration velocity profiles can have profound effects on velocity simulations (Anon, 2001). Standard procedure uses velocity profiles for the lowest calibration flow to simulate downwards to the lowest flows and for the highest calibration flow to simulate upwards to higher discharges.

The following three calibration sets were available and used for simulations as follows:-

1. CALSET 1 measured between late July and mid September and used to model summer velocities for the five month period from June to October.
2. CALSET 2 a winter low flow measured in early December and used to model winter velocities for the five month period from November to March.
3. CALSET 3 a winter high flow taken in late January and used to model winter velocities for the five month period from November to March.

Selection of appropriate calibration sets for a given flow range was made from an assessment of monthly flow exceedance percentiles based on mean daily flows (1993-2000). Median and minimum flows (Nov-Mar) were used to assess the lowest appropriate discharge for use in winter simulations and corresponded closely to the low winter calibration flow (calset 2). Median and maximum flows (June-October) were used to determine the highest flow to simulate using the summer flow (calset 1). This ensured that simulations accurately modelled different hydrological conditions for different seasons. Where changes from use of one calibration set to another were necessitated the velocity regression option within VelSIM was used to apply a smooth transition between predicted velocity profiles based on a two point regression that assumed log-log linear change in velocity distribution.

Changes in channel cross section geometry at different discharges often radically altered velocity profiles. Differences between high and low flow channel shapes occurred at bends and in riffles at very low flows resulting in wide variations between velocity profiles at different calibration discharges. This produced significantly different velocity predictions depending on which velocity profile was used in model calibration. This was an important factor affecting selection of velocity calsets. Observed velocity distributions were examined to identify cross sections where differences between measured discharges were most evident and simulated water surface levels were used to identify changes in geometry associated with changes in depth. This allowed discharges at which velocity distribution patterns were likely to change to be identified and assisted selection of appropriate velocity calibration sets. WSL simulations were used to establish bankfull stage for a reach to determine the highest discharge for which velocity simulations were necessary (as out of channel flows were not modelled).

At certain cross sections (e.g. bends) significant geometry change often occurred at discharges below the high calibration flow, making use of calset 3 for simulating down to lower discharges inappropriate. Where calsets 2 and 3 had similar velocity distribution profiles calset 2 was used to accurately simulate velocities at higher flows. However, velocity distribution profiles often differed radically between calsets, especially at cross sections with substantial geometry change. Under these circumstances the low calset which best mirrored the velocity profile at the high calibration flow was selected and a velocity regression approach used for intermediate discharges to give a better smoothing of velocity distributions over the range of flows. At cross sections with a good match between velocity profiles at high and low calsets the regression option was routinely used to smooth the distributions at intermediate flows giving a more hydraulically accurate velocity representation. This worked best for cross sections such as glides with a relatively symmetrical shape. However, at cross sections with an asymmetric profile, it was found that using the low calset to simulate velocities for intermediate discharges up to the high calibration flow better reflected the likely velocity pattern rather than using a smoothing regression which produced an unrealistically uniform transition between flows.

The lowest calibration flow available (calset1) was always used for summer velocity simulations and to simulate down to very low discharges because these only occurred during summer months. However, where radical geometry change occurred at very low flows such as in riffles, extreme contrasts in velocity profiles between calset 1 and calsets at higher flows necessitated use of a regression approach at intermediate flows to provide a smoother transition in the velocity distribution.

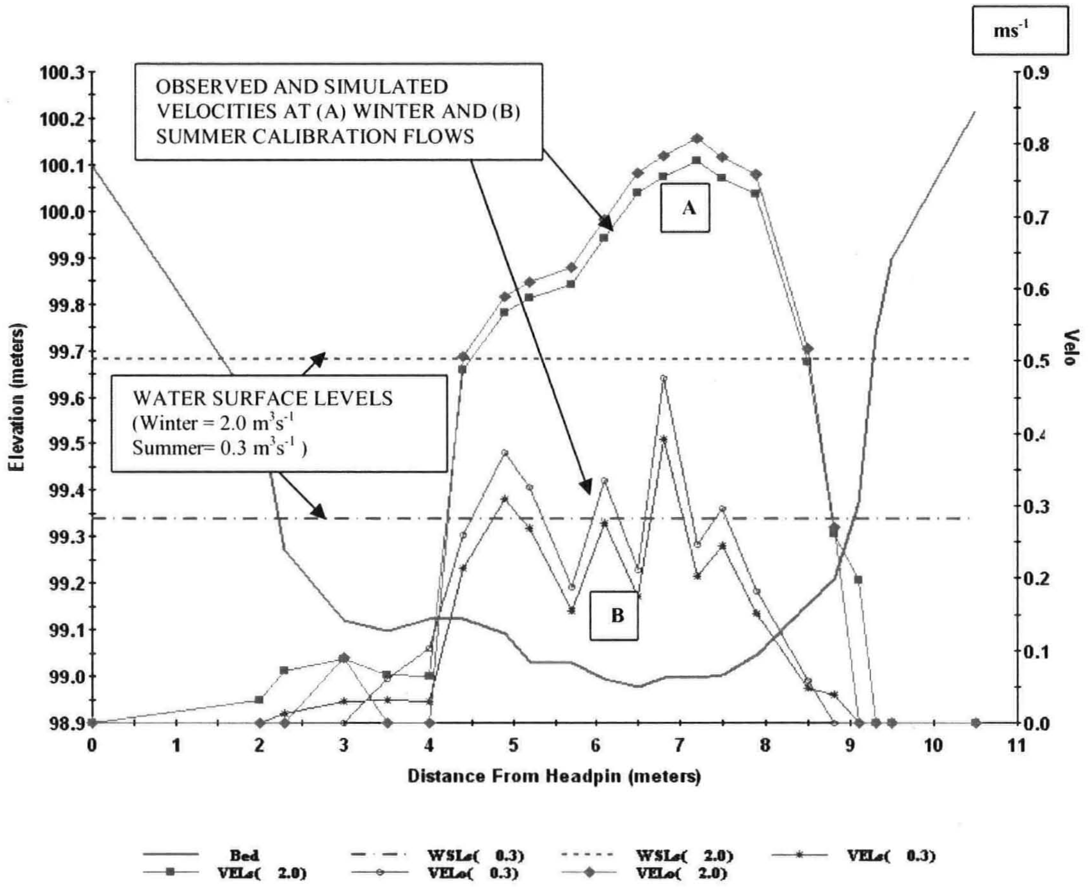

Fig. 5.2. Cross section showing match between measured and predicted velocity distributions for winter and summer calibration discharges

5.4. HABITAT MODELLING TO PREDICT SPATIAL VARIATION IN TROUT HABITAT

Following hydraulic calibration the HABTAE model was used to produce habitat predictions in accordance with standard procedures (see Bovee *et al.,* 1998). HABTAE integrates measured channel cross section and hydraulic parameters with biological information to derive a numerical representation of suitable habitat for brown trout. This takes the form of a functional relationship between discharge and habitat which quantifies habitat availability under various conditions of flow (Fig.5.3).

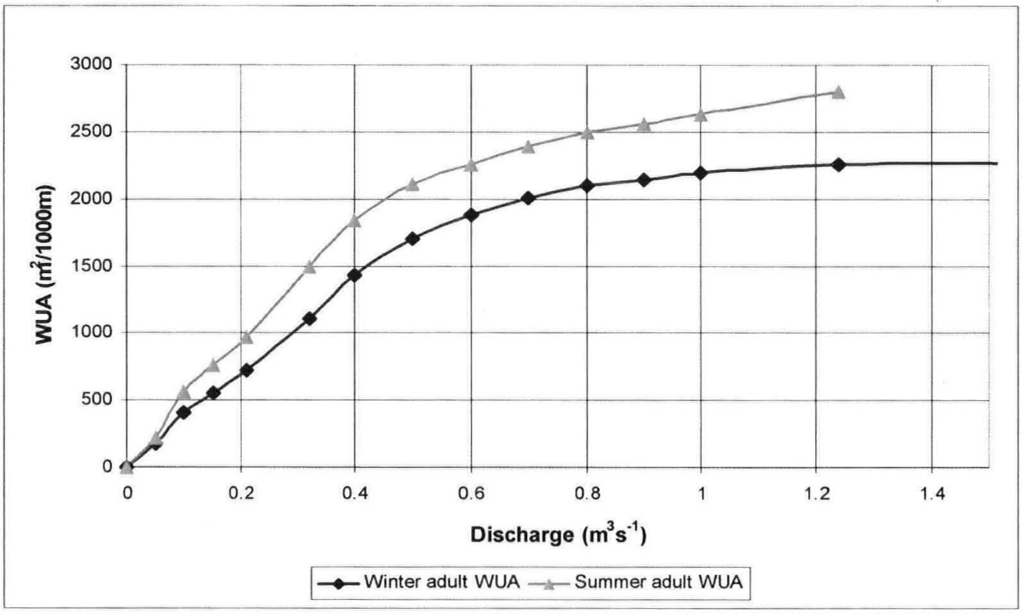

Fig.5.3. Functional relationship between habitat (expressed as WUA) and discharge for adult brown trout

Habitat is expressed as Weighted Useable Area (WUA) which is a composite measure that integrates both habitat availability/quality in terms of suitable area of stream bed per km (m^2 / 1000m) as follows;-

$$\text{WUA} = \frac{n(Ai \times Ci)}{1000} \times \text{RL}$$

Where;

WUA = Weighted Useable Area at specified discharge
Ci = composite suitability of cell i,
Ai = cell surface area
RL = reach length in m
n = cell number

The composite suitability of a cell comprised the combined suitability for the measured microhabitat variables – depth, velocity and substrate/cover. Different life stages of brown trout select habitats according to well defined preferences for different ranges of these microhabitat variables (Armstrong *et al.,* 2003). Habitat Suitability Index Curves (HSI) which represented these habitat preferences were used in the HABTAE model to express habitat conditions in each cell as a single Composite Suitability Index (C.S.I) as follows;

$$Ci = Vi \times Di \times Si$$

where;

Ci = composite suitability of cell i,
Vi = velocity suitability in cell i ,
Di = depth suitability in cell i,
Si = channel index suitability in cell i

5.4.1. Habitat Suitability Index (HSI) Curves

HSI curves are biological response curves which define habitat suitability as a value between 0.0 (unsuitable) and 1.0 (optimal). The area between the peak and curve tails indicates useable ranges. This format expresses behavioural characteristics in that trout often preferentially select narrower ranges of conditions within a broadly suitable range (Armstrong *et al,* 2003). Three categories of HSI curves have been defined according to the means used in their development (after Bovee, 1986):-

Category 1 - derived from life history literature and developed by professional judgement and peer review.
Category 2 – suitability of different microhabitat conditions determined by direct observation of frequency of use by trout at different life stages.
Category 3 – combination of category 2 curves together with additional information to take account of the effect of habitat availability on frequency of use.

Constraints of time and resources made development of habitat suitability curves for the present study impractical. However, HSI curves demonstrate considerable specificity to the stream in which they were developed and problems regarding transferability to other stream types have been well documented (see chapter 2). Category 3 curves have been found to introduce additional bias and be less transferable than generic curves developed in a range of similar stream types (Dunbar *et al.,* 2001). Thus, Category 2 curves developed on the river Piddle by Bird *et al.* (1995) were modified for use in this study (appendix.4). Curve shapes were reviewed, especially for optimum habitat ranges in the light of recent literature (reviewed in Armstrong *et al,* 2003) and found to be broadly in accordance with observed values. However, some changes to curves were made to reflect recent research regarding uncertainty in habitat preferenda (Dunbar *et al,* 2001). This significantly altered the shape of the depth curve for adults at larger depths together with the depth and velocity HSI for PYOY relative to YOY.

The HABTAE programme only handles one "Channel Index" at a time such that simulations could not incorporate suitability data for both cover and substrate. Studies commonly use substrate as the flow independent channel index, partly due to HSI curve availability and to complexities involved in quantifying cover, which cannot be "measured" in the same sense as substrate particle size. Substrate condition is a critical habitat parameter for spawning where gravels are required for redds. Thus, for spawning simulations substrate was employed as channel index. A binary HSI curve was also developed for substrate and used in spawning habitat simulations to test the effect on WUA/discharge relationships relative to univariate curves covering all substrate types. Binary curves define a habitat variable as either suitable (1.0) or unsuitable (0.0) and medium/coarse gravel was defined as optimal but all other substrates types were counted as unsuitable.

In upland streams with coarse rocky bottoms substrate is also an important habitat component for later life stages providing sheltering cover and velocity niches. However, in lowland chalk streams this function is provided by in-stream and riparian vegetation. Smaller mean particle size of gravel means that limited cover value is provided by substrate. Consequently, cover was used for all simulations except those for spawning. A simple HSI curve for cover was developed from the numerical cover coding derived from observed cover in the field. This curve assigned a number to each cover type based on its size, function and complexity after Bovee *et al,* (1994).

5.4.2. Habitat Modelling Strategies

Within PHABSIM the composite suitability index (CSI) of a stream cell is derived from multiplication of habitat suitabilities for depth, velocity and substrate/cover. However, standard multiplication implies synergistic action and recognises no interaction terms between microhabitat variables (Anon, 2001). Thus, the geometric mean of suitability indices was used in the calculations which allowed for a compensation effect between Habitat Suitability Indices. Where two HSI curves were within an optimum range and the third was low the influence of the latter on the Composite Suitability Index was reduced. This had the effect of increasing WUA magnitude but this was immaterial as relative rather than absolute changes in WUA were important and the same methodology was applied to all habitat calculations. However, in some spawning simulations the lowest limiting factor approach was used to compare habitat differences when cell suitability was limited to the value of the poorest habitat attribute. Although this reduced absolute values of predicted habitat the general shape of habitat-discharge functional curves remained broadly similar and no significant differences to overall relationships with trout densities were subsequently found.

Separate habitat simulations were generated by HABTAE for summer and winter habitat. Seasonal variations in cover necessitated use of separate Channel Index files and altered some properties of the hydraulic simulations. Increased summer biomass increased channel roughness effecting both depth and velocity predictions. Separate velocity calibration sets for summer and winter undertaken within VELSIM were employed in the habitat modelling process to ensure a more accurate representation of stream conditions.

In the Lower sector where two adjacent reaches were hydraulically modelled as one contiguous reach, separate simulation files were created and habitat modelling conducted for both reaches individually. This resulted in a small amount of overlap in which the same area of bed was included in both simulations. However, this approach facilitated a more robust analysis which allowed two sets of trout population data to be treated separately rather than combining these into average densities for a single modelled river sector. WUA calculations in the Upper sector used bank length weights to account for sinuosity. This allowed more accurate representation of the reach because HABTAE used trapezoidal rather than rectangular cells where bends were present. The lower sector was rectilinear and no bank weightings were necessary.

Standard WUA computations for both reaches comprised an aggregation of total habitat availability which made no distinctions about variations in habitat quality. Thus, large amounts of low/moderate habitat quality sometimes resulted in the same aggregate WUA as a small amount of high quality habitat. The following modelling strategies were adopted to overcome this problem and to better elucidate habitat mechanisms regulating trout populations:

Minimum Effective Composite Suitability

Parallel habitat simulations were run applying minimum values to composite suitability indices. Cells below a predefined CSI threshold were computed as zero and discounted from total WUA calculations. This prevented small composite suitabilities from accumulating large areas of low quality habitat and allowed only medium and high quality habitat to contribute to total WUA.

Near Shore (Marginal) Habitat.

Aggregate WUA for near shore habitat zones was computed in all reaches because stream margins provide important cover and shelter for trout. All cells more than 2m from the bank edge were eliminated from the WUA computation. The HABTAE model adjusts for those cells falling within the near-shore distance as the bank edge moves with increasing and decreasing depths and computes WUA according to the composite suitability indices of those cells.

Feeding Stations Conditioned on Adjacent Velocity

Feeding stations consist of a low energy holding station in close proximity to a high energy drift delivery zone (Fausch, 1984). Summer (growing season) habitat simulations were run for adult and fry life stages using the adjacent velocity approach to simulate combinations of habitat features providing high energy feeding stations for drift feeding fish. HABTAE computed cell suitability using a combination of an occupied velocity and an adjacent velocity in cells within a specified "sight distance" favourable for food delivery. In the absence of suitability criteria to describe adjacent velocity ranges and appropriate lateral search distances, judgement based on observation was used to define limits. Occupied velocities were set to approximate life stage optima and only those adjacent cells containing significantly greater velocities were included in WUA calculations. Sight distances were arbitrarily defined as 1m either side for adults and 0.5m for fry.

Meso-habitat analysis

HABTAE simulations were run to generate WUA output by individual cross sections to assess the contribution of different habitat types to overall habitat quality in a reach. This method generated a Weighted Useable Width (WUW) versus flow curve as a function independent of length which was used to evaluate relative habitat quality of different meso-habitats (riffle, glide, pools etc.). This approach was useful for evaluating the importance of particular habitat types to different life stages especially during critical periods of the year. WUW of transects representing particular habitat types were multiplied by transect lengths and aggregated to produce a composite meso-habitat WUA which was used to develop habitat-specific flow functional curves. This approach was used to assess the effect of habitat type on local trout population structures and to examine the role of local habitat juxtaposition.

5.4.3. Summary

Graphical outputs from habitat modelling were used to visually assess those parts of the stream providing the most "valuable" habitat for different trout life stages under different scenarios of discharge and season. These were useful for evaluating spatial changes in habitat suitabilities and for highlighting relative importance of single habitat parameters, such as dynamic variations in depth - velocity distributions, in relation to specific meso-habitat types.

The WUA – discharge curves produced from habitat simulations formed the basis for development of habitat time series which represented the starting point for an analysis of time dependent characteristics of habitat availability.

5.5. DEVELOPMENT OF HABITAT TIME SERIES TO SHOW TEMPORAL VARIATION IN TROUT HABITAT

Trout populations are limited by time dependent habitat events which act to limit particular life stages or act as population bottlenecks (Nehring and Anderson, 1993; Elliott, 1994). Thus, temporal variations in fish abundance reflect patterns of antecedent habitat availability that may fundamentally affect long term population change. In order to examine the importance of temporal habitat variations for trout population dynamics, habitat time series were developed as part of the modelling process as shown in figure 5.5.

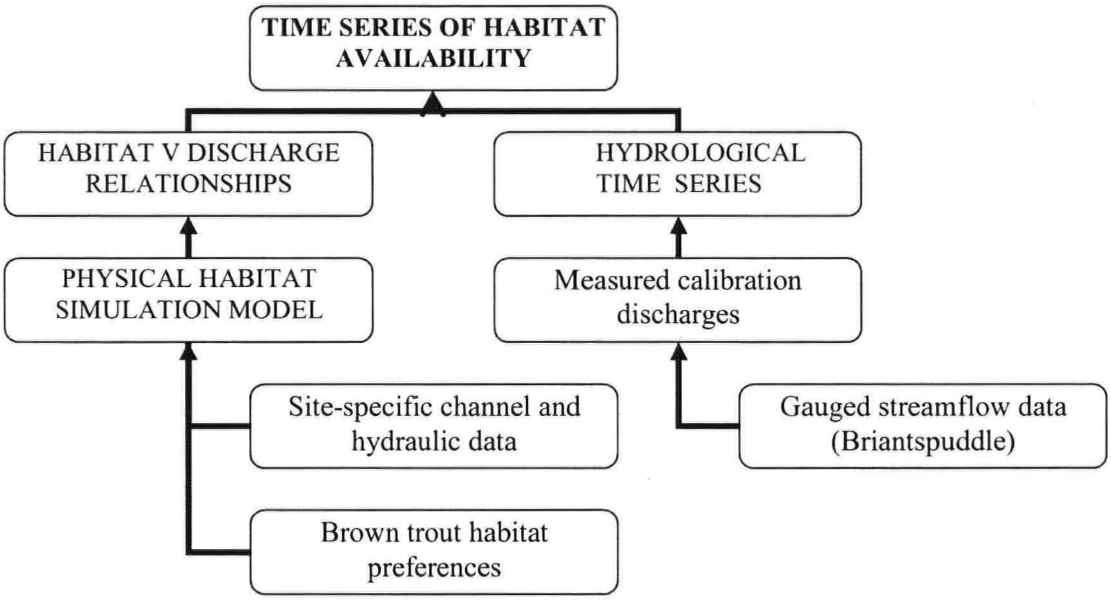

Fig.5.5. Schematic showing component linkages used to model temporal habitat availability in the river Piddle.

5.5.1. Development of Habitat Time Series

Time series were derived as follows (see fig. 5.6.);-

1. Mean daily flow data from Briantspuddle for 1993 – 2000 were used to establish annual hydrographs for the study reaches based on a conversion factor derived from a linear regression of measured discharge at the study site against flow at Briantspuddle (appendix.3).

2. Monthly flow exceedance percentiles and seasonal flow exceedance percentiles for the study reaches were constructed for 1993 – 2000.
3. Daily flow gauge data were used to derive mean monthly time steps for discharge and hydrographs of mean monthly flows were constructed for both river sectors.
4. WUA – discharge curves derived from habitat modelling were used to convert mean monthly discharge to mean monthly WUA for all trout life stages.

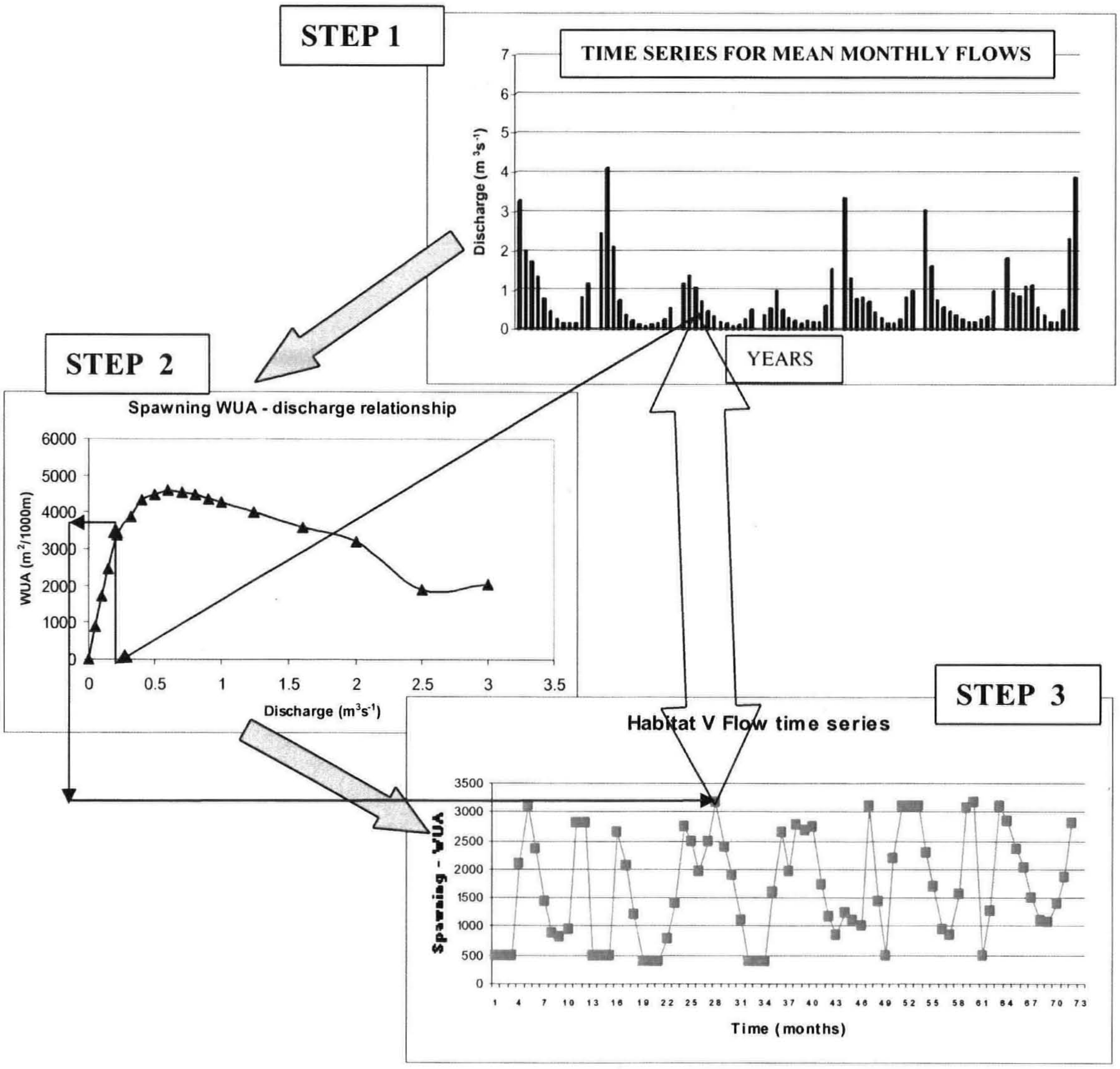

Fig. 5.6. Schematic showing steps in the generation of habitat time series. *(The hollow arrow linking steps 1 and 3 shows that low mean monthly flows equate to high values of spawning habitat).*

Monthly time steps were used both to reduce amounts of data to be processed and to ascertain whether biologically significant events could be identified at a relatively coarse temporal scale (Bovee *et al.*, 1994). Once generated habitat time series were aggregated into seasonal time steps. Winter habitat durations (Nov – Mar) were determined for spawning/incubation and adult life stages. Summer growing season (June – Oct) habitat durations were produced for fry and adult life stages. Habitat specific time series were also generated using the same procedure to assess the importance of different meso-habitat types at different times of year. Time series were not constructed for spring (April – May) due to complexities of hydraulic calibration during this period and the absence of H.S.I curves for early fry life stages.

5.5.2 Development of Habitat Metrics

In order to test the effects of temporal variations in habitat on different life stages of trout metrics were developed that described different aspects of the habitat time series (appendix.5). Mean WUA was used to integrate all habitat events occurring over the relevant portion of a time series. Maximum WUA reflected periods of high habitat availability. Effects of habitat shortages during a particular season were represented using minimum WUA for acute low habitat events and the mean of the lowest 50th percentile WUA was used to depict longer-term effects of habitat minima. Similar habitat metrics were also developed for "near-shore" zones within 2 metres of the bank and for specific meso-habitat types.

5.6. BROWN TROUT POPULATION DYNAMICS

Population age structure was determined for both river sectors from length-frequency histograms which allowed three age cohorts to be clearly identified corresponding to YOY (age 0+), PYOY (age 1+) and adult trout (age >1+). Population size was estimated for each reach using the Zippin maximum likelihood method (Zippin, 1956) and trout abundance (N) in each age class was expressed in terms of density (N/m^2) to take account of variations in area between reaches. Mean lengths of individuals in each cohort were calculated for each reach in each year. Length data from mark and recapture of tagged individuals were used in a von Bertalanffy growth model to derive predicted growth curves for trout in both the Upper and Lower river sectors.

5.7. TESTING RELATIONSHIPS BETWEEN HABITAT AND TROUT POPULATION STRUCTURE

Habitat metrics were input to a statistical analysis package (*SPSS for Windows, Version 9*). Pearsons correlation coefficient and simple linear regression were used to test for associations between habitat metrics and trout densities in each reach over a seven year period. Descriptive statistics were generated for population and habitat metrics to determine means, variance and skew of the data. A one-sample Kolmogorov-Smirnov test was used to test that data were normally distributed. Some habitat metrics with a skewed distribution were natural log transformed in order to stabilise variance and approximate a normal distribution which followed procedures adopted by Nehring and Anderson (1993) for testing correlations between WUA and trout density. Frequency histograms were used to assess the fit to a normal curve and transformations were only used where both skew and Kolmogorov-Smirnov z scores were significantly reduced indicating better approximation of normality. Two-tailed tests of significance were employed and relationships were considered significant for $p < 0.05$.

Linear regressions of trout density (dependent variable) against habitat metrics were used to determine coefficients of variation and to plot lines of best fit and 95% confidence intervals on a scatter-graph. Statistical significance of regressions was tested using one-way analysis of variance to derive F values. Significant F values indicated a 95% probability of a true linear relationship between habitat and trout density. Performance of regression models was assessed by comparison of standard deviation and standard error of the estimate and normalised plots of standardised residuals for dependant variables. Plotting standardised residuals against predicted values indicated linearity and variance equality. Linear plots indicated normality in the regression residuals and that the function used was appropriate to the data.

This approach allowed PHABSIM derived predictions of physical habitat (WUA) to be validated against long term trout population data. This enabled the value of WUA for predicting trout population responses over time to be evaluated and habitat effects on population dynamics of brown trout to be explored.

CHAPTER 6: RESULTS

This chapter summarises the main outputs from the PHABSIM modelling and gives an overview of the trout population dynamics in each river sector. The final section presents the principal relationships between life stage specific densities and habitat.

6.1. HABITAT MODELLING RESULTS

Results from PHABSIM simulations consisted of;

1. habitat – discharge relationships for trout life stages
2. time series showing temporal variations in habitat
3. reach plans showing spatial variations in local habitat

6.1.1. Life Stage Specific WUA – Discharge Relationships

Spawning Habitat

Habitat-discharge relationships for the three study reaches showed broadly similar patterns of spawning habitat over the simulated flow range with maximum habitat occurring between 0.6 - 0.8 m^3s^{-1} and declining as flows increased above 1.0 m^3s^{-1}. Spawning WUA was substantially higher in the downstream reach of the lower sector (Tolpuddle 1) at flows between 0.2 – 2.0 m^3s^{-1} (Fig. 6.1).

Juvenile Trout Habitat (YOY/PYOY)

Lower sector reaches had greater rearing habitat in summer for YOY trout than the upper sector where rearing habitat was limited (Fig.6.2). PYOY habitat was more abundant than YOY habitat in summer especially in the upper sector where it was 5 – 6 times greater at Q >0.2 m^3s^{-1}.

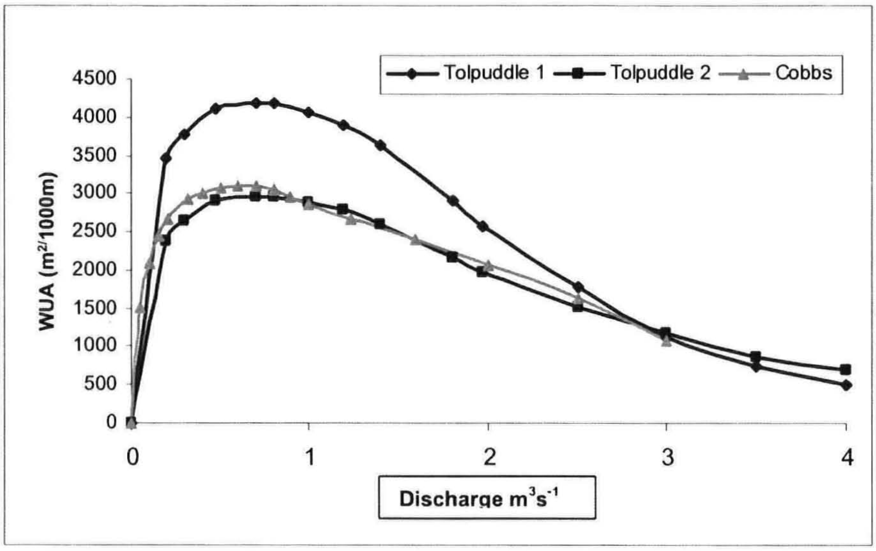

Fig. 6.1. WUA – discharge curves for spawning habitat

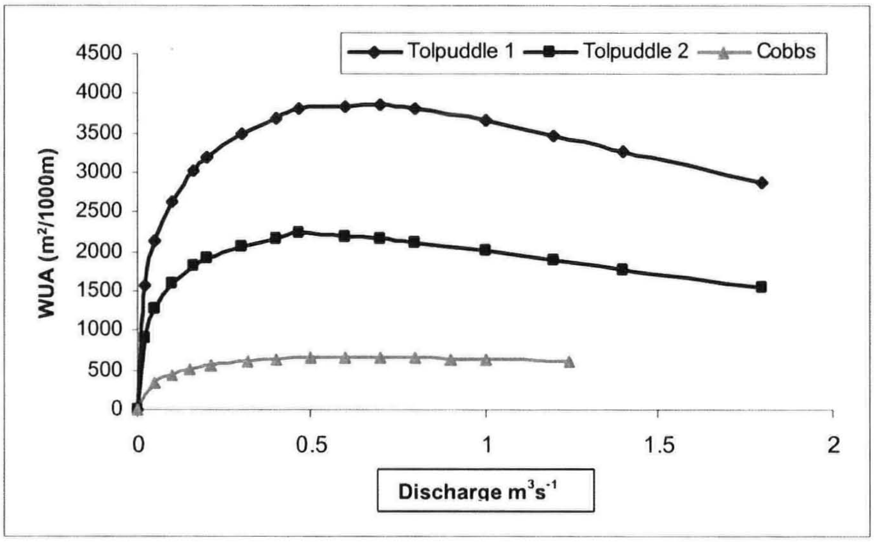

Fig. 6.2. WUA – discharge curves for YOY rearing habitat in summer

Adult Trout Habitat

Habitat availability for adults (>1+) increased rapidly with discharge reaching an optimum at flows between 1.0 – 2.5 m^3s^{-1}. Habitat quality in all reaches was slightly higher in summer than winter due to increased cover but optimum habitat was primarily available during winter (Dec – Mar). This was because flows >1.0 m^3s^{-1} were rarely exceeded in summer but in winter were exceeded 70% of the time (Q50 = 1.7 m^3s^{-1}).

Seasonal comparisons between reaches (Figs. 6.3 & 6.4) showed that YOY habitat in summer was high in the lower sector, where it exceeded adult habitat at summer flows ($<0.6\ m^3s^{-1}$). However, in the upper sector YOY habitat during summer was very low at all but the lowest flows ($< 0.1\ m^3s^{-1}$). PYOY habitat was the most abundant in summer and winter but was broadly similar to adult habitat in both the upper and lower river sectors.

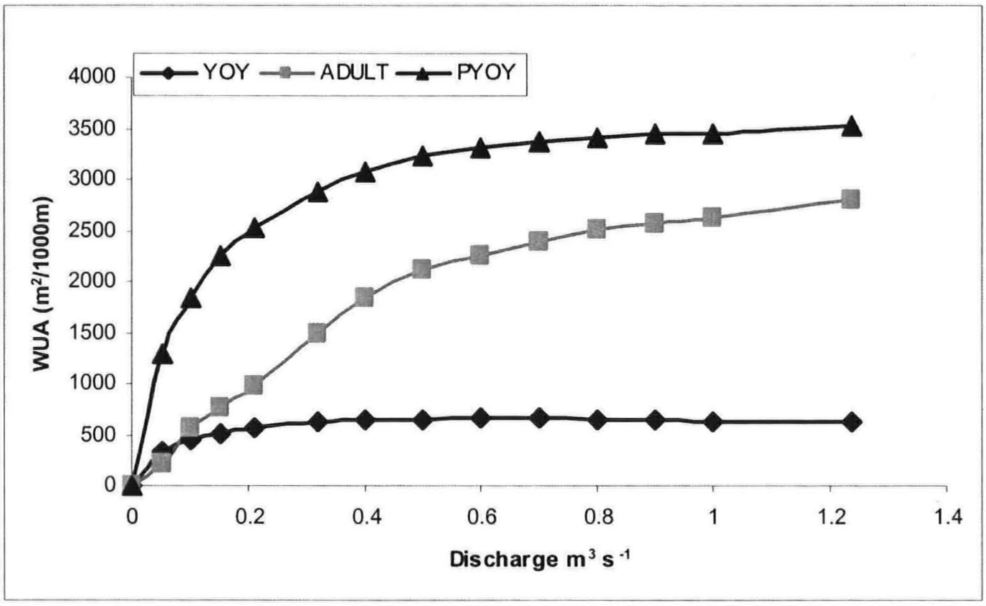

Fig. 6.3. Upper sector: WUA – discharge curves for trout life stages in summer

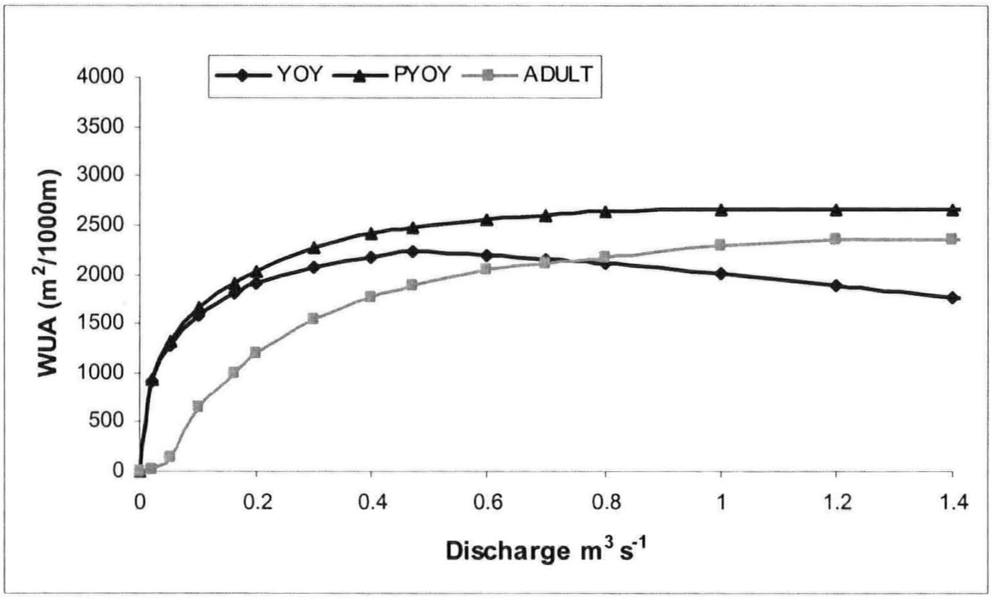

Fig. 6.4. Lower sector: WUA – discharge curves for trout life stages in summer

6.1.2. Life Stage Specific Habitat Time Series

Habitat time series were constructed for the following three life stages:

(i) spawning
(ii) YOY rearing habitat during the first summer
(iii) adult habitat in winter and summer

Spawning Habitat

Spawning WUA was significantly negatively correlated with mean monthly discharge ($r^2 = 0.42$; $p=0.001$). Spawning WUA in all years was greater in the upper sector than the lower sector and showed less variability in relation to flow fluctuations (Fig.6.5). Discharges exceeding the 15th annual percentile resulted in the largest habitat reductions but the effects of high flows were much greater in the Lower sector reaches.

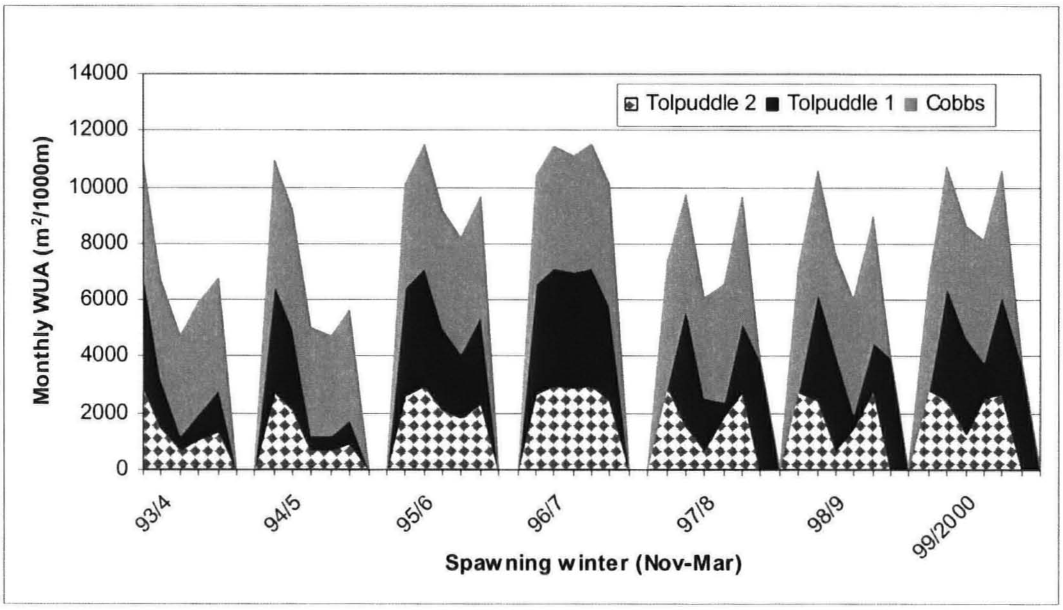

Fig. 6.5. Times series showing monthly variations (Nov-Mar) in spawning habitat between reaches 1993 – 2000

Spawning WUA during the hatching/emergence period (February/March) was significantly negatively correlated with mean monthly discharge ($r^2 = 0.64$; $p<0.001$). During this late winter period spawning WUA was greatest in low winter flow years (e.g. 1996/97). Greater variability in spawning habitat in the lower sector was directly related to the higher winter peak discharges experienced compared to the upper sector.

Discharges greater than the winter *Q*35 (2.0 m^3s^{-1}) substantially depressed WUA in the lower sector (Fig.6.6).

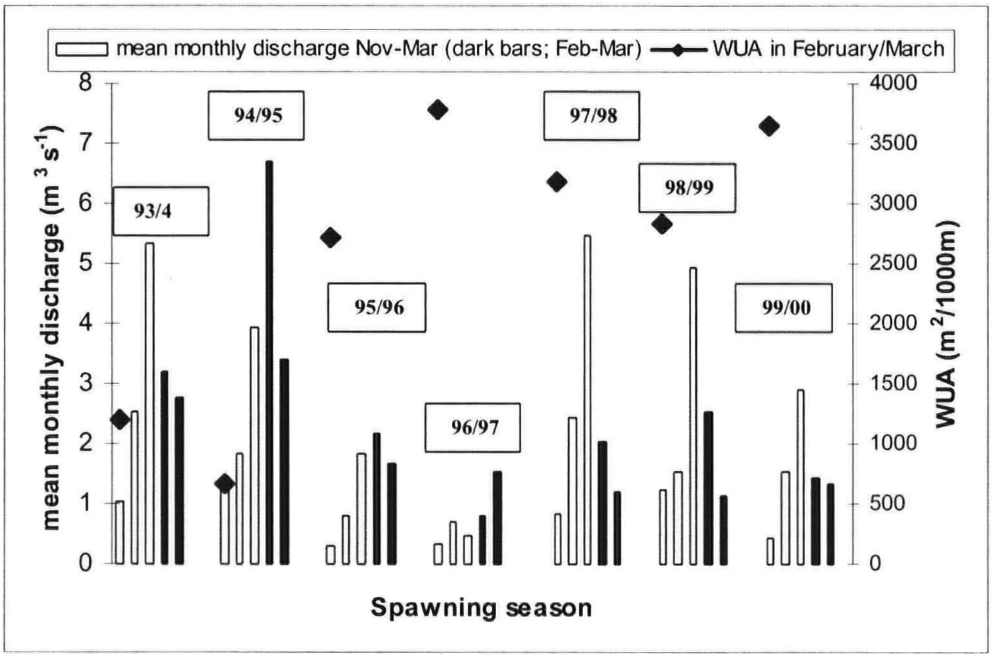

Fig. 6.6. Lower sector variations in spawning WUA relative to mean monthly discharge in February/March

Young-of-the-year (YOY) summer habitat in the first growing season

Time series showed that in the lower sector the downstream reach (Tolpuddle 1) consistently had more summer rearing habitat than the upstream reach (Tolpuddle 2) which had the lowest of all study reaches (Fig.6.7). YOY habitat in summer was substantially reduced in all reaches by low flows such as those in 1995 and 1996.

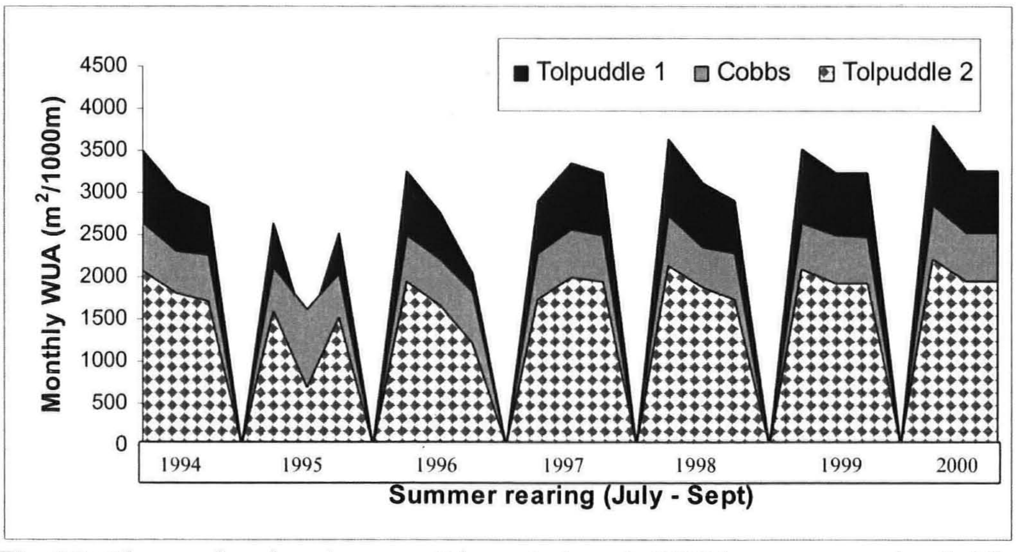

Fig.6.7. Time series showing monthly variations in YOY summer rearing habitat between reaches 1993 – 2000

Adult Trout Habitat

Time series of adult habitat durations in winter (November – March) showed that low winter flows substantially reduced total WUA but that high flows had little effect. In the upper sector (Cobbs) marginal habitat availability (WUA <2m from bank) was depressed by high peak flows but contributed a high proportion of total adult habitat availability in moderate – low flow winters (e.g. winter 1996/97) (Fig.6.8). Seasonal habitat time series showed that marginal habitat for adults was greater in winter than in summer. Summer/winter comparisons over an equivalent five month period (June – October and November – March) showed that marginal WUA in winter exceeded that in summer approximately 80% of the time and was potentially a more limiting resource than total WUA in winter due to greater variations in availability (Fig.6.9).

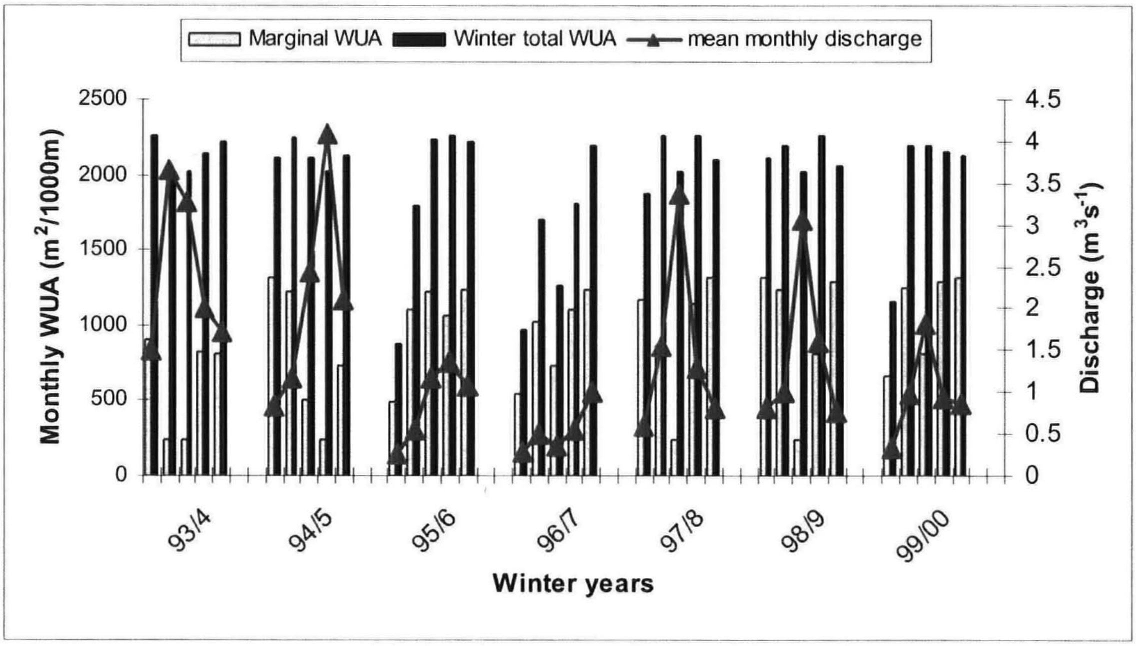

Fig. 6.8. Time series showing adult winter habitat relative to discharge in the Upper sector

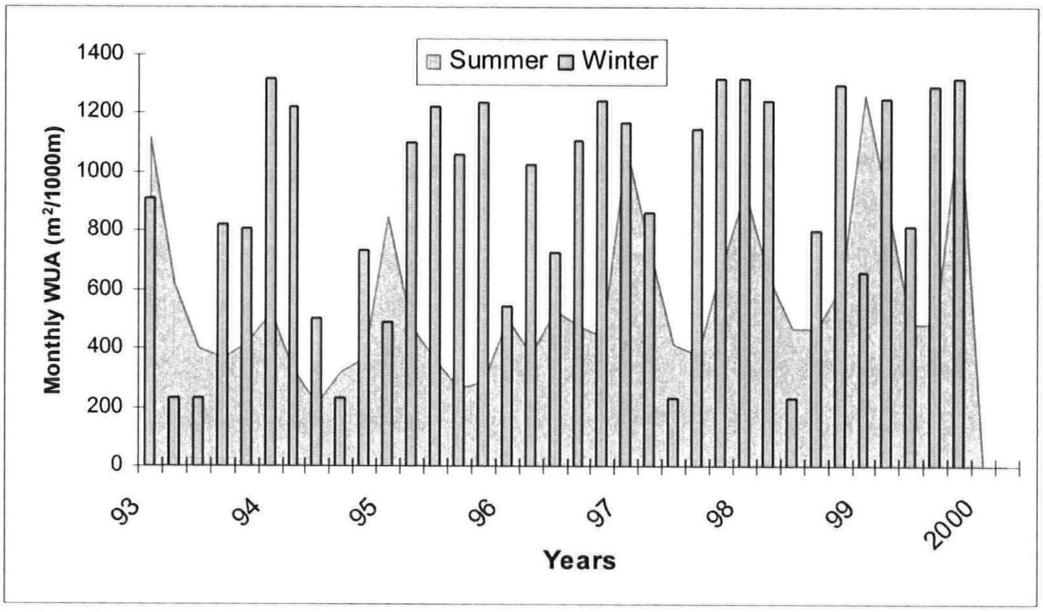

Fig. 6.9. Time series showing seasonal availability of marginal habitat for adults in the Upper sector 1993 – 2000

6.1.3. SPATIAL VARIATIONS IN LOCAL HABITAT DISTRIBUTION

Spatial variations in adult habitat suitability for the upper sector are shown in figures 6.10 – 6.12.

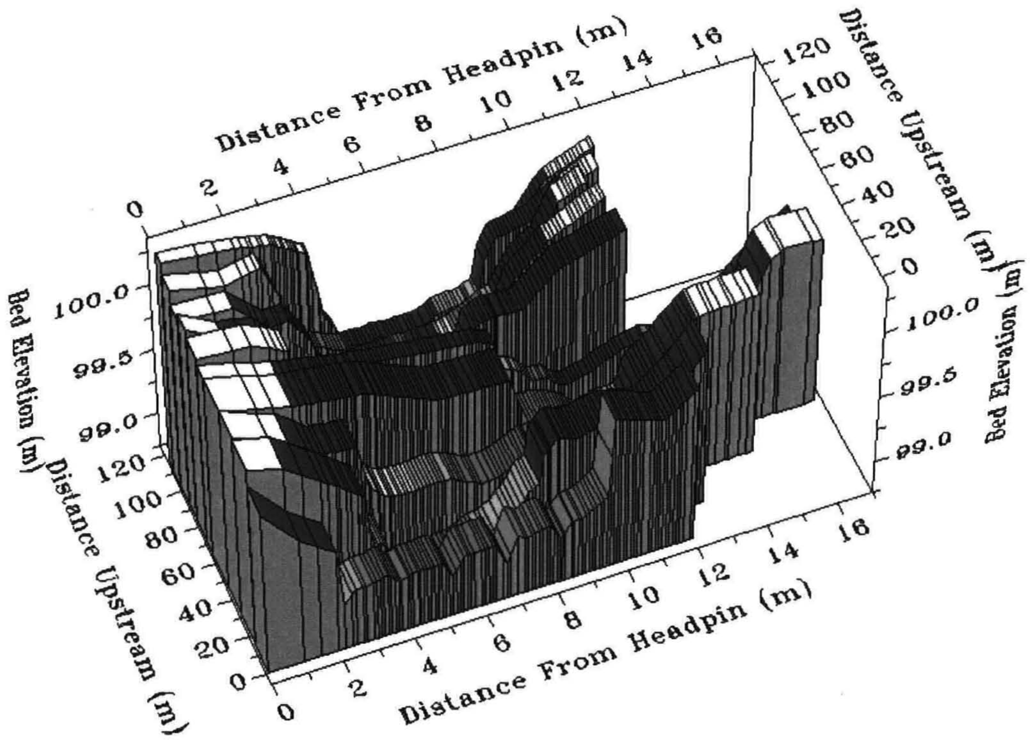

Fig. 6.10. 3D map showing channel morphology and habitat cells in the Upper sector

During high winter flows low velocity niches at stream margins provided better quality habitat as velocity suitability declined at discharges exceeding winter *Q*50. (Fig.6.11a). Areas of prime cover were also heavily orientated towards the margins (Fig.6.11b). In summer depth became a critical resource at flows less than the seasonal *Q*50. Pools became increasingly important as refugia and habitat connectivity was increasingly fragmented (Fig.6.12).

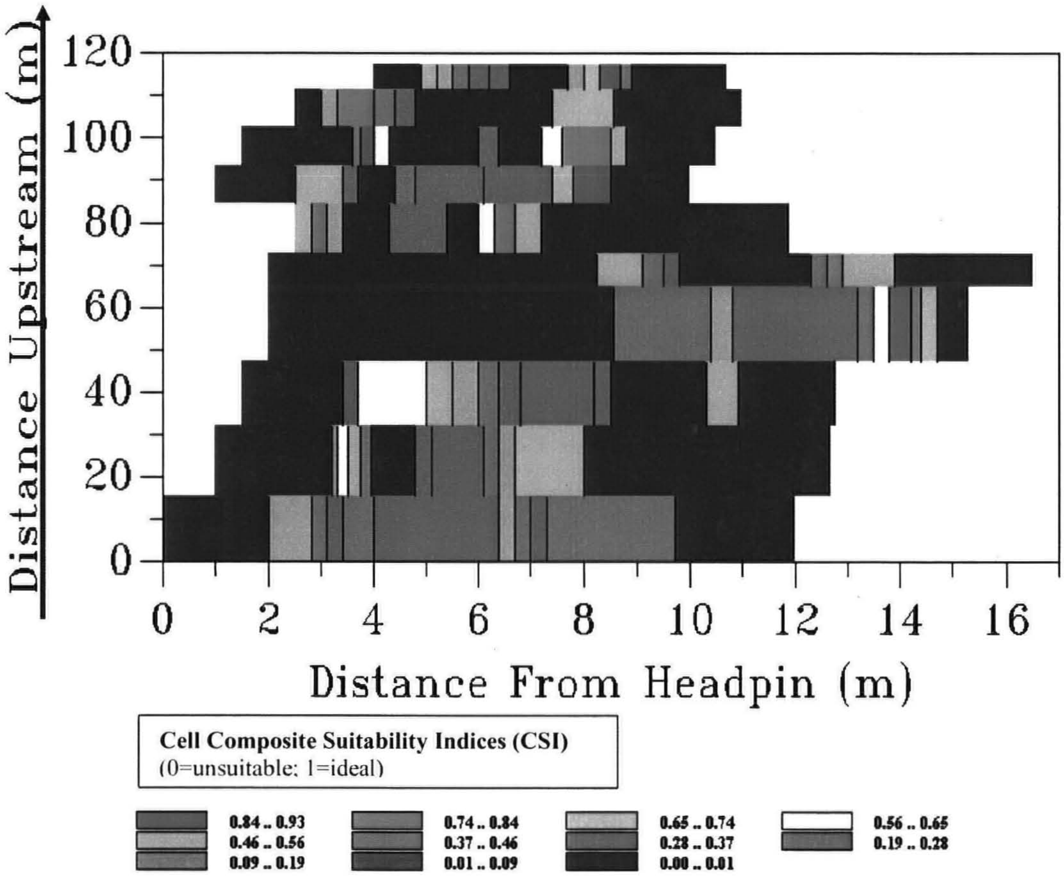

Fig. 6.11.a) Spatial distribution of adult habitat in winter at high flows (Q=2.5 m^3s^{-1})

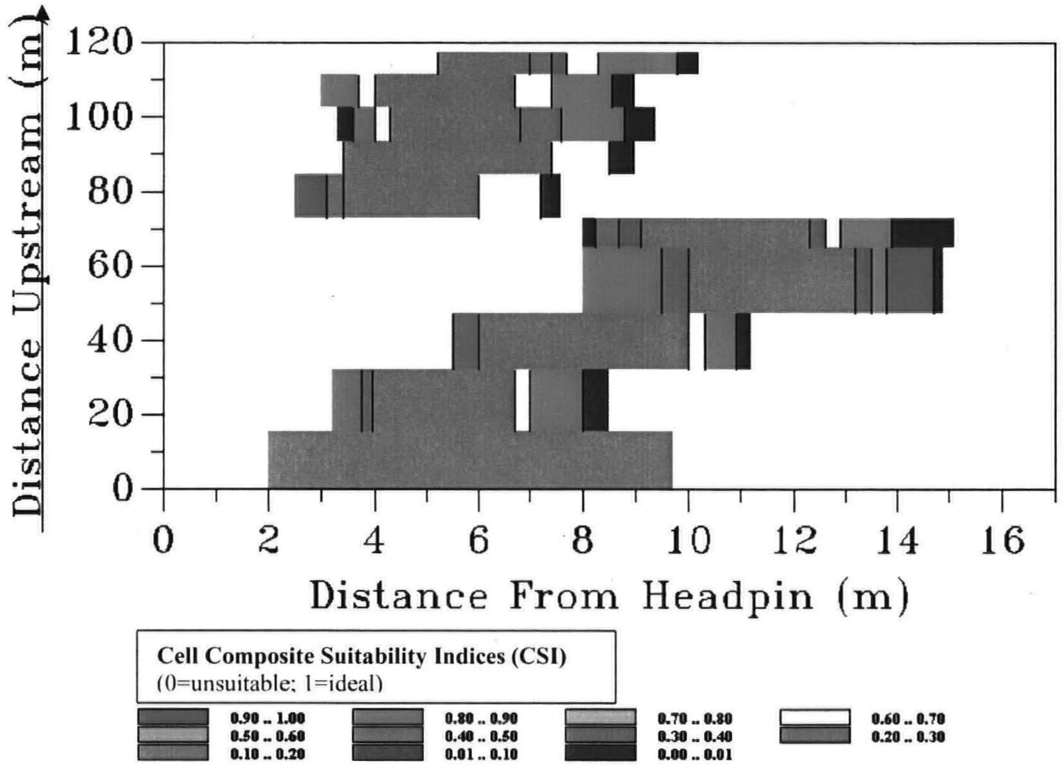

Fig. 6.11.b) Availability of cover in winter in the Upper sector reach (*red/orange areas = highest quality habitat*)

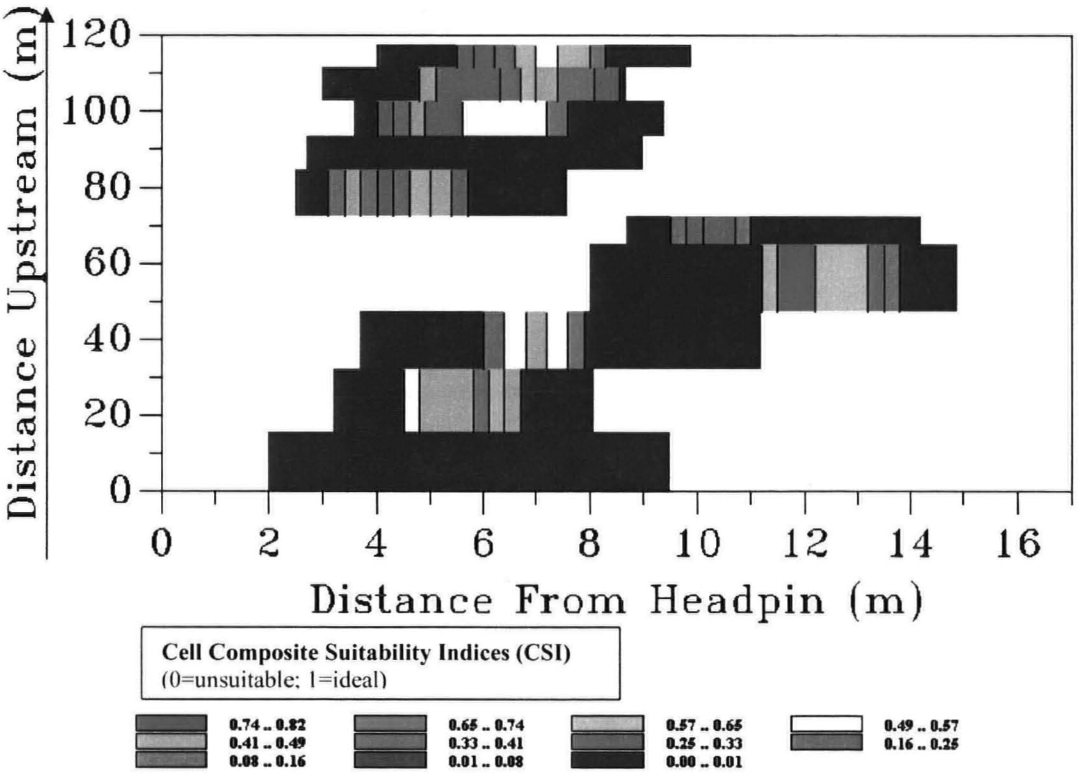

Fig.6.12. Spatial distribution of adult habitat in summer at low flows (Q=0.15 m^3s^{-1}) in the Upper sector reach (*red/orange areas = highest quality habitat*)

6.2. OVERVIEW OF BROWN TROUT POPULATION DYNAMICS

Comparison of trout population data was undertaken separately for the Upper and Lower river sectors.

6.2.1. Length-Age Class Distributions

Frequency histograms of trout lengths showed bi-modal normal distributions indicating 3 distinct age cohorts (fig.6.16). A clear break was apparent at 140 – 150 mm separating trout age 0+ from age 1+ but divisions were less distinct for older trout. Length frequency histograms for the two river sectors indicated cohorts age 2+ and >2+ with modal lengths approximately 260mm and 310mm in the lower sector and 265mm and 325mm in the Upper sector. It was not possible to identify a clear "break" between age classes for older than yearling trout from length – frequency plots. Age – length relationships derived from scale readings indicated that the division between 1+ and older trout approximated to a length of 250mm which was used to define a single age cohort (age >1+) to represent adult trout. Thus, in the present study the three age classes YOY, PYOY and adults corresponded to age 0+, 1+ and >1+ trout.

6.2.2. Trout Year Class Densities

Densities of all age classes in both sectors showed on going upward trends following early year lows (1993 – 1995) with total abundance greatest in the lower sector (Figs. 6.13 – 6.15). Comparison of annual variation in autumn densities showed that YOY and PYOY densities were highest in the lower sector and relatively low in the upper sector. Age-specific mean annual densities showed the lower sector population structure was heavily biased towards juveniles. Adults comprised a higher relative proportion of the total population in the upper sector where a higher ratio of adults to fry was evident. Disproportionately high densities of PYOY relative YOY the previous year were evident in the lower sector with inverse relationships in some years (e.g. fig. 6.14: 1998 – 1999). This was indicated by a near unitary relationship (0.84:1) in the ratio of 0+ to 1+ trout in Tolpuddle 2. Tolpuddle 1 had the highest mean density of YOY and the lowest mean density of adults. Adult densities were similar in both sectors and remained relatively stable after 1995.

Figs. 6.13 – 6.15. Annual autumn densities for 3 age classes of brown trout present in the study reaches 1993 – 2000.
(Densities are expressed as numbers per age class (N) per 10 m² bed area. Numbers are derived using Zippin maximum likelihood of capture method for 3 pass electro-fishing. Year classes are defined from length – frequency data (see 6.2.1)).

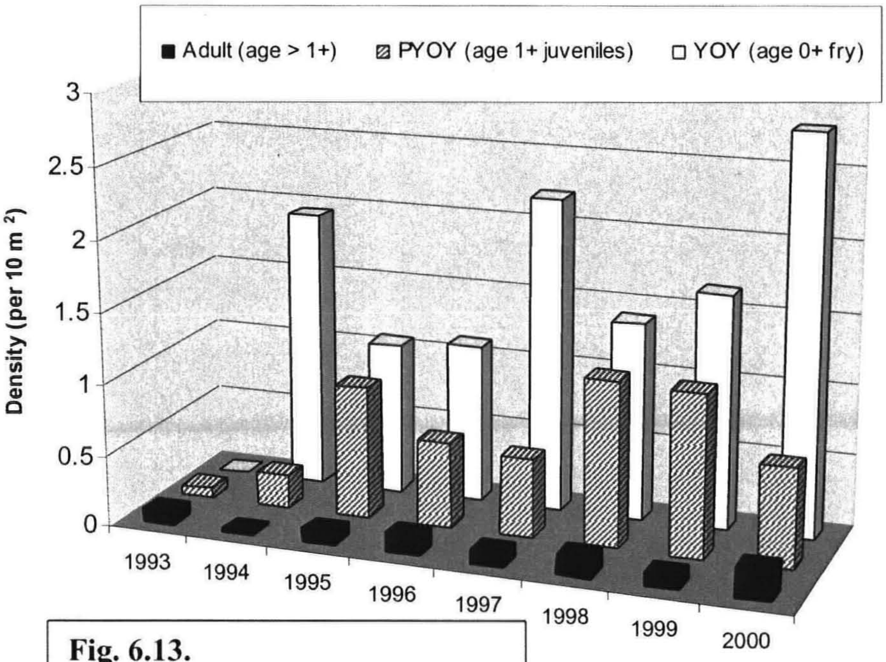

Fig. 6.13.
LOWER SECTOR: Tolpuddle 1

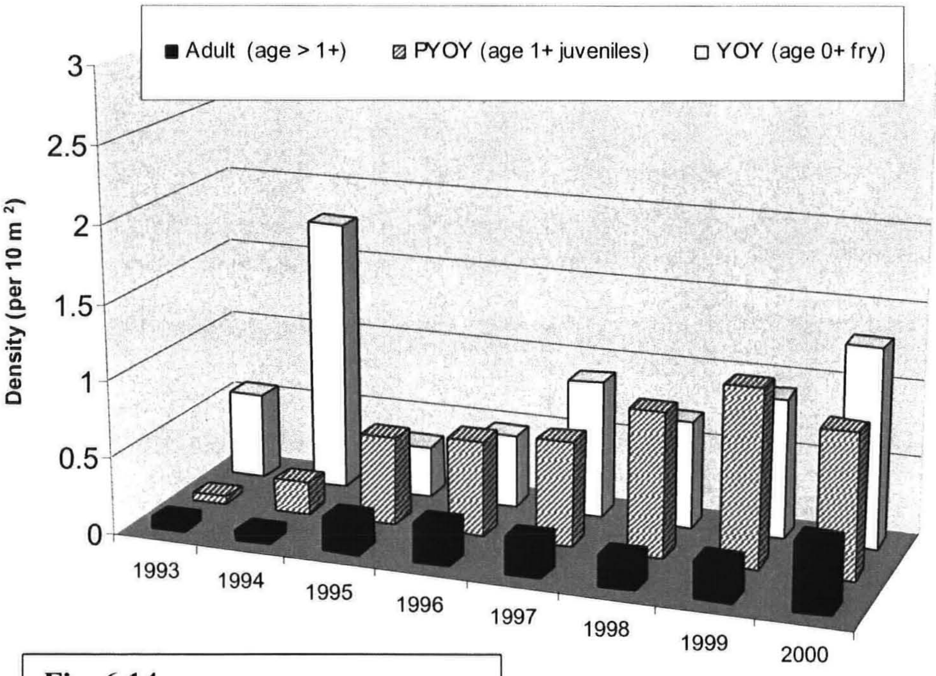

Fig. 6.14.
LOWER SECTOR: Tolpuddle 2

Figs. 6.13 – 6.15. Annual autumn densities for 3 age classes of brown trout present in the study reaches 1993 – 2000.
(Densities are expressed as numbers per age class (N) per 10 m² bed area. Numbers are derived using Zippin maximum likelihood of capture method for 3 pass electro-fishing. Year classes are defined from length – frequency data (see 6.2.1)).

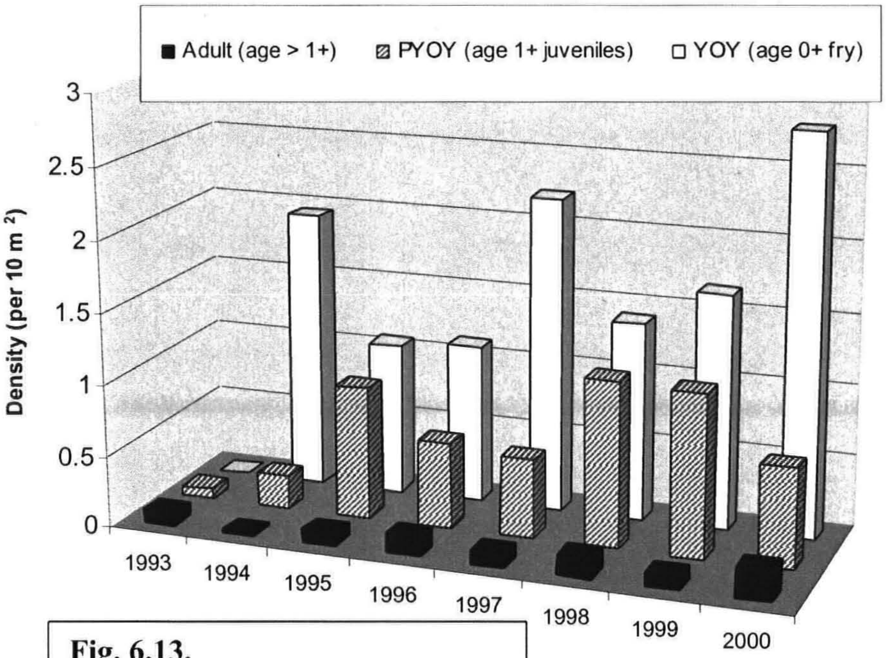

Fig. 6.13.
LOWER SECTOR: Tolpuddle 1

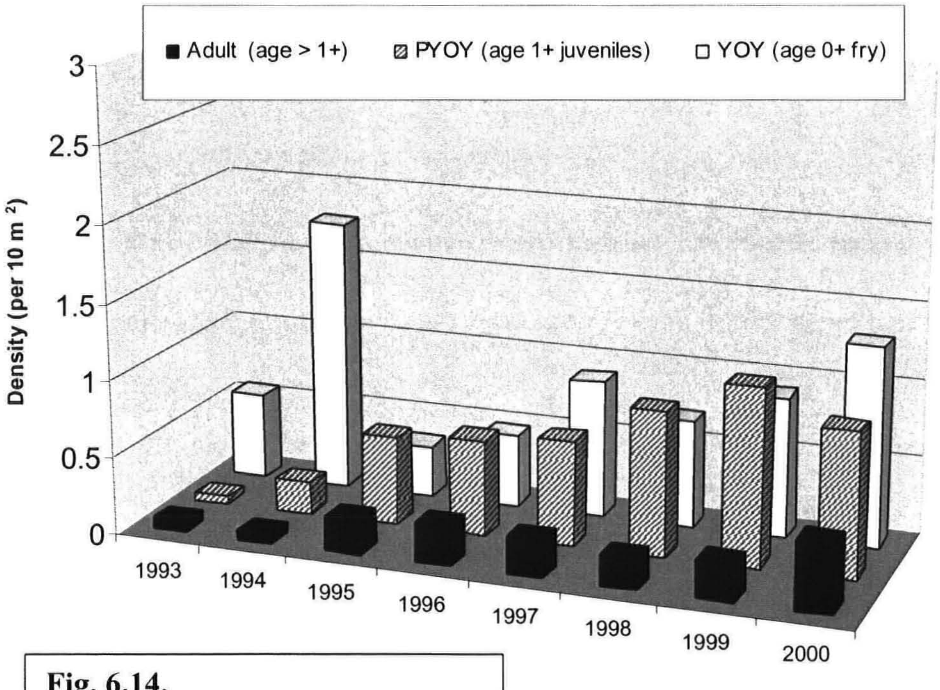

Fig. 6.14.
LOWER SECTOR: Tolpuddle 2

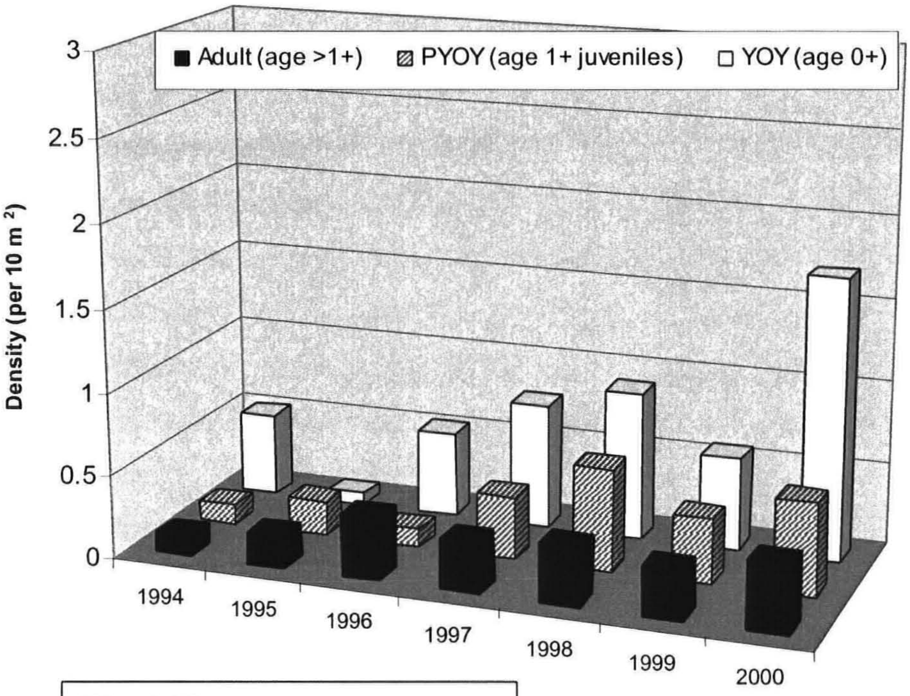

Fig. 6.15.
UPPER SECTOR: Cobbs Wood

6.2.3. Year Class Carry-Over

A significant positive correlation between 0+ year class strength and 1+ density the following year indicated strong first year carry over in both the Upper Sector ($r^2 = 0.59$; p=0.003)) (see appendix.6) and the Lower Sector ($r^2 = 0.50$; p=0.005). A weak positive relationship was also indicated in the Upper Sector between year class strength and adult densities after two years, but this was not significant. No relationships were found between densities of 1+ juveniles and adults (>1+) the following year.

6.2.4. Relationships between Adult Spawning Stock and Subsequent Year Class Strength

In the Upper Sector a positive relationship was indicated between adult density and strength of the succeeding 0+ year class although this was not significant ($r^2 = 0.33$; p=0.057) (see appendix.6). In the Lower Sector no indications of a relationship with adult spawning stock were found.

6.2.5. Trout Growth Rates

Comparison of length – frequency plots for both sectors indicated that cohort modal lengths and maximum adult size were smaller in the lower sector where trout abundance was greatest. This was particularly evident for age 1+ juveniles where a modal length of 190mm compared to 220mm in the upper sector (Fig. 6.16).

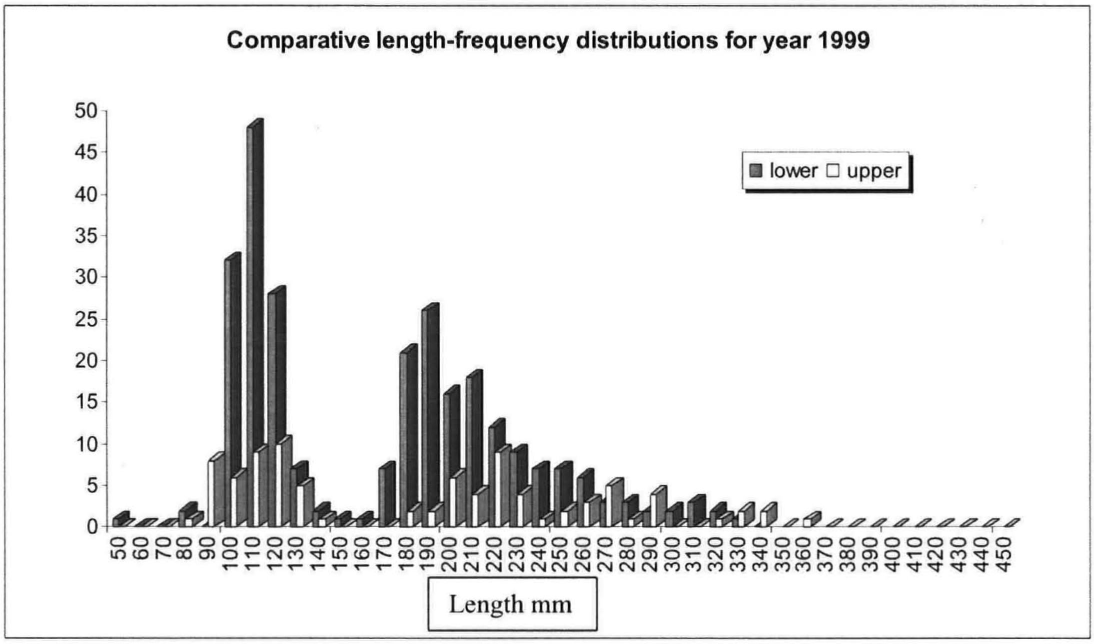

Fig. 6.16. Length- frequency comparisons by river sector after 6 years

A general downward trend in mean size of all trout >0+ was evident over the study period with mean lengths of all age classes smallest in Tolpuddle 1.

Table.2. Mean lengths for age classes of trout

Age Class	Lower sector		Upper sector
	Tolpuddle 1	Tolpuddle 2	Cobbs
	Mean length mm		
0+	103.37	108.94	109.17
1+	205.21	221.84	212.1
>1+	287.92	294.47	302.2

Non-linear von Bertalanffy growth curves derived from mean cohort lengths at age (Table 2) indicated similar early growth in both sectors. Ford-Walford plots predicted maximum adult size to be greater in the upper sector *(L@infinity= 483mm)* than the lower sector *(L@infinity= 336mm.)*. Von Bertalanffy growth curves derived from individual mark and recapture data suggested slower growth in the early years but indicated that in the upper sector trout at age 4 attained a length equivalent to the modal length of the age 3+ cohort (325mm) in the lower sector (appendix.6). Overall growth rates were similar for both sectors (K=0.33 Cobbs and K=0.39 Tolpuddle) but trout took longer to reach maximum size in the upper sector where growth reached an asymptote around age 9+ at a length of 420mm. This was within 1 SE (95% level of confidence) of that predicted by Ford-Walford plots. In the lower sector asymptotic length was less at 342mm, similar to that predicted by Ford-Walford plots.

6.2.6. Length at Age relationships

Mean adult lengths *(Length at age 2+)* were significantly negatively correlated with 1+ densities throughout the study area ($r^2 = 0.43$; p=0.02) and in the lower sector ($r^2 = 0.44$; p=0.02). In the upper sector PYOY mean lengths (*length at age 1)* were significantly negatively correlated with >0+ densities ($r^2 = 0.77$; p=0.02) (appendix.6).

6.3. RELATIONSHIPS BETWEEN HABITAT METRICS AND TROUT POPULATIONS

Table 3 shows the significant relationships between habitat metrics and life stage specific densities. Juvenile trout abundance (YOY and PYOY) was primarily related to spawning and first growing season habitat. Adult abundance was found to be most closely associated with over-wintering habitat.

6.3.1. Adult Life Stage

There were no significant relationships between adult densities (>1+) and mean WUA in summer or in winter. However, adult densities were significantly correlated with winter marginal habitat (ADWNSHAVG) which explained over 90% of variation in adult densities for 2 of the study reaches (Tolpuddle 2 and Cobbs). Figure 6.17 shows this relationship was particularly significant in the upper sector reach at Cobbs (p=0.01).

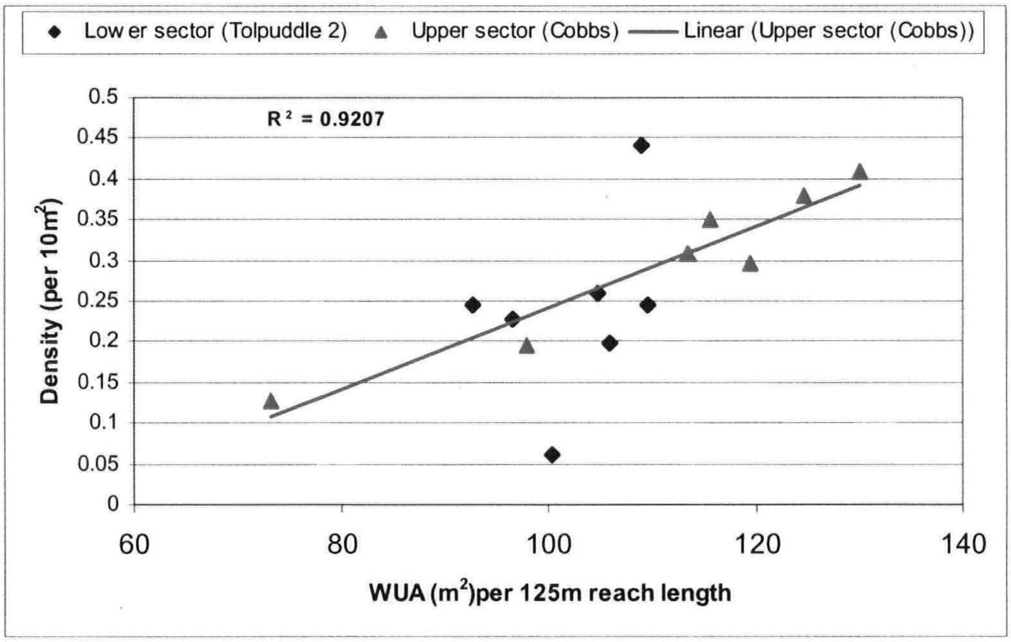

Fig. 6.17. Linear regression showing relationship between marginal habitat in winter and densities of adult brown trout the following summer

Table.3. Significant correlations (P<0.05) between trout density at age *n* and Weighted Usable Area (WUA) for metrics describing habitat parameters.

*(Blanks indicate non-significant correlations. Bold indicates correlations significant at p=0.01 level. Italics indicate relationships where metrics were natural log transformed. * indicates habitat metric applies to whole lower sector).*

HABITAT METRIC	LIFE STAGE	LOWER SECTOR	TOLPUDDLE 1	TOLPUDDLE 2	UPPER SECTOR: COBBS	ALL REACHES
WINTER						
ADWNSHAVG	Adult				**0.959**	
ADWNSHL50	Adult				**0.954**	
SP0AVGHP	PYOY	0.590			0.907	
SP0AVGHP	YOY				0.745	
EFFSP0AVGHP	PYOY	▨	▨	▨	0.835	▨
EFFSP0AVGHP	YOY	▨	▨	▨	0.770	▨
SUMMER						
YSMIN	YOY	**0.826**				**0.698**
YS2AVG	YOY	***0.809***				***0.684***
YS2NSHAVG	YOY	**0.805**			0.779	0.618
ADSMIN	PYOY				*0.810*	
ADSL50	PYOY				*0.805*	
ADSNSHMIN	PYOY				*0.804*	
ADSNSHL50	PYOY				*0.800*	
SPAWNING + REARING						
SPOAVGHP +YSMIN	PYOY	▨	▨	▨	0.843	▨
SPOAVGHP +YSMIN	YOY	▨	▨	▨	0.780	▨
SP0MINHP +YSL50	YOY	**0.862**	0.857*		▨	▨
SP64MINHP +YSMIN	YOY	▨	0.808*		▨	▨
▨	▨	▨	▨	▨	▨	▨

HABITAT METRIC	LIFE STAGE	LOWER SECTOR	TOLPUDDLE 1	TOLPUDDLE 2	UPPER SECTOR: COBBS	ALL REACHES
MESO-HABITAT: SPAWNING						
RIFAVGHP0	YOY				0.807	
GLAVGHP0	PYOY				0.858	
SP0AVGHP* 50125150	PYOY	0.600			▨	▨
SP0AVGHP 50125150+ RIFAVGHP0	PYOY	▨	▨	▨	▨	0.655
MESO-HABITAT: REARING						
RIFAVG2S	PYOY	0.646			▨	▨
RIFSL50	YOY		0.770		▨	▨
GLAVG2S*	PYOY	0.658			▨	▨
GLDSL50	YOY	0.560	0.789		▨	▨
FTAVG2S	PYOY	0.640			▨	▨
FTAVG2S	YOY	0.538			▨	▨
L50-100150	PYOY	0.663			▨	▨
L50-100150	YOY		0.768**		▨	▨
SP0AVGHP* 50125150+ GLAVG2S	PYOY	0.697			▨	▨
▨	▨	▨	▨	▨	▨	▨

6.3.2. Spawning Life Stage

YOY and PYOY trout densities were not related to mean spawning habitat availability (SP0AVG) throughout the winter season (November – March). However, in the upper sector reach spawning metrics for the hatching and emergence period (February/March) were significantly correlated with YOY densities at the end of the first growing season (September/October) and with PYOY trout in the following year. Effective mean spawning habitat during the hatching period (EFFSP0AVGHP) accounted for 59% of annual variation in 0+ densities (F=7.26; p=0.043). This relationship was derived from "effective spawning" simulations which were not carried out in the lower sector but similar results were obtained from standard simulations. Relationships with PYOY densities the year after spawning were found to be more significant for standard spawning simulations and accounted for 82% of variance (F=18.64; p=0.012) in the upper sector (Fig.6.18).

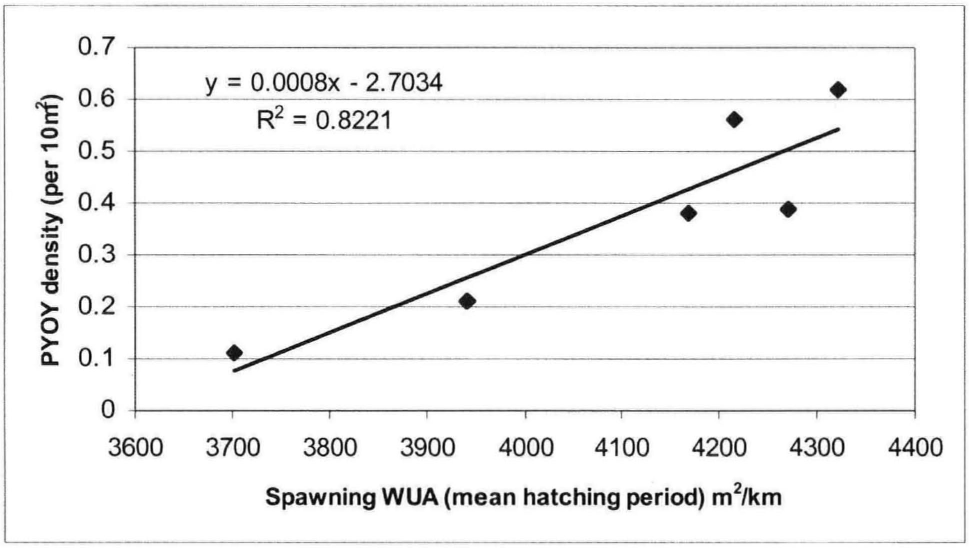

Fig. 6.18. Spawning habitat in February/March related to density of 1+ trout the following year

In the lower sector (Tolpuddle 1+2 combined) there were no significant relationships between spawning habitat metrics and YOY densities. However, a small but significant proportion of total variance in PYOY densities was explained by hatching period WUA (SP0AVGHP) (r^2=0.35; p=0.043).

6.3.3. Young-Of-Year Summer Growing Season

Metrics for juvenile habitat in the first growing season were significantly correlated with YOY densities. Minimum monthly WUA during the first growing season (YSMIN) was the best predictor of 0+ densities explaining 49% of variance (F= 18.1; p=0.002) across all reaches (Fig.6.19). Densities were also significantly correlated (p=0.01) with (log) mean summer WUA (July – September). In the Lower sector minimum first growing season WUA (YSMIN) explained 68% of variance in 0+ densities (F=19.1; p=0.002). Marginal habitat during summer low flows (YS2NSHAVG) accounted for 61% of variance in YOY densities (p=0.04) in the upper sector. There were no relationships between habitat in the first growing season and PYOY densities in any reaches but minimum summer adult habitat significantly explained 66% of variation in PYOY density (p = 0.028) in the Upper sector.

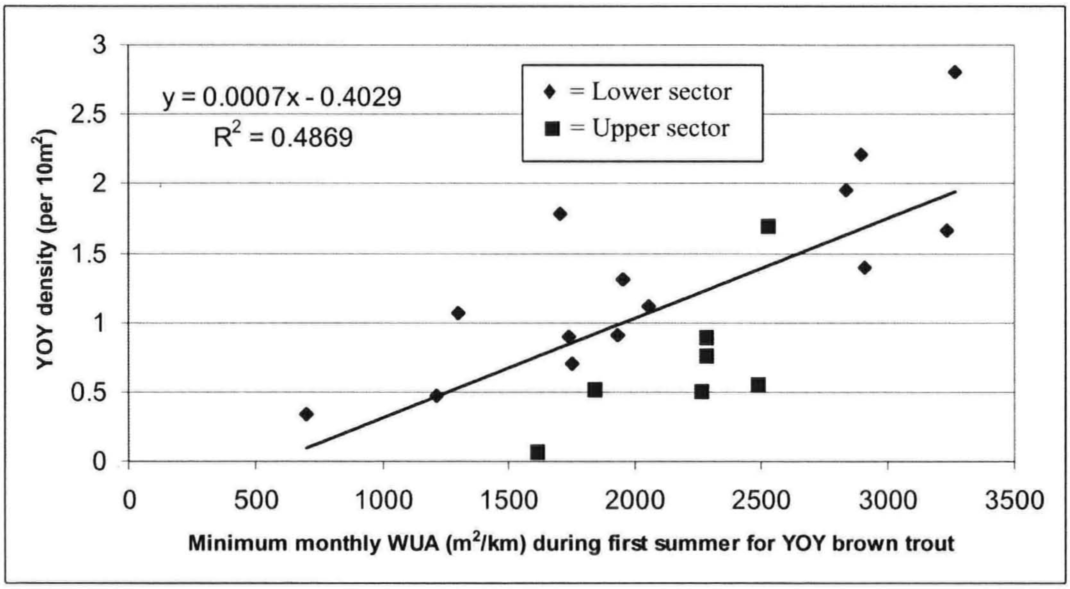

Fig. 6.19. Relationship between density of YOY trout and WUA during first summer growth

6.3.4. Effects of Spawning and Rearing Habitat on Abundance of Juvenile Trout

A multiple stepwise regression model was developed using mean spawning habitat during the hatching period (SP0AVGHP) and minimum summer fry habitat (YSMIN) as predictors to test whether combinations of spawning and rearing habitat across all reaches increased explanatory power for juvenile abundance. The model YOY = -0.12ysmin+ (-0.00029sp0avghp) was the best overall predictor of YOY density accounting for 68% of annual variation across all study reaches (F=19.28; p<0.01) compared to the 49% explained by summer rearing habitat (YSMIN) (Table.4). Model predictors were normally distributed and plots of residuals showed a good fit to the data.

TABLE. 4. Step-wise regression of early life stage critical habitats on YOY densities

Predictor	**F**	**df**	**r^2**	**P<**	**Coefficient**	**Standardised Coefficient**
YOY rearing in summer	18.03	1	0.487	0.001	0.000979	0.952
YOY rearing in summer; Spawning-hatching/emergence	19.282	2	0.682	0.001	-0.00029	-0.508

The extent to which early life stage habitats were limiting juvenile abundance in each sector was examined by aggregating spawning and rearing WUA into single habitat metrics combining spawning during the hatching/emergence period and fry rearing during summer.

a) Upper Sector: Cobbs

Combined metrics accounted for 61% of annual variation in YOY densities (F= 7.96; p = 0.037) and 71% of variation in PYOY densities the following year (F = 9.9; p = 0.035). This did not increase the proportion of variance in YOY densities accounted for by summer rearing habitat (YS2NSHAVG) and reduced the proportion explained by spawning (hatching period) for PYOY densities (see Table.3).

b) Lower Sector: Tolpuddle

Combined metrics accounted for 65 – 73% of annual variance in YOY densities in Tolpuddle 1 depending on the derivations of metrics used to represent spawning or rearing habitat components. Habitat metrics derived from minimum WUA rather than mean WUA during the hatching period (Sp64minHPYSMin) for the lower sector (Tolpuddle 1 + 2) accounted for 65% of variation in YOY densities in Tolpuddle 1 but no relationships were evident in Tolpuddle 2. The relationship in Tolpuddle 1 was increased to 73% when the mean of the lower 50th percentile of summer WUA values (SP0MinHPYSL50) was used to represent rearing habitat.

This metric explained 74% of total variation in YOY densities for the whole Lower sector (Tolpuddle 1+2 combined). However, the scatter-plot of this relationship (Fig.6.20) suggested a clear difference between the strength of the relationship for YOY densities in the downstream reach (Tolpuddle 1) compared to the upstream reach (Tolpuddle 2 – square points). The effect of adding a spawning component only marginally increased the proportion of variance in YOY densities accounted for by habitat minima in the first summer from 68% to 74%.

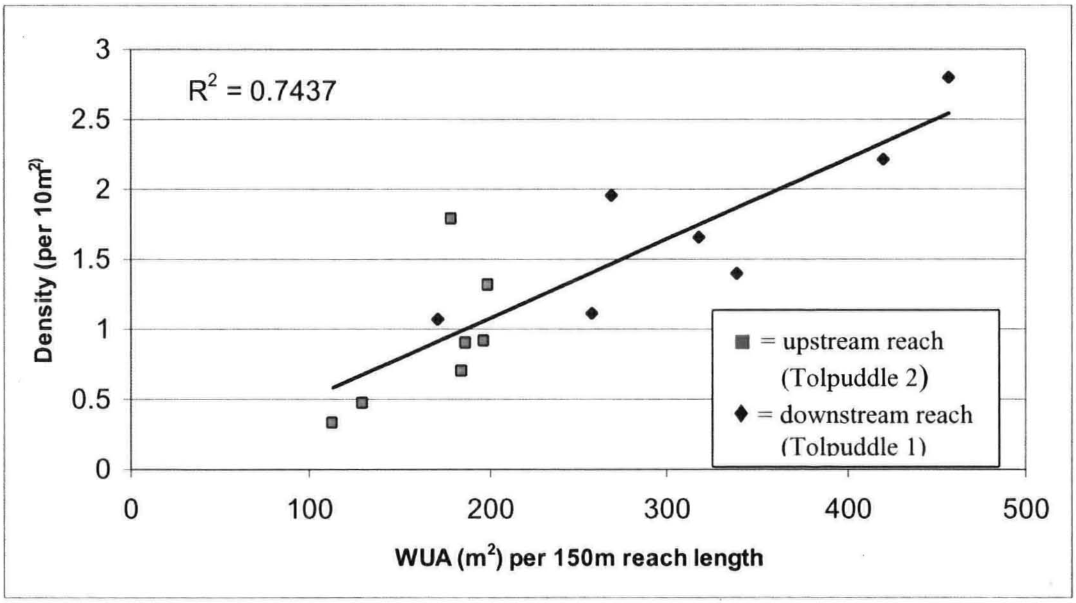

Fig. 6.20. Relationship between spawning and rearing habitat during critical periods and YOY density in the Lower sector

6.3.5. Meso – Habitat Relationships with Juvenile Trout

The relative importance of different meso-scale habitat units (e.g. riffle, glide etc) for spawning and rearing was examined in order to determine whether local scale habitat distribution and type had a significant effect on densities of YOY and PYOY trout. The spatial juxtaposition of meso-habitats is shown in appendix.7.

a) Spawning meso-habitat

(i) Upper Sector:

In the Upper sector three riffles (40, 70, 90) provided the largest combined spawning WUA during the hatching period which was significantly correlated with YOY densities ($p=0.028$). Spawning habitat suitability during the February – March period at these riffles accounted for 65% of annual variation in 0+ year class strength ($F=9.33$; $p=0.028$). This was a significant finding because riffles alone were indicated to be a better predictor of 0+ densities than total spawning WUA (hatching period) for the reach ($r^2 = 0.59$; $p = 0.043$). Combined spawning WUA (hatching period) for Glides 80 and 95 – 110 also accounted for 74% of annual variation in PYOY densities ($F = 11.12$, $p=0.029$).

(ii) Lower Sector:

The highest quality spawning habitats were located at riffle 50 and riffle/glide 120 – 160. Mean WUA for the hatching period at these locations (SP0AVGHP50125150) was significantly correlated with PYOY densities the following year ($r^2 = 0.36$, $p = 0.04$, $F = 5.5$) but was not significant for YOY densities. Thus, these meso-habitats accounted for the same proportion of variation in PYOY densities (36%) as total sector hatching period WUA.

(iii) Combined Sectors:

No overall relationships between juvenile densities and mean spawning WUA during the hatching period (SP0AVGHP) were found. However, the best 3 riffle/glide spawning areas in each sector accounted for 43% of overall variation in PYOY densities the following year ($r^2 = 0.43$, $p = 0.003$, $F = 12.02$).

b) Rearing meso-habitat

(i) Lower Sector:

The Lower sector provided abundant juvenile nursery/rearing habitat. Habitat – discharge relationships and time series for rearing meso-habitats are shown in appendix.8. Relationships were stronger for PYOY which showed similar strengths of association for mean summer WUA in flats, riffles and glides ($p = 0.02 – 0.024$). Glides accounted for the largest proportion of variation in densities for both YOY ($r^2 = 0.31$, $F=5.1$, $p=0.038$) and PYOY ($r^2 = 0.43$, $F=7.63$, $p=0.02$) but were the most abundant habitat type (44%). However, flats comprised only 22% of habitat area but explained 41% of variation in PYOY ($p=0.024$) and 29% in YOY densities ($p=0.05$) suggesting these could be important juvenile rearing habitats during summer low flow conditions (July – September). PYOY densities were also significantly correlated with riffle ($r^2 = 0.42$, $p=0.024$). There were no overall sector relationships between riffle and YOY densities but YOY were found to be significantly correlated with riffle WUA ($r^2 = 0.59$, $p = 0.044$) and glide WUA ($r^2 = 0.62$, $p = 0.038$) in Tolpuddle 1.

The highest quality rearing habitat in the lower sector comprised the glide/riffle/glide 100 – 160 in Tolpuddle 2. This juxtaposition was significantly correlated with total densities of PYOY in the lower sector ($r^2 = 0.44$) and with YOY densities downstream in Tolpuddle 1 ($r^2 = 0.59$). There were no relationships with YOY in Tolpuddle 2.

Summer glide WUA combined with the highest quality spawning habitats (50 and 120 – 160) increased the proportion of variation explained in PYOY densities to 49% compared to 43% for glides ($r^2 = 0.49$, $p = 0.012$, $F = 9.43$).

6.3.6. Summary of Main Relationships between Habitat and Trout Densities

1. adult carrying capacity is potentially constrained by the quality of habitat available in winter and bank-side habitats at stream margins are critical habitat components (Fig.6.17).

2. adult population size appears not to be directly affected by reductions in habitat under low summer flow conditions (but may be indirectly affected by the impact of low summer habitat on juvenile life stages).

3. the quality of spawning habitat during the late incubation and early hatching period (February/March) is a critical bottleneck to juvenile abundance (YOY and PYOY) and which has more marked affect on local population size where recruitment is local (Upper sector) (see sections 6.2.2; 6.2.3; 6.2.4;)

4. availability of rearing habitat during the first growing season is an important mechanism regulating 0+ year class strength (section 6.3.3 and Fig.6.19). Low habitat levels in summer appear to be a critical limiting factor to juvenile abundance given adequate spawning conditions (Fig.6.7 in year 1995).

5. combinations of spawning and rearing habitat in the Lower sector account for a high proportion of variation in annual YOY densities. A particularly strong relationship is evident in the downstream reach (Tolpuddle 1) where 0+ abundance is highest (see section 6.3.4(b) and Fig 6.20).

6. A multiple regression for spawning and summer rearing habitat variables explains significantly more variation in YOY abundance than rearing habitat alone (table.4). However, the relationship suggests that high densities are common when the spawning component of habitat is relatively low but declines rapidly with decreasing availability of rearing habitat (see section 6.3.4).

7. Variability of local meso-scale habitat determines spatial and temporal distribution of early life stage habitats and there is some evidence this may affect juvenile recruitment. Significant relationships were more evident for PYOY although the importance of riffle habitats to YOY trout was identified for spawning in the upper sector (section 6.3.5a(i)).

The implications of these findings are discussed in chapter 7.

CHAPTER 7. DISCUSSION OF MAIN FINDINGS

Results from this study contribute to an understanding of the role of habitat in the mechanisms regulating a wild brown trout population in the river Piddle. The main findings focus on the following aspects of habitat in relation to adult and juvenile life stages.

7.1. EFFECTS OF WINTER HABITAT ON LOCAL CARRYING CAPACITY FOR ADULT TROUT

In both study sectors adult densities were initially low (1993 – 1994) as a consequence of low trout abundance in the early years. This was most likely due to a combination of high predation and degraded habitat. Prior to 1994 pike *(Esox lucius)* were present and were particularly abundant in the lower sector before being removed. In the Upper sector pike were relatively scarce but substantial habitat degradation had resulted from overgrazing. Fencing subsequently led to rapid recovery of the riparian zone after 1994.

Densities of all age classes in both sectors increased significantly after 1994. However, following initial increases adult densities remained stable and showed low annual variation post 1995. In addition, lack of any significant relationships between juvenile (YOY and PYOY) and adult densities suggests an adult population close to carrying capacity after 1995. Population growth is slowest when densities are very low or when approaching carrying capacity and potential for rapid growth is maximised at moderate densities where a population is well below carrying capacity. Under these conditions production of a strong year class would be likely to significantly increase population size. Thus, if the adult population were below carrying capacity it would be expected to decline following poor recruitment years but to rebound rapidly following a strong year class. However, the very strong 0+ year class in the lower sector in 1994 and the very poor cohort in the upper sector in 1995 both had negligible effects on adult population size.

A major finding of this study was that local carrying capacity for adult brown trout was limited by availability of over wintering habitats but not by summer habitat. Seasonal variations in habitat use by brown trout are known to occur in response to water temperature (Cunjak and Power, 1986; Vehanen *et al.*, 2000), habitat availability (Annear *et al.*, 2002) and net energy gain (Fausch, 1984). In summer, feeding is the predominant activity and trout prefer to hold stations in areas of low velocity adjacent to swift currents providing invertebrate drift (Bachman, 1984; Fausch, 1984). Results from this study indicated no relationships between any aspects of summer habitat and adult densities. This finding suggests that adult population size was not directly affected by habitat reductions associated with low flows which have been a recurring problem on the Piddle and other chalk-streams. Indirect effects resulting from possible impacts on juvenile life stages were not evident due to absence of any relationships between juvenile and adult abundance.

However, in winter risk-avoidance, in terms of adverse environmental conditions and predators is probably the principal factor dictating habitat selection by brown trout (Heggenes *et al.,* 1993). Winter is a highly stressful period for stream dwelling salmonids. As water temperatures decrease ($< 8\ ^{0}C$) trout cease feeding or experience reduced ability to assimilate food (Cunjak and Power, 1987). Growth ceases and weight loss is common as energy reserves are mobilised to maintain homeostasis (Cunjak *et al.*, 1987). Simpkins and Hubert (2000) showed that wild trout (*fork length* 200mm) in the Bighorn River, Wyoming lost on average 41% of their September body weight by December. Such losses contribute to mortality by increasing susceptibility to secondary stress factors such as predation and disease (Hebdon, 1999). Consequently, over winter survival is often a critical determinant of adult population size.

Although no relationships were found between overall winter habitat availability and adult densities, results showed that habitat at the stream margins was particularly important to adults in winter. The strength of the association in the upper sector (Cobbs) ($r^2= 0.92$; $p=0.01$) indicated that availability of winter marginal habitats associated with complex cover was a critically limiting resource and a key mechanism regulating adult population size. Habitat simulations clearly demonstrated the importance of marginal areas in the upper sector during winter flow conditions (Figs.6.11a & b). High quality cover was almost entirely restricted to areas immediately adjacent to the bank where low velocity niches (ranging from $0.15 - 0.4\ ms^{-1}$) were increasingly concentrated at higher discharges (e.g. winter calibration flow). Bank-side habitats are of particular importance to brown trout especially in small streams which have a much greater proportion of bank-side habitat relative to stream width (Bagliniere and Arribe-Moutonet, 1985; Eklov *et al.,* 1999). The regression equation for the relationship between density and winter marginal WUA (Fig.6.17) suggests a minimum critical habitat threshold below which reduction in over-wintering territories might become limiting for the adult life stage. WUA less than $70m^2$ (within 2m of the bank) in winter would be likely to significantly reduce adult population size. Maintenance of the existing population requires 100 – 120 m^2 (approx. 1 $m^2/1$ m bank length).

The combination of cover and velocity explains the importance of marginal zones for brown trout over wintering in the upper sector. Lower water temperatures associated with the onset of winter trigger increased sheltering behaviour and a reduction in territoriality (Cunjak and Power, 1986) resulting in habitat niche shift (Smith and Griffiths, 1994; Armstrong *et al.,* 2003). This requires over wintering habitats that provide both cover and velocity shelter from high winter flows. In chalk-streams, absence of boulders and coarser substrates means the natural senescence of aquatic and riparian vegetation plays an important role in determining amounts and types of in-stream cover (Simpkins *et al,* 2000). As a result cover availability shifts increasingly towards the stream margins as biomass of submerged macrophytes declines in winter (Annear *et al,* 2002). Brown trout have been shown to make increased use of sheltering cover in winter, often in close proximity to banks (Cunjak and Power, 1986; Heggenes *et al.,* 1993) where overhead cover, velocity shelter and visual isolation provide trade-offs in forage, competition and predation risk (Kalleberg, 1958; Mortensen, 1977). Winter die-back of lush emergent marginal plants creates long tangled rafts of weed which snag around obstructions and woody debris creating complex cover zones of low overhead and submerged obstacle cover. These complex cover combinations provide excellent winter refugia for adult trout and a major finding of this study has been to demonstrate the importance of these zones in small chalk streams in winter (figs. 6.11(b) and 6.17). These findings are also supported by work elsewhere which has shown that brown trout prefer habitats providing maximum amounts of complex cover combinations in winter (Vehanen *et al.,* 2000). Cunjak and Power (1987) demonstrated that trout utilised submerged cover more frequently than above water cover in winter.

Velocities suitability was of critical importance to over-wintering habitat because at water temperatures <10 ^{0}C brown trout have a clear preference for slower velocities than in summer (Heggenes and Saltveit, 1990; Heggenes and Dokk, 2001). Considerable area of suitable velocities <0.3 ms^{-1} remained available at the margins even at winter flows well in excess of the winter calibration discharge, particularly throughout the upper part of the reach between 60 – 120m. Adult preference for such areas in winter is a response to reduced nutritional requirements, drift availability and the need to conserve energy (Cunjak and Power, 1986). Simpkins *et al,* (2000) noted that 72% of wild trout in a Wyoming stream preferentially selected maximum mean column velocities <0.3 ms^{-1} in January when no such velocity selection had been apparent the previous October.

As winter progresses and aquatic vegetation declines larger trout have been shown to aggregate in deeper, slow pools during the day (Heggenes *et al,* 1993; Griffiths and Smith, 1993). However, pools did not provide significant velocity refuge at flows exceeding 1.0 m^3s^{-1} in the upper sector. Results from the present study suggest this behaviour may be more likely where cover is limited (Cunjak and Power, 1986) and that where bank-side sheltering cover remains abundant in winter relatively shallow water appears to be preferable to pools for adult over-wintering habitat. This is consistent with the findings of Heggenes and Dokk (2001) that showed brown trout used a narrower range of depths in winter avoiding deeper areas in favour of relatively shallow water (20 – 45 cm) often close to banks.

7.1.1. Conclusion

Bank-side cover is an important microhabitat resource in winter. These findings indicate that habitat complexity, particularly availability and diversity of complex cover is a critical determinant of adult winter carrying capacity at the reach scale and may be more important for over-winter survival in chalk-streams than availability of pools. Hunt (1969) noted a 156% increase in brook trout yield after the addition of in-stream cover in a Wisconsin stream, most of which was attributed to increased winter survival. Metcalfe *et al.,* (1999) considered that availability of shelter from predation risk, especially in winter was at least as important as foraging space in determining trout densities and growth. This has important implications for habitat enhancement which often seeks to increase in-stream diversity by creating deep holding pools for adult trout. Fishery management practises often remove dead marginal vegetation in the interests of bank "maintenance." These results emphasise the importance of fencing to allow riparian zone recovery and other techniques such as brush bundle placement where natural regeneration requires assistance.

7.2. ASPECTS OF JUVENILE TROUT POPULATION DYNAMICS

Densities of juvenile trout (YOY and PYOY) were consistently higher in the Lower sector. In the upper sector where juvenile densities were lower significant positive relationships between YOY and PYOY densities the following year indicated strong first year carry over ($r^2 = 0.59$, $p = 0.003$) and there was a positive relationship between adult spawning stock and subsequent year class strength (appendix.6). These findings suggest juvenile recruitment in the upper sector was derived from a resident adult stock spawning locally.

Tagging experiments conducted by the Game Conservancy Trust indicated that 60 – 100% of marked YOY were recaptured in the same or an adjacent reach the following year such that a high proportion of age 1+ trout comprised "local" fish tagged the previous year (Summers, *pers. com*). However, in the lower sector first year carry over was not indicated because PYOY densities were disproportionately high, exceeding YOY densities the previous year in some reaches (e.g. Tolpuddle 2). Tagging also indicated a high proportion of unmarked 1+ trout in the lower sector which may have originated from elsewhere.

These findings suggest that migration may therefore be an important mechanism in the population dynamics of the lower sector reaches with significant in-migration of juveniles possibly occurring between the first and second summers. Juveniles have a natural tendency to drop downstream to establish territories especially at high densities and this movement can distort the age structure of a population (Euzenat and Fournel, 1976). Euzenat and Fournel (1976) showed that spring and autumnal downstream migrations of age 1+ and 2+ brown trout in the river Scorff, France, resulted in major seasonal fluctuations in population structure with a substantial shift towards 1+ in summer.

The absence of any relationships between juvenile densities and adult spawning stock in the lower sector may be due to a combination of in-migration of juveniles together with a small anadromous spawning component. Adult densities in all lower sector reaches plotted against YOY the following year indicated a relationship that did not pass through the origin but intercepted the y-axis as a positive number. Thus, anadromous trout may make a limited but more significant contribution to juvenile recruitment in the lower sector than in the upper sector which may account for the strong 0+ year class in 1994 in the lower sector (Figs.6.13 & 6.14).

7.3. EFFECTS OF CRITICAL HABITAT PERIODS ON JUVENILE ABUNDANCE

A major finding from this study was that juvenile recruitment in the river Piddle was strongly influenced by two critical habitat periods (1) spawning WUA during the egg hatching/alevin stage (February/March) and (2) summer rearing WUA for the YOY life stage (July – September).

7.3.1. Spawning Habitat during the Egg Hatching/Alevin Stage

Spawning habitat was significantly correlated with densities during the hatching/ emergence period (Feb/Mar) but not for other winter months. Relationships were strongest where juvenile densities were lowest and significantly accounted for 59% of variation in YOY densities in the Upper sector (p=0.02). Strong relationships between adult spawning stock and year class strength the following year together with high carry over between 0+ and 1+ year classes (p=0.003) indicated that recruitment in the Upper sector was "local" which probably accounted for the stronger association with local spawning conditions.

Temporal variations in spawning WUA during February and March closely reflected stream flow variability and indicated that increased YOY mortality occurred as a result of high discharges at this time. Winter flow conditions may affect egg survival at any time from egg deposition (November – January in the Piddle) through to emergence (March). During high discharges sediment transport increases and accumulation of fine material in spawning gravels can reduce intra-gravel oxygen availability or physically trap alevins in the gravel preventing emergence (Crisp, 1993). Lack of any relationships between density and spawning habitat between November and January suggested that conditions during the egg stage were relatively unimportant to recruitment and that availability of suitable spawning areas was not limiting. However, in February and March flow conditions were fundamental in determining the suitability of intra-gravel conditions within redds at the time of hatching and during the pre-emergence alevin stage. Extreme floods, such as those experienced in February 1995, put bottom materials into motion and substrate redistribution is likely to have resulted in "wash out" of eggs from the gravel and high mortality of alevins. This accounts for the virtual absence of a 0+ year class in 1995 in the upper sector (Fig.6.15). These findings correspond with those of Jensen and Johnsen (1999) who showed that high spring flood peaks coincident with the hatching and emergence period negatively impacted survival of YOY brown trout and Atlantic salmon. These authors found that high discharges during the alevin stage and the first week after emergence significantly increased mortality but that floods were of minor importance at the egg stage or longer after emergence.

This study shows that alevins and early post-emergent fry are particularly vulnerable to extremes in February and March and stable flows are critical to year class strength during this period. Strongest year classes were associated with low-moderate flows throughout the winter period with an absence of extremes (e.g. 1996 and 1997). These findings support those of Nehring and Anderson (1993) who found that flow stability from egg deposition through to hatching was critical to year class recruitment and that timing and magnitude of variations in fry WUA and mean monthly discharge during incubation were the most important factors limiting trout recruitment in 10 Colorado streams. The relative immobility of early life stages makes them most vulnerable to flow induced habitat variations. Daufresne *et al.,* 2005 demonstrated that post emergent brown trout fry were highly sensitive to increased water velocity for 5 – 6 days after emergence from the gravel and identified a short critical period that corresponded to the time taken for 80% of fry to be displaced downstream from redds. Heggenes and Traaen (1988) demonstrated experimentally a flow sensitive period of 2 weeks for brown trout entering the free feeding stage.

Thus, habitat bottlenecks may be more likely at early life stages with potentially important implications for juvenile recruitment dynamics. Density dependent mortality is high in post emergent fry such that densities are largely independent of egg numbers at high density and bottlenecks tend to trigger density dependent mortality (Elliott, 1994; Armstrong *et al.,* 2003). In addition, high velocities experienced during flood events increase rates of downstream displacement of fry (Crisp and Hurley, 1991a; Daufresne *et al.,* 2005). However, Daufresne *et al.,* (2005) observed experimentally that velocity increases alone did not result in the increased YOY mortality observed in the wild. This may suggest that environmental conditions other than velocity associated with flood peaks (such as increased suspended solids) may reduce YOY survival. Alternatively, more rapid displacement of fry into downstream zones may have implications for utilisation of nursery habitats and density dependent mechanisms which may negatively impact survival.

7.3.2. Rearing Habitat for YOY Trout during the First Summer

Minimum monthly WUA significantly explained 49% of variation in YOY densities across all study reaches ($p<0.001$) (Fig.6.19). Thus, low levels of nursery/rearing habitat in the first summer acted as a critical bottleneck for YOY trout in the river Piddle and was limiting to juvenile recruitment. Low flows occur naturally between July and September and YOY habitat was lowest in months with the lowest summer flows such as in 1995 and 1996. This agrees with the findings of Strevens (1999) who examined the effects of abstraction 2 km downstream of the present study site on juvenile brown trout habitat in summer. Abstraction was shown to have resulted in significant reductions in fry WUA between 1988 and 1992. Low summer habitat was also found to be spatially correlated with a zone of low relative abundance of 0+ trout which was evident during the period 1991 – 1996. In the present study where YOY densities were highest (in the Lower sector) minimum monthly WUA significantly explained the greatest proportion of variation (68%) in density ($p<0.001$). Low flows caused a physical reduction in available habitat and therefore a reduction in carrying capacity which is likely to have increased competition for space and food especially at higher densities. These results suggest that low flows have created a bottleneck leading to density dependent regulation of population size at the fry life stage. Density dependent effects have been shown to be most pronounced during short critical periods usually during the early post –emergent fry stage (Milner *et al.,* 2003). Elliott (1993a) showed that regulation of population size in anadromous brown trout was controlled by density dependent mortality operating for a period between 30 – 70 days following fry dispersal from spawning gravels. This probably occurs during April and May in the river Piddle and is undoubtedly an important period. However, this study has shown that population regulating bottlenecks occur much later in summer and are more significant at higher juvenile densities. Other studies have also suggested that density dependent regulation in brown trout may be sustained during a longer period, at least through the first summer (Gee *et al,* 1978; Egglishaw and Shackley, 1977; Gardiner and Shackley, 1991). Nislow *et al.* (1999) showed that behavioural shift towards risk minimisation occurs later in summer. Where availability of sheltering and refuge habitats is limited by low flows this may result in increased juvenile predation.

7.3.3. Summary

These findings demonstrate that habitat modelling at fine spatial scales but relatively coarse temporal scales (monthly time steps) successfully identified critical habitat periods acting as bottlenecks to juvenile recruitment. Extraction of only three months from an annual time series (February/March + minimum WUA for July – September) was sufficient to identify such critical periods. However, juvenile recruitment dynamics are complex and different aspects of habitat cannot be viewed in isolation. The spatial and temporal inter-relationships between spawning and rearing habitat are also important and need to be considered in the context of trout behaviour.

7.4. SPAWNING AND REARING HABITAT EFFECTS ON JUVENILE TROUT

A diversity of habitat types is important in mitigating brown trout life history strategies because microhabitat availability acts as a limiting factor to trout abundance. The riffle – glide – pool sequence can be regarded as a functional habitat unit (FHU) important in meeting the habitat requirements of different trout life stages which will utilise different habitat types in response to changing ontogenological, seasonal and diel requirements (Roussel and Bardonnet, 1997). Pool-riffle sequences are regularly occurring natural features of alluvial river channels and can be considered meso scale habitat units (1 –

100m). An intermediate meso-habitat unit "glide" tends to dominate proportionally in the river Piddle which is typical in chalk streams (Raven, 1998).

7.4.1. Importance of Meso-Scale Habitats for Spawning and Rearing

Riffles and glides were important meso-habitats for spawning. In the Upper sector both were significantly correlated (hatching period WUA) with YOY densities and glides were correlated with PYOY densities. Time series showed that spawning WUA in riffles was typically in the order of 50% greater than in glides during the study period. This importance of riffles was demonstrated by the fact that a higher proportion of variance in YOY densities was accounted for by riffle WUA ($r^2 = 0.65$; $p = 0.014$) than by total spawning WUA in the upper sector ($r^2 = 0.59$; $p=0.02$). Local recruitment from a resident adult spawning stock may mean lower spawning densities in the upper sector. This would result in more limited competition and efficient reproduction so the numbers of juveniles produced would be more closely related to the spawning level than in the lower sector (Milner *et al.,* 2003).

In the Lower sector WUA – discharge curves showed that young-of-year nursery/rearing habitats were most abundant and juvenile densities particularly PYOY were highest. Different meso-habitat types (riffle, glide, and flat) all provided rearing habitat in summer which was more significantly correlated with PYOY than YOY densities. All meso habitat types were significantly correlated with PYOY density suggesting that different meso-habitats were important for rearing at different times, probably depending on variations in abiotic conditions such as flow and temperature. Thus, at typical summer flows at or above (calibration) base flow, glides provided the most rearing WUA but at low flows (below calibration) flats constituted the largest fry WUA (appendix.8). Flats may have provided potentially important refugia for YOY trout during summer droughts given the relatively high sensitivity of 0+ year class strength to low summer habitat levels.

Flats may also be important to first winter survival of young trout. Behavioural responses to low water temperatures ($< 8\,^0$C) result in reduced tolerance to high velocities and increased importance of slower flowing meso-habitats in winter (Heggenes and Saltveit, 1990; Cunjak and Power, 1986). Heggenes and Dokk (2001) demonstrated that age 0 brown trout showed a marked seasonal shift in meso habitat use from shallower habitats such as riffles and runs in summer towards slow flowing glides and flats in winter. Survival rates in the Lower sector were indicated by tagging to be higher than in the upper sector (Summers. *pers com*). This may reflect better over wintering conditions for juveniles in the Lower sector. Good over-wintering conditions could also account for the substantial in-migration of juveniles between the first and second summers. Studies of juvenile salmon have shown that such movements may be seasonally triggered and lead to redistribution from areas favouring YOY in summer to areas favouring older salmon in autumn (Rimmer, 1983; 1984). However, better over winter survival of juveniles in the lower sector may also be indicative of less competition for shelter from adult trout. Mass is an established determinant of successful shelter competition (Orpwood *et al.,* 2003) and dominant trout are likely out competing juveniles for over wintering habitats in the upper sector.

In summer, the high 0+ densities in the downstream reach (Tolpuddle 1) were probably accounted for by preference of YOY trout for shallow habitats such as riffles (Roussel and Bardonnet, 1997; Heggenes and Dokk, 2001). Fry WUA was greatest in Tolpuddle 1 which consisted almost entirely of riffle and shallow glide that provided young-of-year nursery habitats of similar quality over the typical summer flow range. Both these meso habitats were significantly correlated with 0+ densities in Tolpuddle 1, accounting for approximately 60% of variation during low summer habitat (mean of lowest 50%). This is in accordance with the findings of Heggenes *et al,* (2002) which showed that 0+ brown trout utilised glides as much as riffles under low flow conditions in summer. Riffles and glides were the meso-habitats most affected by low flows. Summer flow augmentation to reduce juvenile habitat depletion (Strevens, 1999) had the effect of increasing the relative amounts of fry habitat in riffles and glides available in summer during the later years of the study (1997 – 2000) (appendix.8). These nursery/rearing habitat increases may have been particularly important as they corresponded with continuing upward trends in YOY trout densities.

These results suggest that a diversity of meso habitat types can be important for juvenile trout because habitat selection is dynamic in response to flow conditions, temperature and habitat availability. Riffles and glides are important for spawning and as summer rearing habitats but deeper, slower flowing areas such as flats may be important over wintering habitats as well as providing refugia during summer low flows.

7.4.2. Spawning and Rearing Habitat Juxtaposition in Relation to Juvenile Recruitment

Results from this study have shown that temporal variation in habitat quality associated with critical periods for spawning and rearing were important limitations to first year survival in the river Piddle. The multiple regression model constructed from metrics representing these two critical periods (spawning WUA during hatching/emergence + minimum rearing WUA for fry in summer) significantly explained 68% of variance in YOY densities for all study reaches (Table.4). Thus, quality and quantity of meso-habitats for spawning and rearing life stages was affecting the productive capacity of habitat and hence juvenile abundance.

The spatial arrangement or juxtaposition of different meso-habitat types in relation to fry dispersal from redds and scales of juvenile movement between habitats as fish develop may also be an important characteristic affecting juvenile production (Kocik and Ferreri, 1998; Armstrong *et al.,* 2003). At larger scales this has been shown to give rise to markedly different population dynamics (Kennedy and Strange, 1982; 1986). However, the relative locations of different habitat types (juxtaposition) and the degree of intermixing between them (interspersion) may also be an important habitat characteristic affecting juvenile production at much smaller reach scales. Recruitment to patches of habitat from any particular spawning area can be expected to be spatially heterogeneous and dependent on distance and fry dispersal patterns from redds (Crisp, 1995). Thus, downstream of spawning habitat fry abundance will remain highly localised, reflecting the pattern of redd distribution, even where nursery/rearing habitat is homogeneous. Armstrong (2005) modelled this process and showed that within 100m of the dispersal point mass and density followed the thinning line as fish saturated the habitat but further downstream the population was below saturation. Thus, rearing habitat that is disconnected from spawning habitat will remain under utilised even where it is abundant such that spatial structuring of spawning and rearing habitats can act to limit local juvenile production (Kocik and Ferreri, 1998).

Tagging studies in the river Piddle showed high site fidelity with limited movement between reaches. This local residency is common in chalk streams (Solomon and Templeton, 1976) and is indicative of abundant and highly interspersed habitat for each life stage and season such that fish do not have to move to acquire requisite resources. The limited range of fry dispersal means that the geographic placement of redds in relation to nursery/rearing habitat may act to constrain local juvenile production in the Upper sector where juvenile rearing habitat was relatively scarce.

In the Lower sector spatial juxtaposition of meso-habitats appeared to be contributing to competitive segregation of YOY and PYOY. Minimum spawning and rearing WUA (SP0MinYSL50) explained 74% of total variation in YOY densities in the lower sector reaches (Tolpuddle 1+2 combined) (Fig.6.20). However, PYOY trout were the dominant age class in the upstream reach of the lower sector (Tolpuddle 2) with YOY more abundant in the downstream reach (Tolpuddle 1). The scatter-plot (Fig.6.20) of the relationship indicates that high YOY densities in the downstream reach (Tolpuddle 1) were strongly associated with minimum spawning and rearing habitat availability throughout the lower sector but YOY densities in the upstream reach (Tolpuddle 2) showed no relationship. Up to 73% of annual variation in YOY densities in Tolpuddle 1 was accounted for by metrics that described minimum spawning and rearing habitat availability for the lower sector as a whole. Meso-habitats providing the highest quality spawning and rearing habitat in the Lower sector comprised a glide-riffle-glide juxtaposition (100 – 160m) located in the upstream reach (Tolpuddle 2) (appendix.7). WUA for this FHU was not related to YOY densities in Tolpuddle 2 but was significantly correlated ($r^2 = 0.57$; $p=0.05$) with YOY densities in the downstream reach (Tolpuddle 1).

These findings suggest that downstream dispersal of fry from areas upstream appeared to be in part driven by inter-cohort competition resulting in habitat use becoming partitioned between Tolpuddle 1 and 2. Competition and predation from older trout is a likely contributor to this downstream movement of 0+ trout. Age 1+ trout tend to be dominant and out-compete fry for preferred habitats as part of cost minimisation expelling 0+ fish to shallow riffles and low velocity river margins (Bohlin, 1977; Cunjak and Power, 1986). Tolpuddle 1 has a lower mean depth and a greater relative area of shallow water than Tolpuddle 2. This may explain why riffle and glide meso-habitats in Tolpuddle 1 were not correlated with 1+ density downstream and why no correlations were evident between any meso-habitats in Tolpuddle 2 and 0+ densities upstream. Heggenes *et al* (2002) showed that under summer low flow conditions age 0+ trout used shallow fast flowing meso-habitats proportionally more whereas 1+ frequented slower flowing deeper habitats such as deeper glides and pools. Bardonnet and Heland (1994) also found that 0+ trout occupied significantly shallower water in the presence of older trout. These authors showed that downstream movement of newly emerged brown trout fry increased by 20% when emergence occurred in an area of high predation risk from 1+ trout and bullhead. Lower densities of 1+ and older trout in Tolpuddle 1 provide the fittest YOY trout competitive advantage and better opportunity to defend territories.

Movements and migrations of trout have the potential to increase distribution and reduce local density – dependent constraints on production enabling fish to capitalise on spatially dispersed habitats most suitable for different life stages (Armstrong, 2005). The fact that the relationship between PYOY trout in Tolpuddle 1 and adult density the following year in Tolpuddle 2 is stronger than in Tolpuddle 1 may suggest that a proportion of "local" 0+ trout move back upstream as they mature to occupy areas of deeper water with more abundant cover available in Tolpuddle 2.

Such movements probably contributed to the trout population in the lower sector saturating the available habitat over time once the cropping effect of pike predation was removed. This habitat saturation resulted in density dependent growth and trout attained a smaller maximum size than in the upper sector where densities were significantly lower. Strong declines in modal lengths of 1+ together with the smaller maximum size of adults suggested the lower sector population was becoming asymptotic and that biological carrying capacity was becoming progressively growth limiting. The apparent "stunting" of cohorts seen in later years indicated a population that was at carrying capacity and according to recent work by Armstrong (2005) is a result of the integration of density – dependent growth and self thinning at high densities. This results in a change in the gradient of the relationship between mass and density at habitat saturation such that fish mass becomes much smaller for a given density.

7.5. SOME COMMENTS ON THE MODELLING APPROACH

The modelling approach used in this study contributes to the debate regarding the validity of outputs from PHABSIM and merits some further consideration.

7.5.1 Habitat Suitability Index Curves

There are a number of limitations associated with use of category 2 HSI curves which are implicit to any application of PHABSIM. HSI curves represent a biological response to habitat that inevitably involves a degree of ecological uncertainty in curve shape which is difficult to quantify (Orth, 1987; Bovee *et al.,* 1998). Errors arising from these uncertainties can significantly influence WUA/discharge relationships under certain conditions (Booker and Dunbar, 2004; Dunbar *et al.,* 2001).

This study used generic curves developed over a wide range of chalk stream sites rather than site-specific HSI curves which are conditioned by habitat availability and increase bias where the range of habitat utilisation is artificially narrow (Dunbar *et al.,* 2001). This afforded greater confidence in the WUA/discharge relationships because curves were not conditioned by site specific habitat availability. This study also benefited from recent research which has indicated that habitat preferences (selection within available habitats) for trout and salmon in the 80 – 200mm size class are broadly consistent for velocities < 0.5 ms^{-1} and for depths up to 0.6 m (Dunbar *et al.,* 2001). The early fry stage (< 80mm) was not modelled and depths > 0.6m were primarily confined to winter. Thus, the HSI curves used reflected a considerable narrowing of uncertainty with regard to habitat selection for YOY and PYOY in summer.

HSI curves used for channel index affected habitat predictions. Relative magnitudes of WUA varied depending on whether cover or substrate was employed in the modelling computations. The distribution of suitable cover was spatially heterogeneous and highly skewed towards the margins whereas substrate was relatively homogeneous which resulted in a relative increase in the effect of depth/velocity suitability. Thus, simulations using substrate predicted significantly greater habitat availability than cover, even when a minimum composite suitability factor was applied (Fig.7.1). Therefore, cover was a more limited resource and WUA at stream margins became relatively more important when cover was used. Use of different HSI curves for channel index in the Lower sector had negligible effects on correlations between growing season habitat and juvenile densities which suggested that depth and velocity were more important in determining YOY summer habitat than substrate or cover.

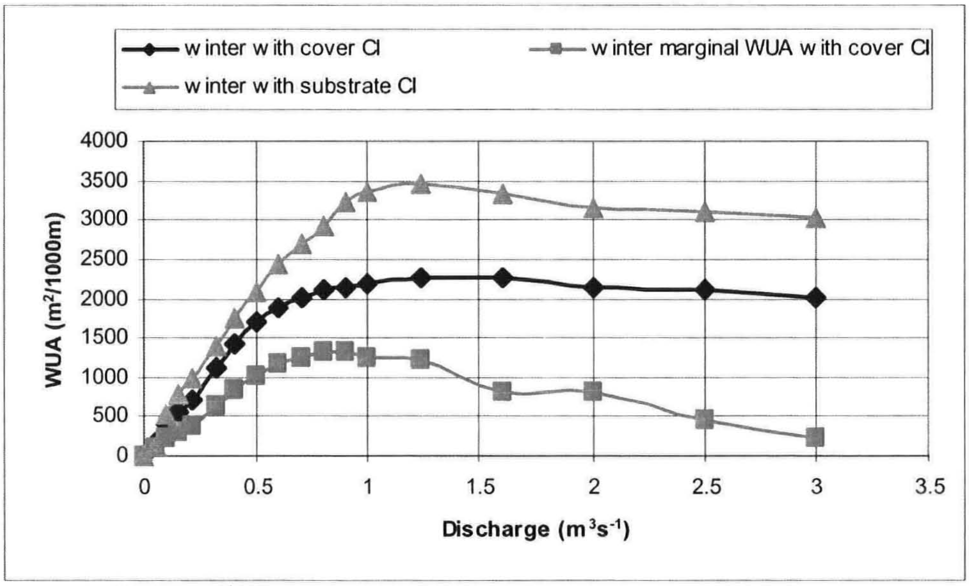

Fig.7.1. Variations in WUA predictions for adult trout in winter based on channel index

HSI curves for cover were not readily available and none had been previously developed on the river Piddle. A "curve" was developed by the author for use in this study that assumed an approximately linear increase in suitability values depending on type, size and complexity of cover based on approaches used elsewhere for cover criteria classification (Nehring and Anderson, 1993: Bovee *et al,* 1994). However, this was not a habitat preference curve as it was not based on frequency of use data.

7.5.2. WUA – Discharge Relationships

Spawning simulations in the Upper sector used a binary curve to define optimal substrate conditions in addition to univariate suitability indices. Bovee *et al,* (1994) considered that binary curves were a more robust approach for quantifying actual habitat area than conventional suitability indices because they avoided problems associated with assigning a quality to each part of a biological response curve. Use of binary curves resulted in very similar WUA/discharge relationships to univariate curves because most substrates consisted of medium – coarse gravel which was within the optimal range used for the binary curves.

An examination of the effects of different simulation strategies on spawning habitat predictions in the Upper sector demonstrated no appreciable difference between mean WUA and "effective" WUA during the hatching period (Fig.7.2). However, greater relative variations in high quality habitat (minimum composite suitability factor = 0.5 applied) were demonstrated during the hatching period than over the whole winter period.

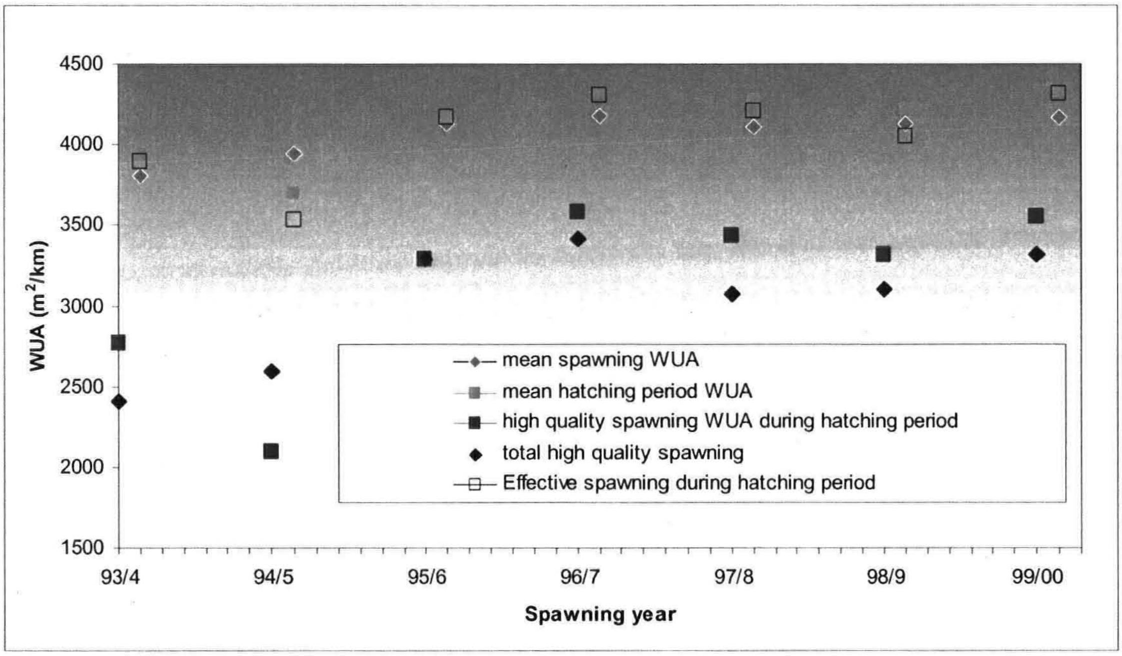

Fig. 7.2. Effects of different simulation strategies on spawning habitat predictions in the Upper sector

WUA/discharge relationships were also found to be sensitive to hydraulic considerations and seasonal differences. Increased hydraulic complexity magnifies differences in calculated physical habitat (WUA) (Booker and Dunbar, 2004). The sensitivity of hydraulic models to seasonal changes in biomass of submerged macrophytes was of particular significance because hydraulic roughness in chalk-streams increases significantly as discharge drops in summer (Johnson *et al.,* 1993). This caused particular problems in spring/early summer when Ranunculus reached maximum biomass resulting in a stage increase with declining discharge. Hearne *et al,* (1994) demonstrated that macrophytes distorted habitat results by up to 34% where hydraulic models were calibrated to a non-macrophyte scenario. This was overcome by undertaking separate hydraulic calibrations using different combinations of calibration flow sets for different times that reflected the natural senescence of in-stream vegetation and using WSP to modify roughness (see chapter 5).

Vegetation also had substantial impacts on velocity distribution through a cross section. Seasonal and annual variability in biomass is unpredictable and locations of individual macrophytes, insofar as they affect velocity at a given point, cannot be considered "fixed" in the same way as an obstruction such as a boulder. Velocity predictions have a substantial degree of uncertainty because velocity profiles are by their nature transient and vary chaotically. A significant finding of this study is that, in chalk-streams, seasonal variations in WUA predicted by PHABSIM are most sensitive to the calibration sets used to model velocity. Use of different velocity sets to calibrate the VelSIM model for summer and winter periods of the hydrological cycle had a substantial effect on WUA-discharge relationships (Fig.7.3).

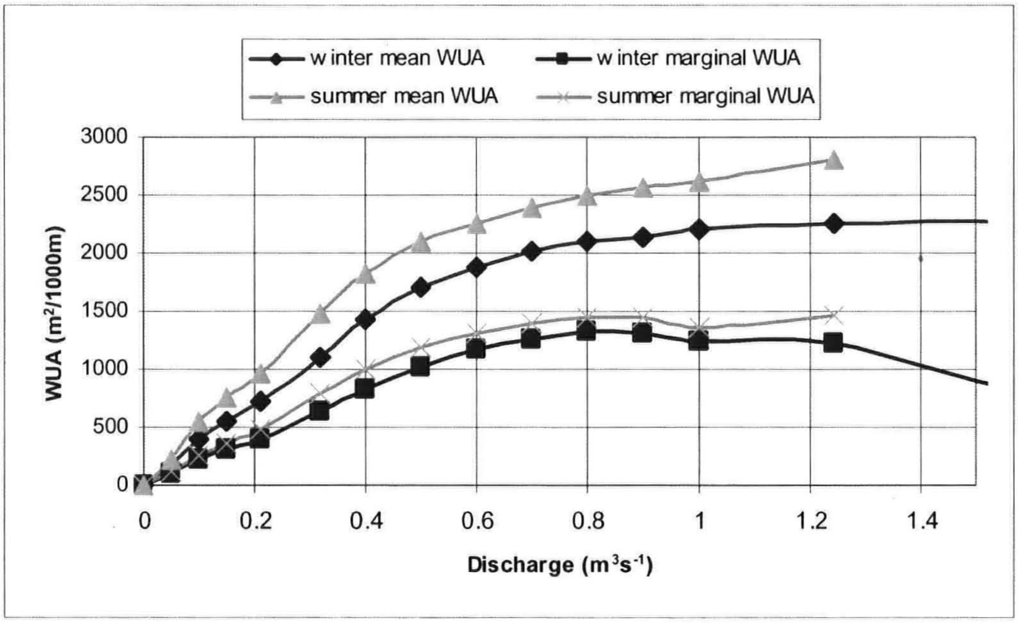

Fig.7.3. Effects of season on WUA – discharge relationships for adult trout

Unlike depth - discharge changes which were relatively linear, velocity changes were non-linear in both magnitude and pattern of distribution. Velocity distributions not only changed with spatial and temporal variations in particular plant assemblages, but the "mobility" of submerged macrophytes meant that subtle changes in velocity constantly occurred as plants waft in the current and funnelled flows creating significant habitat features at certain times of the year which disappeared at others. In these respects, chalk-streams are more complex to model hydraulically than upland streams and the physical complexity of modelled reaches necessitated a considerable degree of care to achieve accurate model calibrations which fundamentally affected predictions of trout habitat.

7.5.3. Other Methodological Considerations

The present study has highlighted that use of relatively coarse temporal resolutions (monthly time steps) can be successful in identifying biologically important events but interpretation of results is sensitive to the time series used. A finer temporal resolution focussed on hatching/swim-up (February – March) and YOY first summer (July – September) periods would be beneficial for identifying critically limiting habitat durations regulating 0+ year class strength in chalk-streams. Daily time series would identify periods within these months when higher and lower than average habitat levels were occurring that could represent critical thresholds and act as bottlenecks in trout populations (Capra *et al.,* 1995). Temporal intervals should be small enough to avoid masking biologically significant events but sufficiently large to reduce the volume of data processing. An averaging period of 7 days probably represents the most practical compromise (Bovee *et al.,* 1994).

The value of the results in this regard would be enhanced by the addition of temperature time series to estimate starting dates for reproductive and early life history phases and to calculate degree day accumulations (Bovee *et al.,* 1994). Degree day accumulations are linked energetically to juvenile growth rates and are useful for evaluating critical habitat durations when temperature conditions are favourable for a particular life stage. For example, periods of high quality spawning habitat that occur during sub-optimal temperatures will be much less important to subsequent year class strength and could be excluded from a critical habitat thresholds analysis. These approaches would enable managers to better understand the multiple linkages that exist between microhabitat, thermal regime, first year growth and year class strength which ultimately limit populations.

CHAPTER.8.   CONCLUSION

The aim of this thesis was to examine habitat – population relationships for a wild brown trout population in the river Piddle, Dorset and to model the effects of seasonal fluctuations in habitat availability/quality for different life stages of trout. The primary objectives were as follows:-

Objective 1: Analyse the dynamics of the brown trout population in the river Piddle

Objective 2: Quantify habitat quality for juvenile and adult trout in contrasting reaches during summer and winter.

Objective 3: Examine effects of temporal changes in habitat on trout abundance and identify aspects of habitat acting as population limiting factors.

Objective 4: Assess the importance of spawning and rearing habitats in relation to juvenile recruitment

This chapter examines the extent to which these aims and objectives have been met and evaluates the contribution of the main findings to an understanding of habitat limitations to trout production in self sustaining wild populations. The significance of these results is assessed in relation to habitat enhancement and the efficacy of PHABSIM for the management of chalk rivers.

8.1. Objective 1: BROWN TROUT POPULATION DYNAMICS

Main Findings:

Population size was primarily regulated by year on year variations in 0+ recruitment and adult spawning stock size. However, there were considerable differences between the trout populations of the Upper and Lower river sectors. In the Upper sector 0+ densities were more closely related to adult stock size suggesting that recruitment was primarily derived from a resident adult population. In the Lower sector substantial increases in the ratio of adults to young-of-year indicated predation was a likely factor that was limiting the population at the commencement of the study period. Tagging indicated limited movement of individuals aged 1+ and >1+ but there was evidence of significant in-migration of juvenile trout into the lower sector between autumn and the following spring.

Trout lengths were strongly negatively correlated with density and growth rates showed clear density dependent effects. Trout grew more rapidly and attained larger maximum size in the upper sector where densities of age 0+ and 1+ were significantly lower. Stunting was apparent in the Lower sector following year on year abundance increases which suggested that habitat saturation was occurring.

Significance:

The effects of reduced predation have allowed optimal use of previously under-utilised habitat over time. Reductions in asymptotic lengths in the Lower sector with increases in abundance suggest that habitat carrying capacity can be described by the slope of the self thinning line (Armstrong, 2005). In later years habitat saturation led to a marked reduction in fish mass for a given density producing a stunting effect not apparent in the upper sector. This suggests that at high densities biological productivity becomes a potentially more important limiting factor than physical habitat even in high productivity chalk streams. This is consistent with findings of Bagliniere and Maisse (1990) who developed a growth model for 0+ trout which showed that biological carrying capacity became progressively growth limiting.

8.2. Objectives 2 & 3: ADULT TROUT

Main Findings:

1. Habitat availability in winter is more critical than in summer

There were clear distinctions between summer and winter habitat effects on adult trout in the Upper sector. Summer low flows depressed WUA mainly due to associated loss of depth but had no effect on density. Peak flows in winter reduced WUA due to increased velocities. Lack of velocity shelter and cover away from the stream margins probably accounted for the absence of any relationships between (aggregate) winter habitat and adult densities. However, marginal habitats were more abundant in winter than summer due to depth – dependent habitat gains at higher flows which occurred where the combined effects of complex cover and low velocities were concentrated.

2. **Riparian marginal zones are particularly important over wintering habitats for adult trout and limit local carrying capacity at the reach scale**

In the Upper sector adult trout comprised the largest proportion of the total population and marginal habitat in winter accounted for over 90% of variation in densities. The strength of this relationship and the lack of variation in adult population size after 1995 suggest that marginal habitats associated with riparian zones were a critical determinant of adult carrying capacity.

Significance:

These findings emphasise the importance of habitat complexity which affords velocity shelter and overhead cover in winter. Riparian zone habitats may have a more important influence on over-winter survival in small streams than availability of pools and will be a key determinant of carrying capacity at a reach scale where complex bank-side cover remains present throughout the year. This highlights the importance of fencing of riparian zones and has important implications for the management of wild chalk-stream fisheries.

8.3. Objectives 2 & 3: JUVENILE TROUT

Main Findings:

3. **Two flow related critical periods significantly affect juvenile recruitment:**
   - **(i) spawning habitat during the hatching/emergence period**
   - **(ii) minimum fry habitat during the first summer.**

High peak flows reduced spawning habitat and maximum WUA occurred during low winter flows. Spawning WUA during the hatching period was sensitive to winter flows

>*Q*35 percentile especially during February. Spawning habitat during the critical period was significantly correlated with PYOY densities and explained 59% of annual variation in YOY densities in the Upper sector (p=0.043).

Summer habitat for YOY during the first growing season was most impacted by low base flows. Minimum summer WUA accounted for 68% of variance in YOY densities in the Lower sector and 49% overall (p=0.002). In the Lower sector the addition of a spawning component only resulted in a small increase in the proportion of variance explained by the regression (74% compared to 68%) indicating that rearing habitat was more limiting to year class strength than spawning habitat.

Significance:

Consistent with the findings of Nehring and Anderson (1993) a stable flow regime during the critical period (February and March) is fundamental to spawning success. Summer low flows act as a bottleneck at the YOY life stage, a finding that supports the inference of Strevens (1999) that abstraction induced habitat losses were negatively impacting juvenile populations in the river Piddle. These findings have important implications for habitat management which requires that critical periods causing bottlenecks are understood so that managers avoid the risk of manipulating habitat that is already in excess, or increasing fish numbers at a life stage that will subsequently be constrained. Thus, increasing spawning habitat will not increase juvenile production if fry habitat is limiting in summer.

Future climatic change has the potential to disturb the natural hydrological stability of chalk streams with increased frequency and magnitude of winter flood events together with more prolonged summer droughts. Results from this study clearly demonstrate that any shift towards flow regimes with higher winter peaks and longer duration of summer low flows would have the potential to adversely impact brown trout populations during these critical habitat periods.

8.4. Objective 4: SPAWNING AND REARING HABITAT EFFECTS ON JUVENILE RECRUITMENT

Main Findings:

4. Juvenile rearing habitat in summer is a critical factor limiting juvenile production and is more important than spawning habitat.

A multiple regression model consisting of spawning and rearing habitat metrics for the two critical periods significantly explained 68% of total variation in YOY densities. Comparison of standardised beta coefficients for the two variables showed that increases in the standard deviation of summer rearing habitat (YSMIN) result in a proportional (almost equal) increase in YOY densities but increased spawning habitat appeared to negatively affect densities.

5. Juxtaposition of spawning and rearing zones affects local distribution of juvenile trout and may be mechanism affecting recruitment

In the Lower sector the downstream reach (Tolpuddle 1) had the highest YOY densities. Total Lower sector WUA for the critical periods accounted for up to 73% of variance in YOY densities in Tolpuddle 1 but was not related to YOY/PYOY densities in Tolpuddle 2.

6. Riffles and glides are the most important meso habitats for spawning and rearing but deeper meso habitats are important refugia in summer

Riffles provided significantly more spawning WUA than glides and where local recruitment was occurring accounted for a greater proportion of variance in YOY densities (65%) than spawning WUA for all meso-habitats combined. However, glides occurred more frequently and also provided good spawning habitat. Riffles and glides were both important summer rearing habitats and were highly correlated with YOY densities. Deeper, slower flowing areas such as flats provided refugia from summer low flows which appeared to be important for PYOY trout in the Lower sector.

Significance:

These results demonstrate that juvenile abundance in the river Piddle is related to temporal variations in the quality of local spawning and rearing habitats. The fact that rearing habitat availability in summer is a more important limiting factor than spawning habitat supports the findings of Elliott (1994) who demonstrated that spawning success in a Cumbria stream had no effect on densities of surviving fry, which were regulated by density-dependent mortality in response to availability of nursery habitats. Thus, given sufficient spawners, increased amounts of spawning habitat result in increased density dependent mortality of fry at the swim up stage (Heland, 1999) which accounts for the negative influence of the spawning component in the multiple regression model.

This study highlights the value of habitat studies at small spatial resolutions. A variety of meso-habitat types are important under different environmental conditions such that small scale habitat heterogeneity can be an important mechanism influencing juvenile recruitment dynamics. Riffles and glides are the most important rearing habitats and time series analyses show that summer low flows act as bottlenecks to juvenile production mainly because they cause greatest reductions in fry WUA associated with these meso habitats. However, flats provide refugia from low flows and may also be important for over winter survival. Spatial juxtaposition of different meso- habitats can be important at the reach scale. Competitive segregation of the 0+ and 1+ year classes in the Lower sector is partly a response to spatial habitat partitioning with YOY utilising abundant nursery habitat downstream of high quality spawning/rearing areas for which they are out competed by older trout.

8.5 . IMPLICATIONS FOR MANAGEMENT OF CHALK- STREAMS

Chalk streams are a unique ecotype rich in biodiversity and which support important native populations of wild brown trout. In 2004 the UK Biodiversity Action Plan Steering group for chalk rivers produced its first report summarising the current status of English chalk rivers and setting out a vision for future conservation and management (Environment Agency, 2004). In addition, the Game Conservancy Trust and the Wild Trout Trust are currently funding research looking at the interactions between wild and hatchery reared trout in chalk rivers and the effects of different stocking densities on wild trout biomass. Against this background findings from the present study have some important implications for management of wild brown trout populations and the chalk-stream fisheries they support.

8.5.1. Habitat Enhancement

Habitat manipulations have tended to focus on reach or site scales and only limited efforts have been made to assess net gains in terms of increased trout standing stocks over time (e.g. Hunt, 1969, 1971, 1976). Fish responses to in stream conditions at a population level reflect broad scale abiotic influences which provide the environmental setting and determine carrying capacity (Rabeni and Sowa, 1996; Armstrong *et al,* 2003). Therefore, although habitat improvements may appear beneficial at a local scale they may affect trout distribution rather than abundance and the success of management interventions should be measured in terms of increases in production (Armstrong *et al.*, 2003).

A major benefit of this study has been to show that temporal variations in meso-scale habitat quality can limit juvenile abundance. Thus, where habitat shortages are evident trout productivity can be optimised by restoring a juxtaposition of meso-habitats that maximises spawning WUA under moderate flows and YOY rearing habitat downstream under summer low flow conditions. Maintenance of habitat diversity is important for mitigating temporal fluctuations in flow and environmental conditions. Results from this work suggest that reach scale habitat enhancements have the potential to increase trout productivity locally with an understanding of the role of different meso-habitats and the links between spawning and rearing. For example, riffle placement in degraded chalk-streams will improve spawning habitat but will not necessarily increase YOY abundance due to early density dependent mortality as the multiple regression model suggests. However, riffles also enhance physical habitat diversity for fry life stages, which are out-competed for deeper habitats, thus increasing the likelihood of a self sustaining population being maintained by "local" adult stock. Findings from this study contribute to a better understanding of different meso-habitat combinations and their importance to early life stages of trout. This is vital to enable managers of river rehabilitation schemes to more effectively manipulate natural population regulating mechanisms.

8.5.2. Management of Riparian Zones

River rehabilitation approaches focused at the channel and riparian scale remain the most important from a fishery management point of view (Zalewski and Frankiewicz, 1998). In-stream enhancement structures have an important role to play, especially in low diversity habitats, but protection of natural stream components should precede use of traditional structural techniques (White and Brynildson, 1967). The current study has demonstrated that in chalk streams riparian vegetation provides critical over wintering habitats in shallow streams and as such plays a crucial role in determining carrying capacity at the reach scale. The importance of these riparian margins in winter indicates the need for a more hands-off approach to management which allows for natural senescence of riparian vegetation rather than clearing decaying margins in winter.

Riparian vegetation increases habitat diversity as roots, overhanging brush and woody debris provide cover for trout and influence velocity, depth and substrate coarseness. In addition, it serves to increase invertebrate biomass and thus food availability (Harrison, 2000) and is important for seasonal structuring of in-stream habitats which assists resource partitioning and spatial segregation between life stages which can stimulate increases in fish biomass (Zalewski and Frankiewicz, 1998). Thus, riparian zone recovery should be regarded as the "building block" for rehabilitation of degraded chalk streams (Holmes, 2002). Intensive grazing has caused this aspect of these unique ecosystems to be often the most impacted. This approach can achieve the dual functions of; (i) structuring and regulating abiotic habitat and (ii) improving trophic conditions and increasing fish productivity (Zalewski and Frankiewicz, 1998). Unlike more expensive structural techniques which are spatially limited, fencing of over-grazed riparian zones can lead to the regeneration of kilometres of river habitat in a relatively short timescale.

8.5.3 Management of Flow Regimes in Relation to Maintenance of Habitat Connectivity

This study demonstrates the efficacy of PHABSIM as a tool for the management of flow regimes in respect of groundwater abstraction in chalk rivers. The setting of ecologically acceptable flow (EAF) targets should form the basis for defining sustainable water resource exploitation. The setting of EAFs should be based on maintaining suitable amounts of habitat for juvenile trout during the critical periods and in particular fry WUA using the lowest flow month between July and September. Connectivity between habitats under different flow scenarios can be simulated graphically which has potential for use in conjunction with other ecological models such as models of fry dispersal patterns.

8.5.4. Habitat Modelling as an Aid to River Management

Modelling complex biological interactions between fish populations and their physical environment is a daunting challenge and models are imperfect tools. Models assume a linear relationship between habitat and fish abundance which is over-simplistic and their performance varies depending on the ability of selected variables to represent complex functional links between habitat and standing stock ((Fausch *et al.* 1988; Armstrong *et al,* 2003). The scale at which models are applied can affect the way causal mechanisms are attributed and stochastic habitat models typically over-emphasise the importance of spatial variation at the expense of temporal variation (Rabeni and Sowa (1996; Wiley *et al.,* 1997). Thus, caution should be applied when using models to predict effects of altering specific habitat components to guide habitat improvements.

A particular strength of PHABSIM is that it is a dynamic model that integrates temporal dimensions through habitat time series and threshold analysis (Capra *et al.,* 1995). Analysis at different temporal scales is important to understanding habitat – population relationships as habitat demand is dynamic according to time of year and life cycle requirements. One criticism of PHABSIM is that it has not yet been well validated in biological terms, partly due to difficulty in obtaining biological time series over a sufficiently long period to study population response to habitat temporal variability (Capra *et al.,* 2003). A significant contribution of the present study has been the application of empirical population data over a relatively long timescale (7 years) to demonstrate fish population response to habitat changes over time. A rigorous study design directed at controlling complicating factors enabled PHABSIM to accurately predict the magnitude and direction of brown trout population responses to temporal changes in habitat.

In recent years advances in ecological modelling have led to more sophisticated ecological models incorporating biological and behavioural attributes. Nislow *et al.,* (1999) demonstrated that availability of favourable foraging habitats during the early first summer significantly improved retention of YOY salmon in streams at the end of summer. Behavioural changes from maximising energy gain towards minimising predation risk reduced the influence of late summer habitat availability on 0+ performance. Such foraging-based habitat models can increase the generality of habitat models by incorporating biological mechanisms involved in microhabitat selection and help better determine the impacts of habitat modifications on population levels. Such factors need to be integrated into PHABSIM if HSI curves are to be developed which accurately reflect changing habitat preferences in response to these biological mechanisms.

There is a clear need for more advanced models of the relationships between habitat and fish production in order to assist fishery managers understand population – limiting habitat durations and predict the effects of habitat management on wild populations. PHABSIM integrates the temporal dimension but effects of biological mechanisms cannot be isolated from physical habitat and this has been a criticism of the way habitat preference curves treat trout responses to habitat variables. Thus, more recent approaches which integrate population dynamics models offer a way forward. Coupling PHABSIM modelling with dynamic population models has been shown to be effective for identification of critical periods during which carrying capacity becomes limiting and for understanding mechanisms which interlink different cohorts of a population in relation to temporal changes in environmental parameters (Gouraud *et al.,* 2001; Capra *et al.,* 2003). Used in conjunction with models of fry dispersal this study has shown the potential for PHABSIM to elucidate how juxtaposition of spawning and rearing areas may act to regulate juvenile recruitment under different flow conditions. Such approaches have the potential to provide managers with tools to determine the conditions under which habitat is limiting and to simulate population responses to habitat improvements and changes in river management.

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GLOSSARY OF TERMS

The following terms and their definitions are provided to help the reader understand some of the specialised vocabulary utilised throughout PHABSIM in the description of open channel hydraulics, suitability curves, and habitat modelling.

ADULT: Sexually mature fish usually age 2+ and >2+

ALEVIN: Post egg life stage during yolk-sac absorption prior to emergence as swim-up fry

ANADROMOUS: Salmonids which migrate to sea to mature returning to freshwater to spawn

AREA, CONVEYANCE: Cross-sectional area of a stream perpendicular to the flow.

AREA, CROSS-SECTIONAL: The area of the cross section containing water, perpendicular to the direction of flow. (Units: square feet or square meters).

AREA, USABLE: The surface area of a stream that can be used by an aquatic organism. (Units: square feet or square meters).

AREA, WEIGHTED USABLE (WUA): The surface area of a stream weighted by its suitability to an aquatic organism. (Units: square feet or square meters).

AREA, WEIGHTED USABLE BED (WUBA): The bed area of a stream weighted by its suitability to an aquatic organism. (Units: square feet or square meters).

AQUIFER: Saturated porous rock (e.g. chalk) which acts as a groundwater store

ASYMPTOTIC LENGTH: maximum (theoretical) size likely to be attained by adult fish in a population under prevailing growth conditions

BACKWATER: (1) A region of a stream where the water surface level is governed by a downstream control (Hence the term step-backwater is applied to the WSP model, see below.). (2) An off-shoot from the main channel with little flow and where the water surface elevation is maintained by conditions in the main channel.

BANKFULL STAGE: Discharge at maximum channel conveyance sometimes known as channel-forming flow

BASE FLOW: Discharge maintained entirely by groundwater during minimum summer flow levels

BEST ESTIMATE Q: discharge computation attained from the most reliable/accurate cross section in a given channel length

BETA COEFFICIENT: (1) A coefficient used to represent the change in Manning's roughness with discharge or hydraulic radius. (2) Ratio of the bed shear stress to the resisting forces of the bed material (Shield's Parameter).

BOTTLENECK: A point in time or space which limits survivorship at a life stage such that population size at subsequent life stages is reduced (see limiting factors)

BRUSH BUNDLES: Series of branches bound together and lashed into bank at downstream angle to create friction. Induces deposition to help stabilise weak banks and provides cover/velocity shelter for juvenile fish

CALIBRATION FLOW: empirically measured discharge used to calibrate PHABSIM hydraulic models by comparing measured flow with model predictions

CARRYING CAPACITY: the number (or biomass) of fish that an environment can support in terms of space and resources.

CARRY OVER: number of individuals from an age cohort surviving to a subsequent year (e.g. YOY-PYOY)

CELL: As used in PHABSIM, an increment of width of a stream channel weighted for its relative importance by a length to give an area. Defined by verticals.

CELL FACTORS: See Factors, Cell.

CHANNEL INDEX: A suitability index to the channel characteristics, usually substrate or cover.

CHANNELISATION: Section of channel artificially straightened and smoothed in order to maximise conveyance factor. Typically trapezoidal in cross section

CHANNEL ROUGHNESS: A coefficient of resistance to flow caused by particle or vegetative friction and channel features such as bends and constrictions.

CHANNEL WIDTH: See Width, Channel.

COMPOSITE SUITABILITY OF USE FACTOR: See Factors, Cell.

CONVEYANCE, FACTOR: See Factor, Conveyance.

COVER: Areas of shelter in a stream channel that provide aquatic organisms protection from predators and/or a place in which to rest and conserve energy due to a reduction in the force of the current or visual isolation, e.g., pools, undercut banks, boulders, water depth, surface turbulence, etc.

CRITICAL FLOW: See Flow, Sub-Critical and Super-Critical.

CRITICAL PERIODS: Biological events which are likely to limit subsequent population size e.g. early post emergence of fry

CROSS SECTION: A section across a stream channel that is perpendicular to the direction of the flow. Sometimes called a transect.

CROSS SECTION Q: discharge computation attained at any individual transect

CURVES, PREFERENCE: The criteria used to weight an area as to it worth for a specific aquatic organism. The organism prefers certain conditions.

CURVES, SUITABILITY-OF-USE (SI): Same as Preference Curves except the concept of the suitability of the conditions for a specific organism is stressed.

CURVES, USABILITY: Same as Preference Curves except the concept of usability of the conditions for a specific organism is stressed.

DATUM: An agreed standard point or plane of stated elevation, noted by permanent bench marks on some solid immovable structure, from which elevations are measured, or to which they are referred.

DEFLECTORS: Artificial constructions protruding from the bank to channel flow and create scour typically towards the centre of the channel.

DEPTH: The vertical distance from a point on the bed to the water surface.

DEPTH, HYDRAULIC: Equivalent to mean or average depth.

DEPTH, MEAN: The cross section area divided by the surface width.

DEPTH, THALWEG: The vertical distance of the lowest point of a channel cross section to the water surface, i.e., maximum depth of cross section.

DISCHARGE: The rate of flow, or volume of water flowing in a given stream at a given place and within a given period of time, expressed as cubic meters per second

ECOLOGICALLY ACCEPTABLE FLOWS: PHABSIM defined discharges determined to maintain a minimum level of life stage specific habitat availability

FACTOR, CELL: Also referred to as Composite Suitability of Use Factor. The function of velocity (v), depth (d), and the channel index (CI) used to weight an area of stream for its value as habitat. The term is defined within the context of specific habitat models

FACTOR, CONVEYANCE: In uniform flow situations, the area available to transport water is directly proportional to Q. The Conveyance Factor (K) is the relationship between the channel and flow characteristics.

FLOW: The movement of a stream of water and/or other mobile substances from place to place; discharge; total quantity carried by a stream.

FLOW EXCEEDANCE PERCENTILE: Length of time that a given discharge is exceeded during an annual hydrological cycle expressed as a percentage e.g. Q95 is the flow exceeded 95% of the time

FLOW, STEADY and UNSTEADY: Flow in an open channel is said to be steady if the depth of flow does not change or can be assumed constant over a specified time interval. The flow is unsteady if the depth changes with time.

FLOW, SUB-CRITICAL and SUPER-CRITICAL: In any body of moving water both inertial and gravity forces are acting on the water body. The effect of gravity on the state of flow is represented by the ratio between inertial and gravity forces, i.e., Froude Number. If the Froude Number is less than unity, gravity forces predominate, so the flow has low velocity and is described as tranquil or streaming. If the Froude Number is greater than unity, the effects of inertia are more pronounced, so the flow has high velocity and is described as shooting, rapid, or torrential.

When the Froude Number is equal to unity, flow is defined as critical.

Most instream flow studies are concerned primarily with the sub-critical state of flow.

FLOW, UNIFORM and VARIED: Uniform flow means that the depth of flow is the same at every section of the channel. Thus, the hydraulic, energy, and bottom slopes are parallel. If the flow is varied, the depth of flow changes along the length of the channel. Varied flow is classified as either rapidly or gradually varied, depending on the distance within which the change in depth occurs. Rapidly varied flow is manifest in an abrupt change in depth, resulting in hydraulic jumps, hydraulic drops, and related phenomena. The criterion for uniform or varied flow is change in depth with respect to space.

FORK LENGTH: Fish length measured from snout to fork of tail

FROUDE NUMBER: A dimensionless number used as an index to characterise the type of flow in a hydraulic structure that has the force of gravity (as the only force producing motion) in conjunction with the resisting force of inertia.

FRY: Young fish during their first summer post emergence (see YOY)

GABIONS: Series of wire mesh baskets filled with stones used to armour banks

GEOTEXTILES: Synthetic material used as a substrate for infilling of eroded banks

GRADIENT: The rate of change of any characteristic per unit of length. See Slope.

HABITAT CONNECTIVITY: Degree of spatial interlinking or fragmentation of habitat types suitable for different life stages
HABITAT DURATION: period of time that a given value of habitat is maintained or exceeded – similar concept to that of flow exceedance
HABITAT JUXTAPOSITION: Interspersion of habitat types suitable for different trout life stages (see habitat connectivity)
HABITAT SUITABILITY: Available habitat weighted according to its suitability for a given life stage.
HATCHING/EMERGENCE PERIOD: Period between February and April from first hatching to initial dispersal of swim-up fry
HEAD PIN: The terminal points in a cross section. Usually marked by something (a "pin") pounded into bankside
HEIGHT OF INSTRUMENT: The elevation of the sight plane through a level.
HYDRAULIC CALIBRATION: Hydraulic modelling process undertaken as part of PHABSIM which utilises empirically measured discharges to calibrate the models prior to running habitat simulations
HYDRAULIC CONTROL: downstream flow check such as a weir or natural break of slope which determines height of the water surface over a given distance upstream
HYDRAULIC GEOMETRY: The dimensions of certain stream features with respect to both the wetted and unwetted portions of the channel.
HYDRAULIC RADIUS: Ratio of the cross-sectional area to the wetted perimeter, $R = A/P$.

JUVENILE: Fish less than age 2 years

K-DAMS: K shaped weir typically of log construction pinned into bed and banks to act as both an upstream gravel trap and to deflect flow downstream to create scour in centre of the channel

LIFE STAGE: An arbitrary classification of the age of an organism into stages related to body morphology and reproductive potential, e.g., "fry" for YOY
LIMITING FACTOR: Any biotic or abiotic factor which acts to reduce population size
LOWEST LIMITING FACTOR: Method for computation of WUA which utilises the lowest composite suitability index

LWD: large woody debris; typically logs and tree trunks etc

MACROHABITAT: Habitat conditions in a reach of river controlling longitudinal distribution of aquatic organisms.

MANNING'S EQUATION: An empirical formula for the calculation of velocity in a channel.

MANNING'S ROUGHNESS or MANNING's n: A factor used when computing the average velocity of flow of water in a channel that represents the effect of roughness of the confining material upon the energy losses in the flowing water. Also referred to as "n" or roughness coefficient.

MASS BALANCE: relationship between channel conveyance and velocity for a given discharge

MEAN DEPTH: See Depth, Mean.

MESO-HABITAT: Intermediate scale habitat features such as pools, riffles and glides; typically at the 10 – 100m scale

MESO-HABITAT TYPES:

- RIFFLE: shallow, broken standing wave, fast and audible flow
- RUN: unbroken standing wave, swift/fast flowing but not audible
- POOL : Deep and slow flowing, smooth and unbroken surface
- FLAT : smooth laminar flow, unbroken surface, very slow flowing with insufficient velocity to create ripple when obstruction is placed in flow
- GLIDE: smooth laminar flow, unbroken surface, sufficient velocity to create ripple when obstruction is placed in flow
- CASCADE: steep gradient with white, broken water typically in a “stepped” sequence

METRICS: numerical expression representing the value of a particular component of habitat to a given life stage

MICROHABITAT: Habitat small area (cell) of a river controlling specific locations or home ranges.

OVER-WIDENING: Channel section where lateral erosion of both banks has resulted in wide, shallow reaches with associated loss of habitat heterogeneity

PHABSIM: the Physical Habitat Simulation System. Computes a relationship between streamflow and physical habitat for various life stages of an aquatic organism PHABSIM is a component of IFIM.

PHYSICAL HABITAT: The place where a population lives and its surroundings as defined by physical conditions, most commonly depth, velocity, and channel conditions such as substrate and cover objects.

POACHING: Banks grazed and trampled by cattle resulting in collapse and severe erosion. Typically leads to over-widening of channel

POINT BAR: Sloping crescent shaped deposit of fine material on inner bank of meanders

PROFILE or PROFILE, LONGITUDINAL: (1) In open channel hydraulics, it is a plot of water surface elevation against channel distance and/or bottom elevation. (2) A line of elevations along a river usually following the thalweg. Most often includes the bed and water surface elevations.

PROFILE, TRANSVERSE: Same as a cross section.

PYOY: Post-young-of-the year; juvenile fish (parr) in their second year after hatching (age 1+) sometimes called yearlings

RATING CURVE: A curve that expresses graphically the relation between mutually dependent quantities, e.g. curve showing the relation between gauge height (stage) and discharge of a stream.

REACH: A comparatively short length of a stream. The actual length is defined by the purpose of the study.

REACH LENGTH: The length of a section or piece of a river.

RECRUITMENT: Level of survivorship from one life stage to a subsequent life stage

REVETMENT: Artificial reinforcement of bank face to increase resistance to erosion

RIFFLE: Shallow rapids in an open stream where the water surface is broken into waves by obstructions wholly or partly submerged.

RIP-RAP: Coarse angular boulders used to form an erosion resistant face to stabilise banks

ROOT WADS: Exposed roots of bank-side trees

ROUGHNESS: Amount of resistance to flow resulting from friction with channel bed, banks and vegetation

ROUGHNESS COEFFICIENT: See Manning's Roughness.

ROUGHNESS MODIFIERS: weighting factor applied to values of Mannings n to adjust for relative changes in n with increases or decreases in discharge.

SEGMENT: Relatively homogeneous section of a stream composed of two or more reaches.

SELF THINNING: Process by which numbers/biomass of fish in a given area decline with time due to increasing demand for resources (space and food) as fish grow.

SHEAR STRESS, BED: The stress on the river bed caused by the flowing water.

SIMULATION FLOW: PHABSIM model predictions at discharges not measured in the field

SLOPE: The inclination or gradient from the horizontal of a line or surface. The degree of inclination can be expressed as a ratio, such as 1:25.

SLOPE, BOTTOM: The change in the average elevations of the bed between two cross sections, divided by the distance between them.

SLOPE, ENERGY: Change in total energy (potential and kinetic) available at a point. Usually approximated as the change between the cross section divided by the distance between cross sections.

SLOPE, HYDRAULIC: The change in elevation of the water surface between two cross sections, divided by the distance between the cross sections.

SLOPE, THALWEG: The change in the elevation of the bed, measured at the points of maximum depth, divided by the distance between cross sections.

SLOPE, WATER SURFACE: The slope of the water surface at a point and is usually approximated as the difference in water surface elevations at two points divided by the distance along the flow path between the points.

SPAWNING STOCK: Number of spawning adult fish

STAGE: The elevation, or vertical distance of the water surface above a datum (a plane of known or arbitrary elevation).

STAGE-DISCHARGE RELATIONSHIP: Log-linear regression for the relationship between discharge and the height of the water surface; sometimes called depth-discharge relationship

STAGE OF ZERO FLOW (SZF): The water surface elevation at a cross section when the flow reaches zero. This is either the lowest point of the bed or the pool water surface when no flow occurs (i.e., a downstream low bed point acts as the pool water surface control).

STEADY FLOW: See Flow, Steady and Unsteady.

STREAMBED: The bottom of the stream channel; may be wet or dry.

STREAM WIDTH: See Width, Stream.

SUB-CRITICAL FLOW: See Flow, Sub-Critical and Super-Critical.

SUBSTRATE: The material on the bottom of the stream channel, e.g., rocks, vegetation, etc.

SUPER-CRITICAL FLOW: See Flow, Sub-Critical and Super-Critical.

THALWEG: The longitudinal line connecting points of minimum bed elevation along the stream course.

THREE PASS DEPLETION METHOD: standard multi-pass electrofishing technique for population estimate based on rate of decline in captures between passes for an enclosed population over a fixed area

TOE WIDTH: See Width, Toe

TOP WIDTH: See Width, Top.

TRANSECT: Same as cross section.

UNIFORM FLOW: See Flow, Uniform and Varied.

UNSTEADY FLOW: See Flow, Steady and Unsteady.

UPSTREAM WEIGHTING FACTOR: value between 0 – 1 assigned to a surface area of stream to indicate its worth as a particular meso- habitat type.

USABLE AREA: See Area, Usable.

VARIED FLOW: See Flow, Uniform and Varied.

VELOCITY: The time rate of motion; the distance travelled divided by the time required to travel that distance.

VELOCITY, ADJACENT: A velocity in a cell near the cell being considered.

VELOCITY, MEAN: The mean velocity may represent either a cell or a cross section. It is calculated as: $V=QxA$

VELOCITY, MEAN COLUMN: The velocity averaged from the top to the bottom of a stream. Usually measured at 6/10 depth or an average of values measured at 2/10 and 8/10 of the depth

VELOCITY, NOSE: The velocity at the point where a fish is located. This is the point velocity expressed in terms of an organism.

VELOCITY, POINT: The velocity at a depth in the stream.
VELOCITY ADJUSTMENT FACTOR (VAF): The ratio of the discharge for which velocities are being simulated to the sum of simulating cell velocities times cell areas:
VERTICAL: As used in PHABSIM, sample locations across a cross section.

WATER SURFACE ELEVATION (WSL): The elevation of the water's surface in relation to an arbitrary datum.
WEIGHTED USABLE AREA (WUA): See Area, Weighted Usable.
WEIGHTED USABLE BED AREA (WUBA): See Area, Weighted Usable Bed.
WEIGHTED USABLE VOLUME (WUV): The volume of a stream weighted for its worth as habitat.
WETTED PERIMETER: The distance along the bottom and sides of a channel cross section in contact with water. Roughly equal to the width plus two times the mean depth.
WETTED WIDTH: See Width, Wetted.
WIDTH: The distance across a channel at the water surface measured normal to flow.
WIDTH, BANKFUL: The width of the stream just before the flow overtops the channel.
WIDTH, CHANNEL: An arbitrary width based on what the observer sees as a channel.
WIDTH, STREAM: Either the same as the channel width or the width of the wetted stream.
WIDTH, TOE: The width of the base of a trapezoidal channel.
WIDTH, TOP: The width of the wetted area of flow across a stream channel.
WIDTH, WETTED: The width of the stream with water in it.

YEAR CLASS: Age cohort of fish hatched at same time
YOY: Young-of-the year; juvenile fish in their first year after hatching (age 0+)

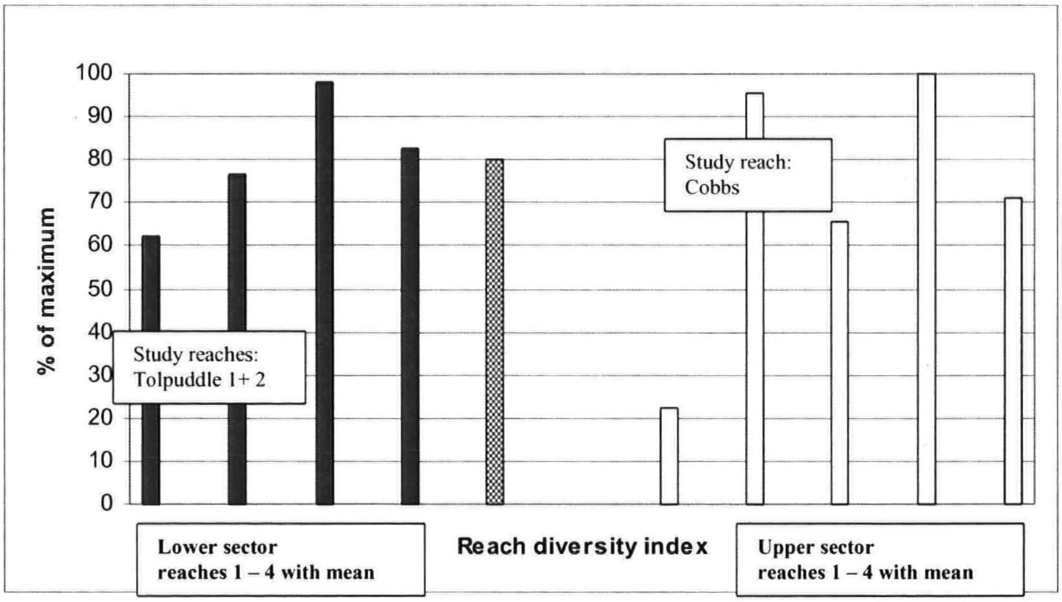
APPENDICES

APPENDIX.1.

HABITAT CHARACTERISTICS OF RIVER PIDDLE STUDY REACHES

RIVER SECTOR	**Lower sector**		**Upper sector**
STUDY REACH	**Tolpuddle 1**	**Tolpuddle 2**	**Cobbs**
LOCATION	Tolpuddle – upstream Affpuddle weir	Tolpuddle – upstream of and contiguous with Tolpuddle 1 reach	Cobbs Wood – upstream of Blue bridge
REACH LENGTH	65m	85m	125m
MORPHOLOGICAL DIVERSITY INDEX (% of max)	62.1	76.7	95.6
RIFFLE / RUN (%)	30.8	5.9	40
GLIDE (%)	69.2	35.3	40
FLATS (%)	0	58.8	0
POOLS – MEANDER (%)	0	0	14.4
POOLS – OTHER (%)	0	0	5.6

Relative habitat diversity for study reaches based on proportions of different meso-habitat types present in each reach.



The Upper and Lower river sectors both comprised four contiguous electrofishing reaches of which one was selected from the upper sector (Cobbs) and two from the lower sector (Tolpuddle 1 and 2) for application of PHABSIM. Habitat walk-over mapping determined the proportions of different meso-habitat types present in each reach. A simple diversity index was used to calculate morphological diversity in each reach based on these proportions. The graph represents this morphological diversity for each reach as a percentage of the reach with the highest diversity score (Upper sector: reach 4) taken as 100%. Selected reaches were coterminous with electrofishing sections and were chosen to represent the contrasting habitat characteristics present throughout both sectors.

APPENDIX.2.

COVER CLASSIFICATION SCHEME (adapted from Trihey and Wegner, 1981).

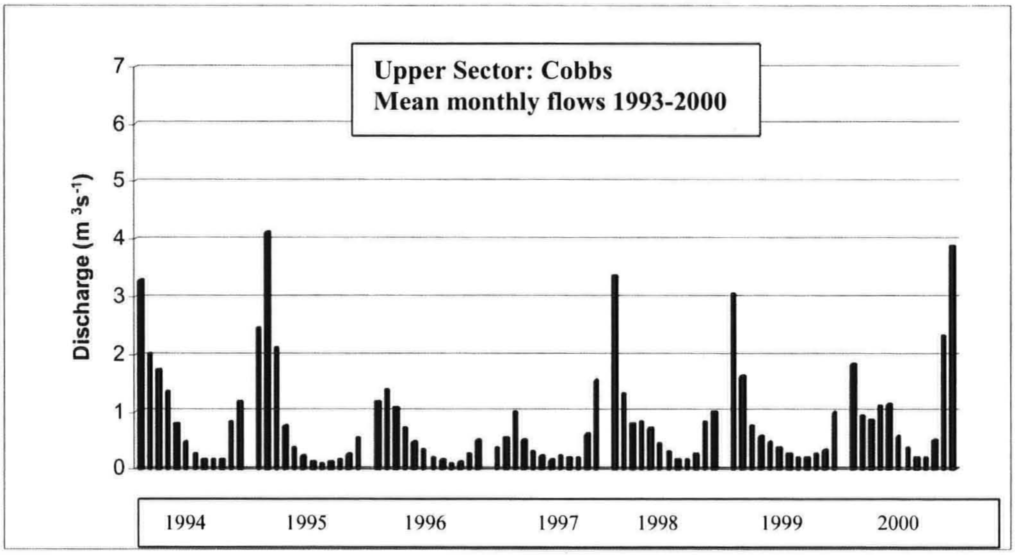
Cover	Description	(A)		
0	No cover present	**OBJECT COVER**		
1		0 - 25 % of cell affected	**(B)**	
2		25 - 50 % of cell affected	**OVERHEAD COVER**	
3		50 - 75 % of cell affected		
4		75 - 100 % of cell affected	0 - 25 % of cell affected	**(C)**
5			25 - 50 % of cell affected	**UNDERCUT BANK**
6			50 - 75 % of cell affected	
7	**(D) OBJECT+**		75 - 100 % of cell affected	0 - 25 % of cell affected
8	**OVERHEAD COVER**			25 - 50 % of cell affected
9	0 - 25 % of cell affected	**(E) OBJECT+**		50- 75 % of cell affected
10	25 - 50 % of cell affected	**UNDERCUT BANK**		75 - 100 % of cell affected
11	50 - 75 % of cell affected	0 - 25 % of cell affected		
12	75 - 100 % of cell affected	25 - 50 % of cell affected	**(F) OVERHEAD COVER**	
13		50 - 75 % of cell affected	**+ UNDERCUT BANK**	**(G) OBJECT+OVERHEAD**
14		75 - 100 % of cell affected	0 - 25 % of cell affected	**COVER +**
15			25 - 50 % of cell affected	**UNDERCUT BANK**
16			50 - 75 % of cell affected	0 - 25 % of cell affected
17			75 - 100 % of cell affected	25 - 50 % of cell affected
18				50 - 75 % of cell affected
19				75 - 100 % of cell affected

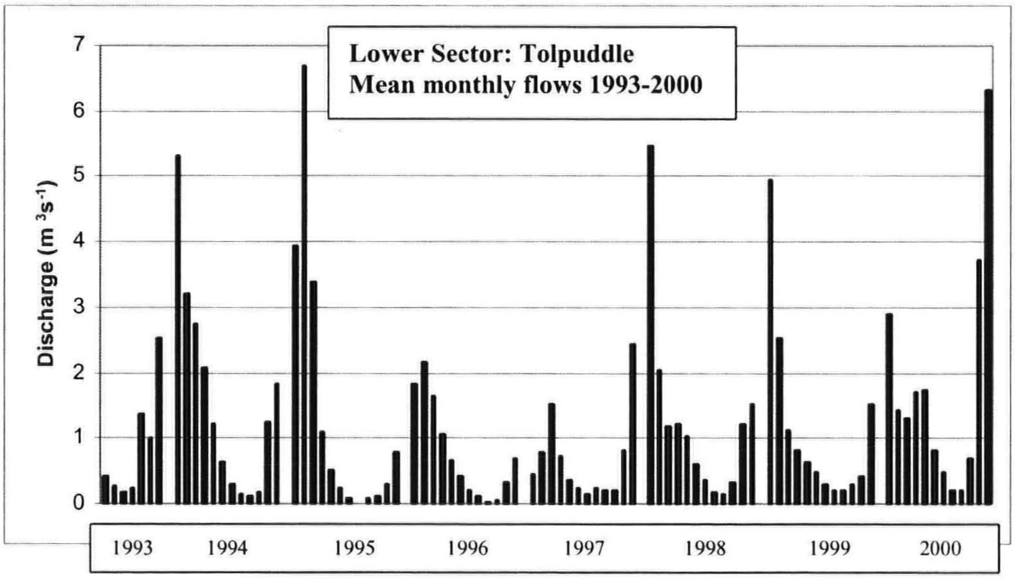
APPENDIX.3

HYDROLOGICAL REGIMES AND CALIBRATION DATA

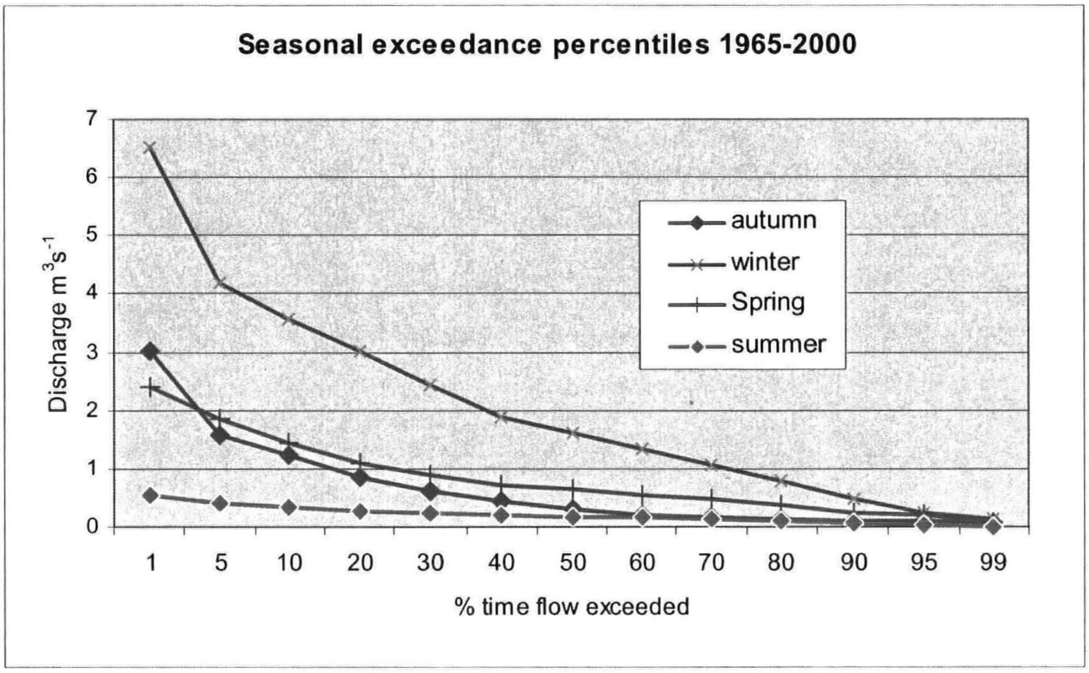
Long term discharge data indicated median flows (*Q*50) were 0.54 m^3s^{-1} with *Q* >1.0 m^3s^{-1} exceeded 33% of the time. During the study period (1993 – 2000) median discharge (*Q*50) in the Lower river sector (Tolpuddle) was 0.62 m^3s^{-1} with flows > 1.0 m^3s^{-1} exceeded almost 40% of the time. In the Upper river sector (Cobbs) median discharge (*Q*50) was 0.50 m^3s^{-1} for the same period.

Mean monthly flows (1993 – 2000) for the Upper and Lower river sectors

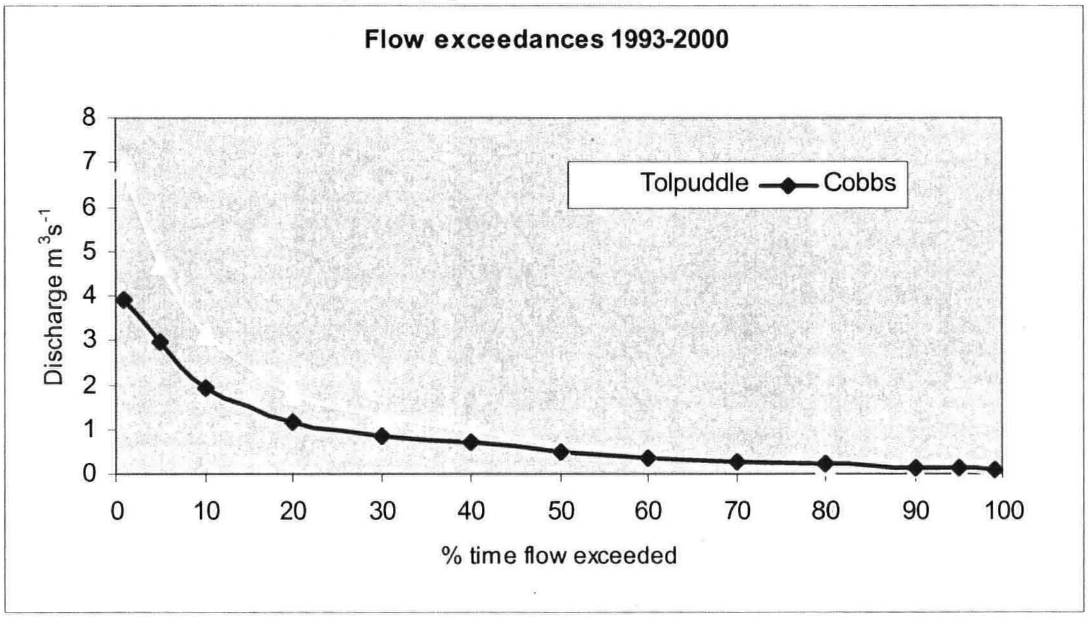




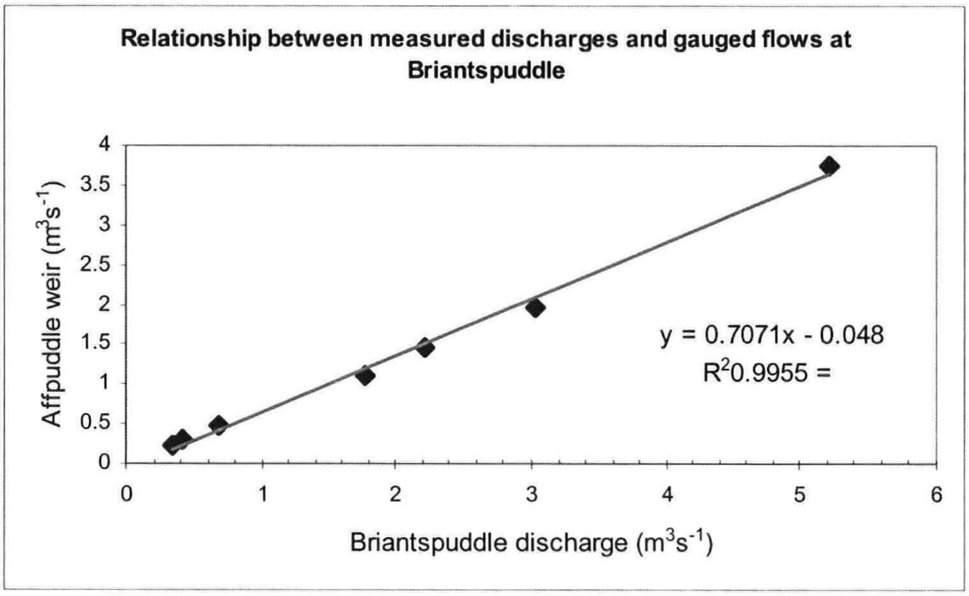
Seasonal flow exceedance curves (based on mean monthly discharge) at Affpuddle weir (downstream end of study area) for period 1965 - 2000



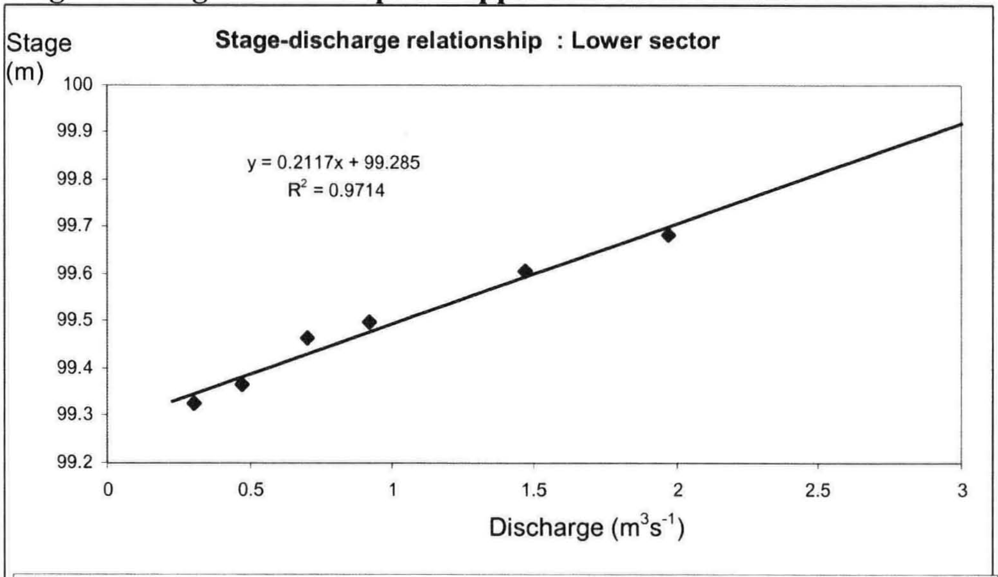
Flow exceedance curves (based on mean monthly discharge) for upper and lower river sectors during study period 1993- 2000

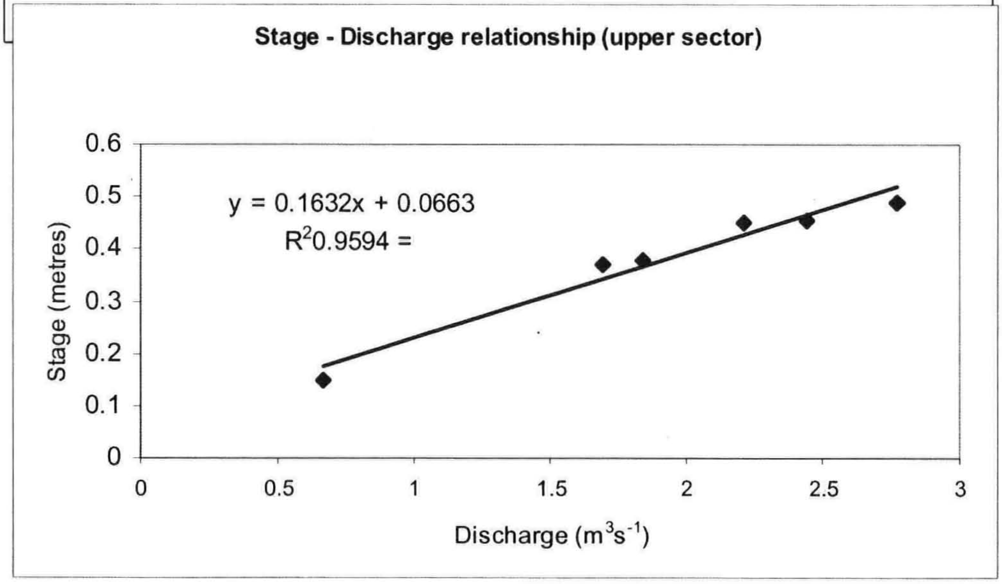


Relationship between discharge at Briantspuddle and at the Tolpuddle study site



Stage-discharge relationships for upper and lower river sectors

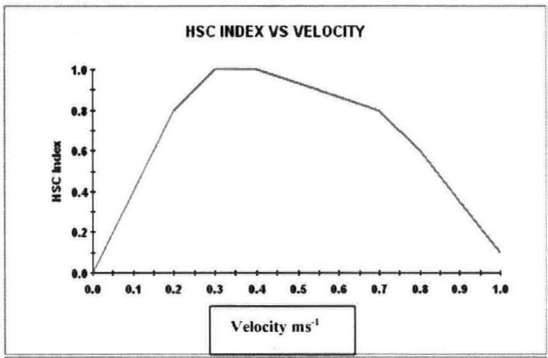


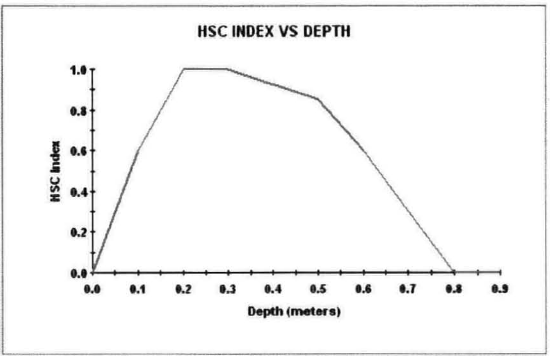


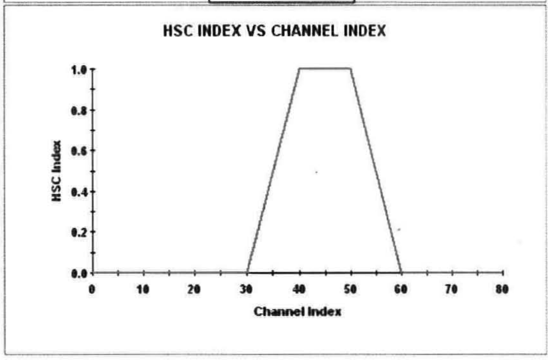
APPENDIX.4

SELECTED HABITAT SUITABILITY CURVES

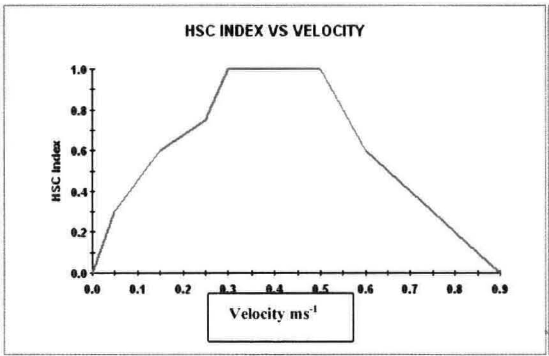
BROWN TROUT SPAWNING

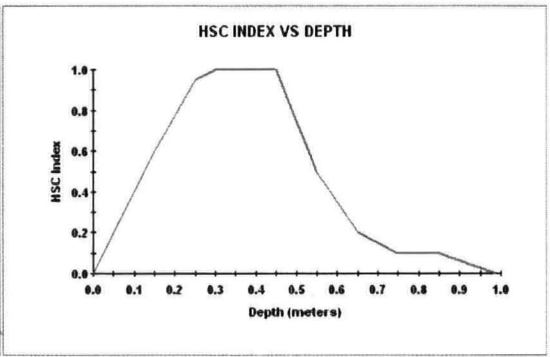


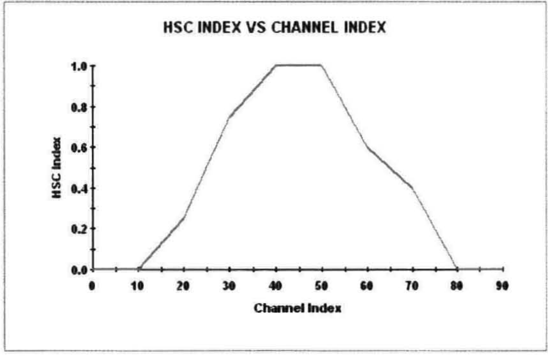




YOUNG OF YEAR BROWN TROUT (age 0+)







APPENDIX.5.

DESCRIPTION OF HABITAT METRICS GENERATED FROM TIME SERIES

Habitat Metric	**Description** (all habitat durations are monthly intervals)
SPAWNING	
SP0AVG	Average spawning0 habitat, all spawning whole season (Nov-Mar)
SP0MIN	Spawning0 minimum habitat
SP0MAX	Spawning0 maximum habitat
SP0L50	Mean of lowest 50% of spawning0 habitat
SP0AVGHP	Average spawning0 habitat during egg hatching period (Feb – Mar)
SP0MINHP	Spawning0 minimum habitat during egg hatching period
SP0MAXHP	Spawning0 maximum habitat during egg hatching period
SPCFAVG	Average high quality spawningCf habitat, whole season (Nov-Mar)
SPCFMIN	SpawningCf minimum high quality habitat
SPCFMAX	SpawningCf maximum high quality habitat
SPCFL50	Mean of lowest 50% of spawningCf high quality habitat
SPCFAVGHP	Average high quality spawningCf habitat during egg hatching period
SPCFMINHP	SpawningCf maximum high quality habitat during egg hatching period
SPCFMAXHP	SpawningCf maximum high quality habitat during egg hatching period
SPEFFAVG	Average Effective Spawning habitat, whole season (Nov-Mar)
SPEFFMIN	SpawningEFF minimum effective habitat
SPEFFMAX	SpawningEFF maximum effective habitat
SPEFFL50	Mean of lowest 50% of SpawningEFF effective habitat
SPEFFAVGHP	Average Effective Spawning habitat during egg hatching period
SPEFFMINHP	SpawningEFF minimum during egg hatching period
SPEFFMAXHP	SpawningEFF maximum during egg hatching period
YOY TROUT	
YGSAVG	Young-of-year average growing season habitat, summer (June – Oct)
YS2AVG	Young-of-year habitat, summer mean (July – Sept)
YSMIN	Young-of-year habitat, summer minimum
YSMAX	Young-of-year habitat, summer maximum
YSL50	Young-of-year habitat, mean of lowest 50% summer habitat
YGSNSHAVG	Young-of-year average growing season nearshore habitat, summer
YS2NSHAVG	Young-of-year nearshore habitat, summer mean
YSNSHMIN	Young-of-year nearshore habitat, summer minimum
YSNSHMAX	Young-of-year nearshore habitat, summer maximum
YSNSHL50	Young-of-year nearshore habitat, mean of lowest 50% summer habitat
YGSAJVAVG	Young-of-year average growing season, feeding stations (June – Oct)
YS2AJVAVG	Young-of-year summer feeding stations, mean (July – Sept)
YSAJVMIN	Young-of-year summer feeding stations, minimum
YSAJVMAX	Young-of-year summer feeding stations, maximum
YSAJVL50	Young-of-year summer feeding stations, mean of lowest 50%

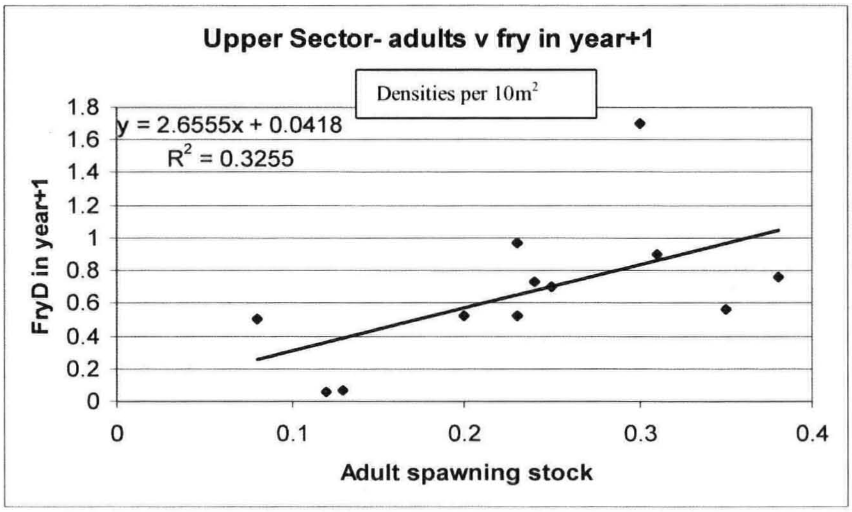
Habitat Metric	Description (all habitat durations are monthly intervals)
PYOY TROUT	
JWAVG	Average 1st winter parr/juvenile habitat (Nov – Mar)
JWMIN	Parr/juvenile habitat, winter minimum
JWMAX	Parr/juvenile habitat, winter maximum
JWL50	Parr/juvenile habitat, mean of lowest 50% winter habitat
JWNSHAVG	Average winter season nearshore parr/juvenile habitat (Nov – Mar)
JWNSHMIN	Parr/juvenile nearshore habitat, winter minimum
JWNSHMAX	Parr/juvenile nearshore habitat, winter maximum
JWNSHL50	Parr/juvenile nearshore habitat, mean of lowest 50% winter habitat
ADULTS	
ADWAVG	Average winter season adult and juvenile habitat (Nov – Mar)
ADWMIN	Adult and juvenile habitat, winter minimum
ADWMAX	Adult and juvenile habitat, winter maximum
ADWL50	Adult and juvenile habitat, mean of lowest 50% winter habitat
ADWNSHAVG	Average winter season nearshore adult and juvenile habitat
ADWNSHMIN	Adult and juvenile nearshore habitat, winter minimum
ADWNSHMAX	Adult and juvenile nearshore habitat, winter maximum
ADWNSHL50	Adult and juvenile nearshore habitat, mean of lowest 50% winter habitat
ADSAVG	Average growing season adult habitat, summer (June – Oct)
ADSMIN	Adult habitat, summer minimum
ADSMAX	Adult habitat, summer maximum
ADSL50	Adult habitat, mean of lowest 50% summer habitat
ADSNSHAVG	Average growing season nearshore adult habitat, summer (June – Oct)
ADSNSHMIN	Adult nearshore habitat, summer minimum
ADSNSHMAX	Adult nearshore habitat, summer maximum
ADSNSHL50	Adult nearshore habitat, mean of lowest 50% summer habitat
<u>Definitions</u>	
spawningCf:	refers to spawning simulations with composite suitability factor Cf applied to remove habitat of low quality
SpawningEFF:	refers to spawning simulations utilising effective spawning habitat option within HABTAE programme
nearshore habitat:	habitat simulations limited to area <2m of bank edge (ie marginal habitat)
feeding stations:	refers to habitat simulations utilising adjacent velocity option within HABTAE

YOY TROUT	**MESO-HABITAT**
RIFAVGS	average riffle habitat, growing season (June – Oct)
RIFAVG2S	average riffle habitat, summer mean (July – Sept)
RIFMINS	minimum riffle habitat, growing season
RIFMAXS	maximum riffle habitat, growing season
RIFL50S	mean of lowest 50% riffle habitat, growing season
GLAVGS	average glide habitat, growing season (June – Oct)
GLAVG2S	average glide habitat, summer mean (July – Sept)
GLMINS	minimum glide habitat, growing season
GLMAXS	maximum glide habitat, growing season
GLL50S	mean of lowest 50% glide habitat, growing season
FTAVGS	average flat habitat, growing season (June – Oct)
FTAVG2S	average flat habitat, summer mean (July – Sept)
FTMINS	minimum flat habitat, growing season
FTMAXS	maximum flat habitat, growing season
FTL50S	mean of lowest 50% flat habitat, growing season
SPAWNING	**MESO-HABITAT**
RIFAVGSP0	Average riffle habitat, spawning season (Nov-Mar)
RIFMINSP0	minimum riffle habitat, spawning season
RIFMAXSP0	maximum riffle habitat, spawning season
RIFL50SP0	mean of lowest 50% riffle habitat, spawning season
RIFAVGHP0	Average riffle habitat during egg hatching period (Feb – Mar)
RIFMINHP0	minimum riffle habitat during egg hatching period
RIFMAXHP0	maximum riffle habitat during egg hatching period
RIFAVGEF	Average riffle habitat, effective spawning (Nov-Mar)
RIFMINEF	minimum riffle habitat, effective spawning
RIFMAXEF	maximum riffle habitat, effective spawning
RIFL50EF	mean of lowest 50% riffle habitat, effective spawning
RIFAVGHPEF	Average riffle habitat during effective egg hatching period (Feb – Mar)
RIFMINHPEF	minimum riffle habitat during effective egg hatching period
RIFMAXHPEF	maximum riffle habitat during effective egg hatching period
GLAVGSP0	Average glide habitat, spawning season (Nov-Mar)
GLMINSP0	minimum glide habitat, spawning season
GLMAXSP0	maximum glide habitat, spawning season
GLL50SP0	mean of lowest 50% glide habitat, spawning season
GLAVGHP0	Average glide habitat during egg hatching period (Feb – Mar)
GLMINHP0	minimum glide habitat during egg hatching period
GLMAXHP0	maximum glide habitat during egg hatching period
GLAVGEF	Average glide habitat, effective spawning (Nov-Mar)
GLMINEF	minimum glide habitat, effective spawning
GLMAXEF	maximum glide habitat, effective spawning
GLL50EF	mean of lowest 50% glide habitat, effective spawning
GLAVGHPEF	Average glide habitat during effective egg hatching period (Feb – Mar)
GLMINHPEF	minimum glide habitat during effective egg hatching period
GLMAXHPEF	maximum glide habitat during effective egg hatching period

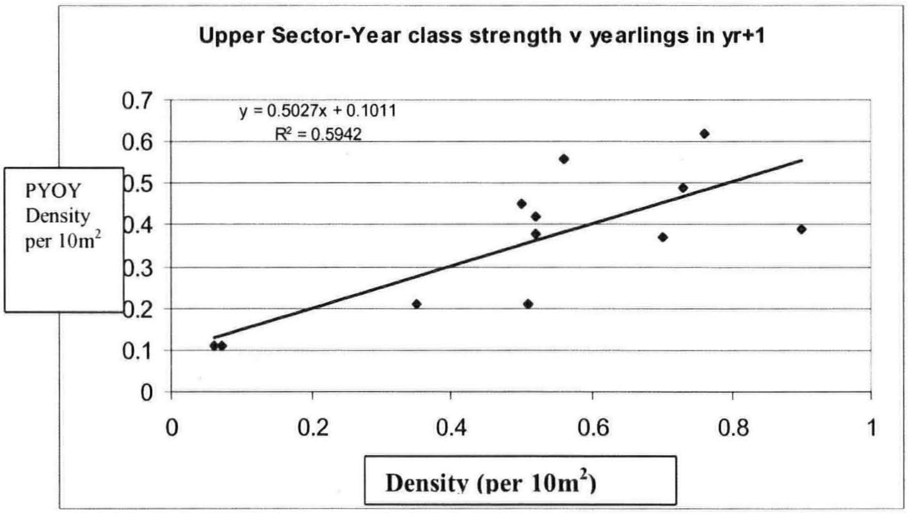
APPENDIX.6.

TROUT POPULATION DYNAMICS

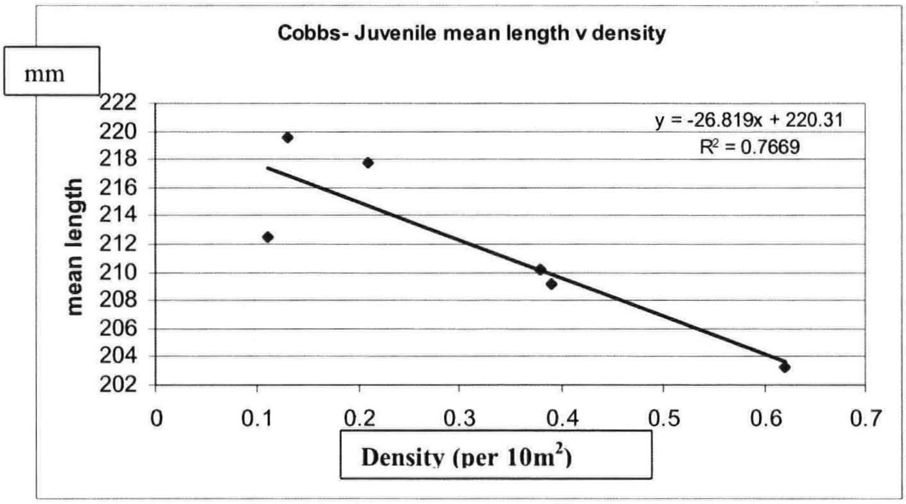
A) Relationship between adult spawning stock and densities of 0+ fry in the following year in the Upper sector (Cobbs)



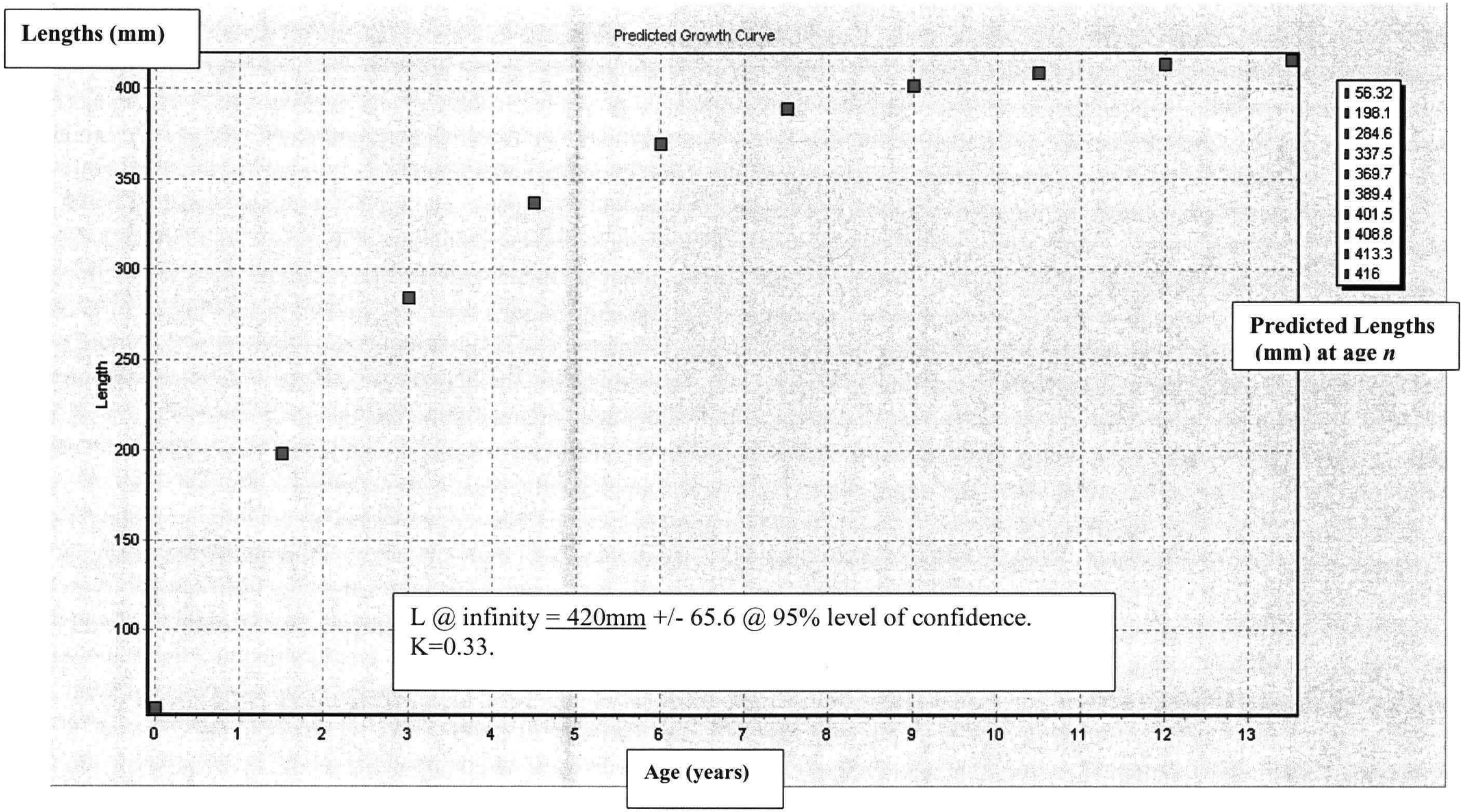
B) Relationship between densities of 0+ fry and age 1+ juveniles the following year in the Upper sector (Cobbs)



C) Self thinning line for age 1+ trout showing reduction in mean size with density in the Upper sector (Cobbs)



Von bertalanffy growth curve from 33 tagged trout marked and recaptured at Cobbs.



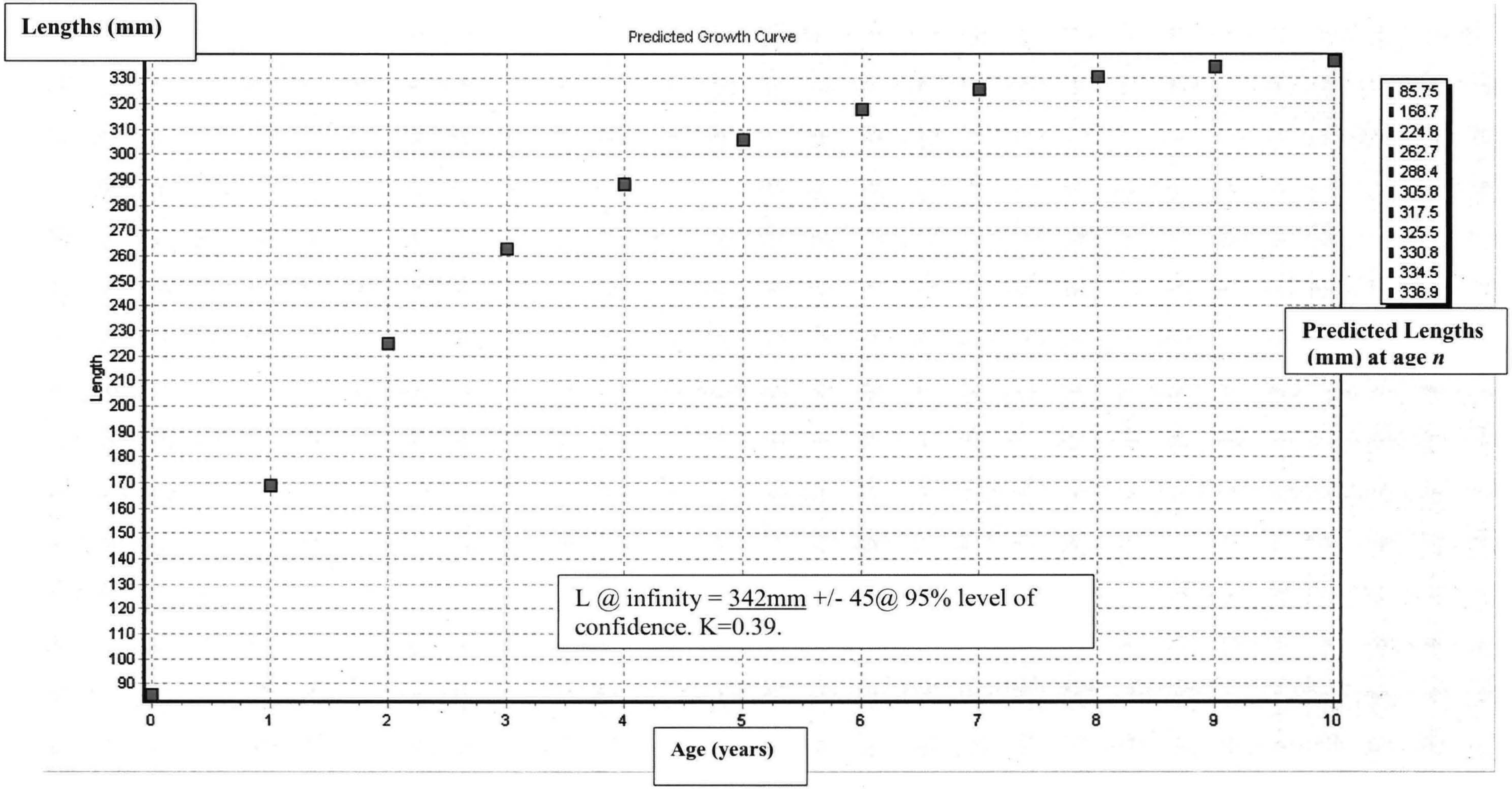
Lengths (mm)

Predicted Lengths (mm) at age *n*

Age (years)

L @ infinity = 420mm +/- 65.6 @ 95% level of confidence.
K=0.33.

Von Bertalanffy growth curve from 30 tagged trout marked and recaptured at Tolpuddle.

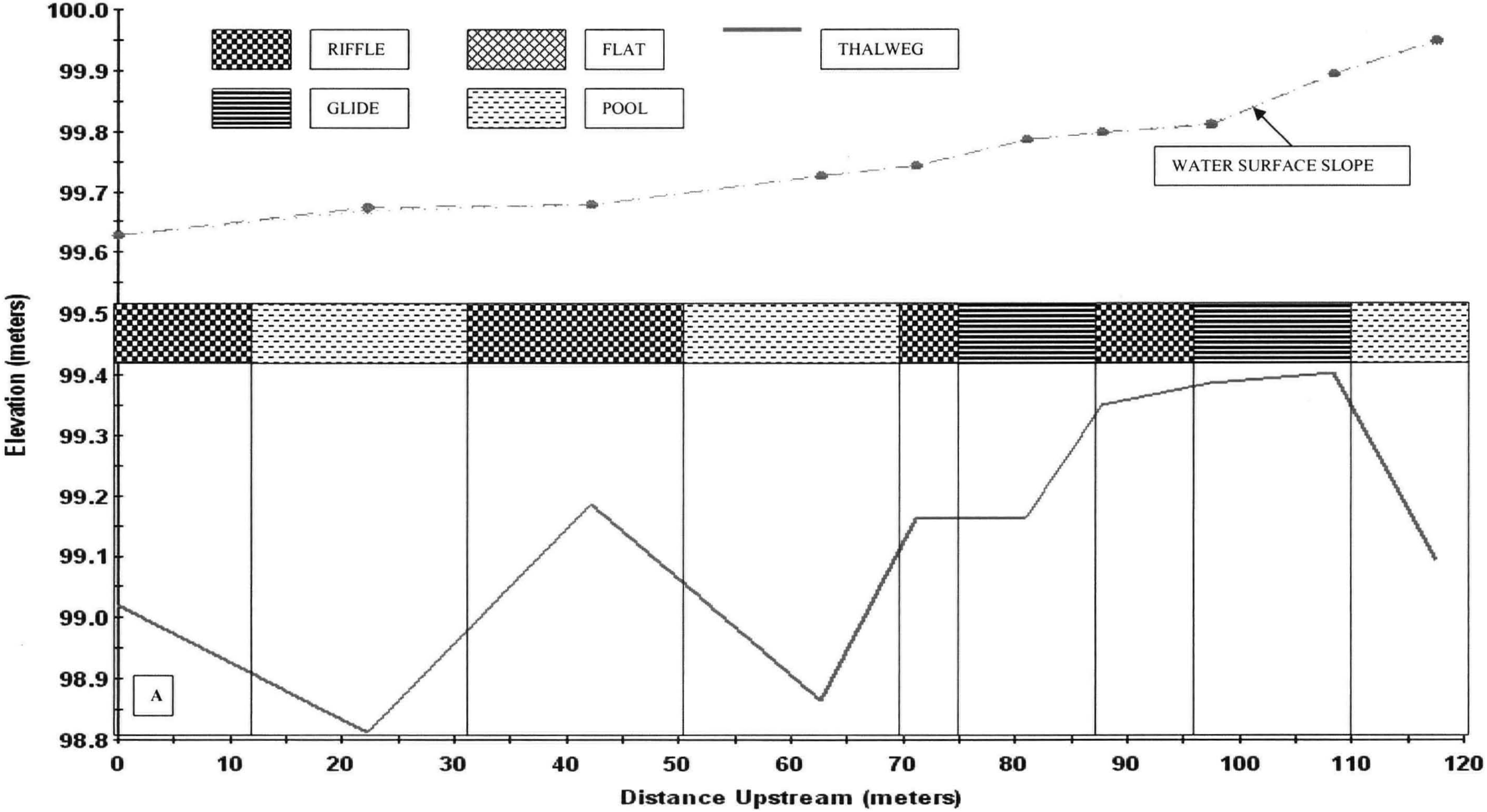


L @ infinity = <u>342mm</u> +/- 45@ 95% level of confidence. K=0.39.

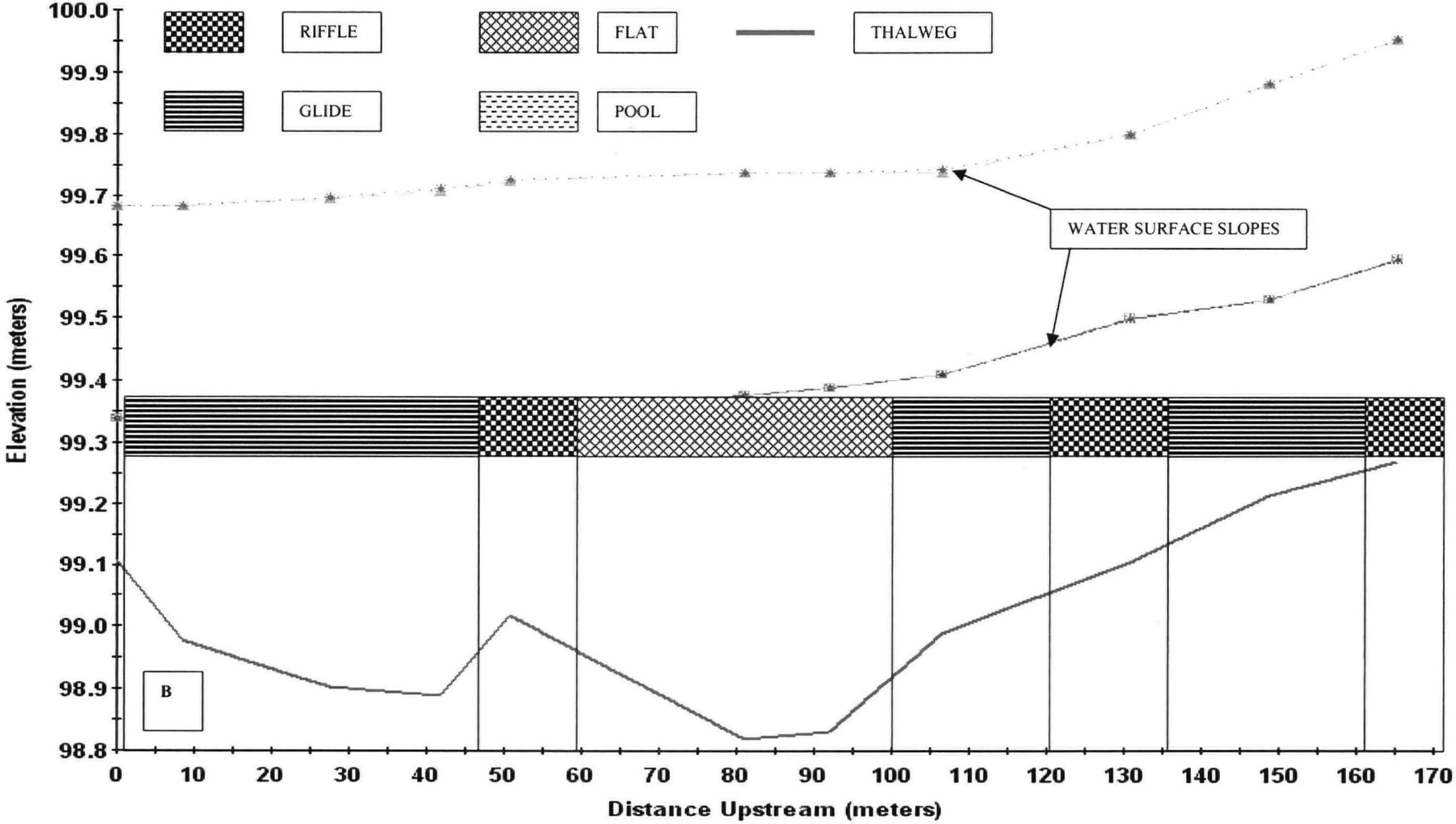
APPENDIX. 7.

LONG PROFILE PLOTS SHOWING MESO-HABITAT JUXTAPOSITIONS FOR UPPER AND LOWER RIVER SECTORS

Distribution of meso-habitat types (relative to thalweg depths) in the upper sector at Cobbs



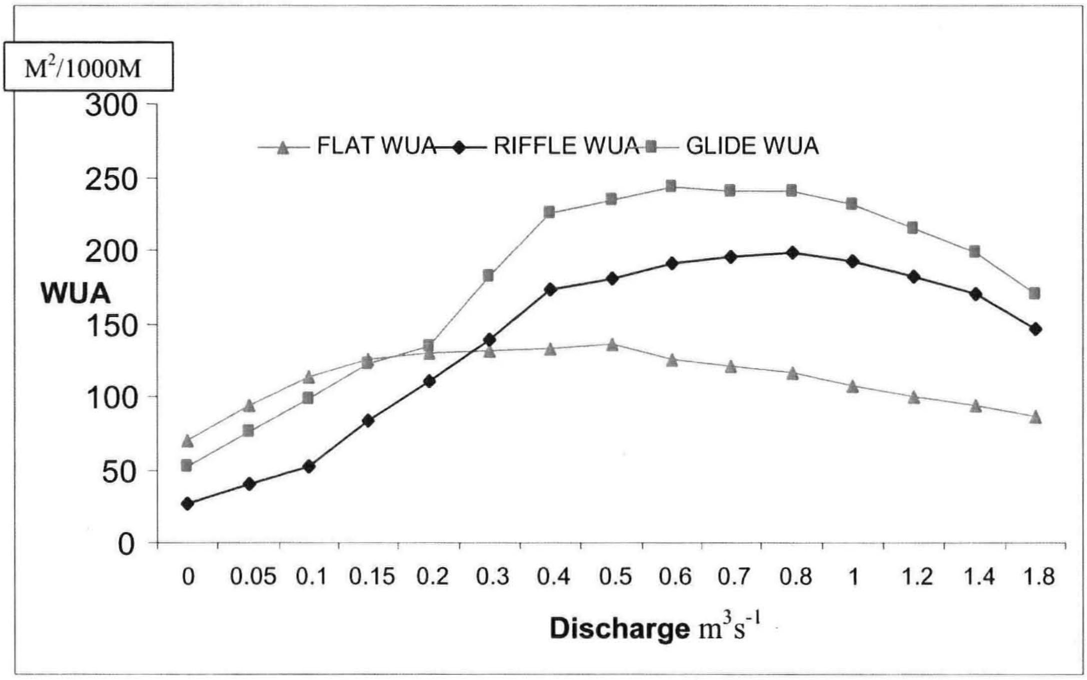
Distribution of meso-habitat types (relative to thalweg depths) in the lower sector at Tolpuddle



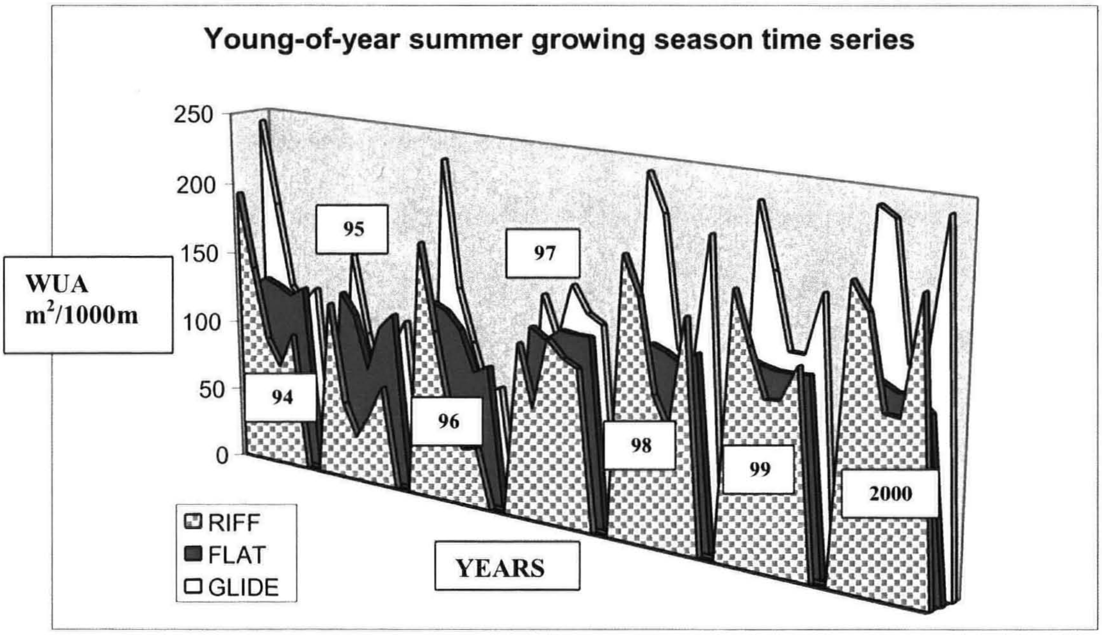
APPENDIX.8.

MESO HABITAT RELATIONSHIPS

WUA – discharge relationships for meso-habitat types in the Lower sector: summer habitat for YOY brown trout



Time series (1994 – 2000) showing summer habitat durations (WUA) for three meso- habitat types for YOY brown trout in the Lower sector



APPENDIX.9.

SUMMARY OF PROGRAMME NAMES WITHIN PHABSIM REFERRED TO IN TEXT

STGQ: The STGQ model uses a stage-discharge relationship (rating curve) to calculate water surface elevations at each cross section. In the stage-discharge relationship and its simulation, each cross section is independent of all others in the data set. The basic computational procedure is conducted by performing a log-log regression between observed stage and discharge pairs at each cross section. The resulting regression equation is then used to estimate water surface elevations at all flows of interest.

MANSQ: The MANSQ program utilises Manning's equation to calculate water surface elevations on a cross section by cross section basis and therefore treats each cross section as independent. Model calibration is accomplished by a trial and error procedure to select a b coefficient that minimises error between observed and simulated water surface elevations at all measured discharges.

WSP: The Water Surface Profile (WSP) program uses a standard step-backwater method to determine water surface elevations on a cross section by cross section basis. The WSP program requires that all cross sections being analysed in a given model run be related to each other in terms of survey controls and sequence upstream i.e. each cross section's hydraulic characteristics in terms of bed geometry and water surface elevations are measured from a common datum. The model is initially calibrated to a measured longitudinal profile of water surface elevations by adjusting Manning's roughness, first for the entire study site and then at each cross section. Manning's roughness is then adjusted for subsequent measured longitudinal water surface profiles at other discharges by setting the roughness modifiers used within the model. This approach requires all hydraulic controls within the modelled study site are represented by cross sections.

VELSIM: The VELSIM program is the principal tool used to simulate the velocity distributions within a cross section over the required range of discharges (i.e., the mean column velocity in each wetted cell in a study cross section at each simulation discharge). The technique relies on an empirical set of velocity observations that act as a template to distribute velocities across a channel by solving for the 'n' in Manning's equation (in this context 'n' acts as a roughness distribution factor across the channel). The channel is divided into cells and the velocity calculated for each of these cells. The usual practice is to use one set of velocities as a template for simulating velocities for a particular range of discharges. When more than one set of empirical velocity measurements is available, a commensurate number of flow ranges can be simulated with different velocity templates. The program can be used when no velocity measurements are available. In this situation, velocity will be distributed across the cross section as a function of flow depth.

HABTAE: The primary habitat simulation program in PHABSIM. Options within HABTAE allow the user to select habitat calculation assuming the condition within a cell establishes the worth of the habitat in the cell. Adjacent cell conditions (for example a "feeding station") are also included in HABTAE. The HABTAE program also allows habitat to be determined in terms of volume (instead of the surface area), and provides a method for determining the habitat conditions at each cross section as well as the aggregate for a study site.

HABEF: Effective habitat analysis in PHABSIM is used to determine availability of physical habitat considering two flows; in other words, the HABitat that remains EFfective when two flows are of importance. This situation often arises, for example, in the evaluation of reducing flows during the spawning period and subsequent incubation period or in hydro-peaking operations that have a daily minimum and maximum flow. In the case of spawning and incubation analyses, the spawning area at a cross section is not 'effective' unless the incubation period flow regime maintains the habitat in a suitable condition for the eggs to hatch.

HABTAM: The second effective habitat model is the HABTAM program. In HABTAM the species can move from cell to cell cross each transect over a range of starting and ending discharges. In this model, effective habitat is defined as the habitat that remains usable when the species is forced to move due to flow fluctuations.

AVDEPTH/AVPERM: The average parameter model, AVDEPTH /AVPERM, calculates a variety of hydraulic characteristics for each cross section in addition to a study site average view. These include wetted width, wetted perimeter, and wetted surface area, cross sectional area, mean channel velocity, and average depths. They can also be utilised to determine the width of a stream with water that is over some arbitrary depth(s) specified by the user.

CALCF4: This utility program calculates a water transport (or conveyance) parameter (WTP) for each cross section. The program uses Manning's equation at each cross section to calculate the WTP for each water surface elevation, develops power relationships between WTP's, area and maximum depth, discharge and width, velocity, and average depth. The exponent (B) in the WTP regression equation between discharge and the channel conveyance factor or WTP for each cross section is an excellent initial estimate for the b coefficient for each transect in the MANSQ program.