HABITAT USE BY 0+ CYPRINID FISH IN THE RIVER GREAT OUSE, EAST ANGLIA

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(Paul Garner held an FBA post-graduate Research Studentship for three years, based at the Eastern Rivers Laboratory of the IFE (see *Freshwater Forum* 3:2, pp. 141-143), and the following article summarises his research for a PhD. Paul is now an FBA post-doctoral Research Fellow, based at the Ferry House, Windermere Laboratory, where he is working on the ecology of minnows and other cyprinid fish.)

The effects of river regulation upon the fish fauna of lowland rivers

". . . *we know very little about large rivers . . . defined as those which are large enough to intimidate research workers."*

Dodge (1989)

Human activity has caused a wide range of impacts upon river ecosystems with, perhaps, the most far reaching being the modification of river channel form and discharge, resulting in the loss of lateral diversity and channel - riparian zone connectivity (Boon 1992; Swales 1994; Zalewski et al. 1994). The rivers of the European continent represent the most regulated rivers in the world (Swales 1994). Hence, it is not surprising that many studies have reported a decline in both the quantity (biomass) and quality (diversity) of the ichthyofauna of these rivers. For example, in the River Danube, out of 52 long-established species, 30 are considered to be endangered or vulnerable, primarily as a result of the loss of specialised biotopes (Schiemer et al. 1991; Schiemer & Waidbacher 1992). Similarly, the fish fauna of the River Morava (Czech Republic) has undergone considerable changes in the relative importance of different species with, currently, an ichthyofauna dominated by a small number of generalist species (Jurajda & Penaz 1994). This appears to be a common result of river regulation and has been reported in the River Rhone (Copp 1992a), the River Great Ouse (Copp 1990a, 1992b) and in the Rivers Elbe and Rhine (Lelek 1976). In North America, habitat degradation has been linked to ca. 70% of all extinctions of freshwater fish species (Miller et al. 1989). Surprisingly, no species of riverine fishes have become extinct in Europe, unlike the North American continent, yet localised extinctions are common (Miller et al. 1989; Maitland & Campbell 1992).

The requirement for models of fish habitat use

There has been a long-held requirement for the classification of riverine fish habitats owing to their economic importance and conservation needs (Huet 1959). Habitat assessment can be applied in three areas of fisheries management (Milner et al. 1985): classification of sites for the conservation of high value sites, assessment of impacts (either *a priori* or *a posteriori),* and enhancement. All of these tasks require that detailed information concerning the habitat preferences of the target species is compiled and can be interpreted in terms of the behaviour of the fish (Milner et al. 1985).

Rivers differ from other aquatic environments in two key characteristics: they have a unidirectional water flow, and are subject to high variability, both in space and time. For an organism to survive in a riverine system it must be well adapted and able to utilise areas which increase its fitness (Hynes 1970). Use of the most suitable habitats results in maximum success, generally thought of in terms of reproductive potential, although in fish aged 0+ years this can be better thought of as survival to the second year and beyond (Conover 1992). Several different habitats may be required at specific periods during the life history of a fish species, owing to variation in physiology and, hence, behaviour of the organism (Balon 1956, 1984, 1986; Copp 1990b). Gustard et al. (1987), in a study of the effects of compensation flows in the UK, concluded that there still remained the need for more primary research into the relationships between the biota and the physical and chemical habitat, particularly at the reach scale.

Investigation of the habitat - biota relationships of stream fishes in North America led to the release of the Instream Flow Incremental Methodology (IFIM) by the Co-operative Instream Service Group of the United States Fish and Wildlife Service (Bovee 1978). Designed to link hydrology and ecology, this approach used data from both disciplines to predict the flow requirements of the biota. The IFIM is considered to be "the most scientifically and legally defensible method available for most instream flow problems" (US Department of the Interior 1979, internal report) and has been described as "the current state of the art" (Orth 1987). The biological component of the IFIM consists of the development of habitat suitability relationships, which predict the suitability of a habitat patch for a target species. A range of methodologies have been developed for producing habitat suitability relationships. These relationships may be based upon expert opinion or field observation and a range of habitat variables. At present few studies have derived habitat suitability relationships for cyprinids, and of these, most have relied upon expert opinion (Armitage & Ladle 1991).

Importance of the Family Cyprinidae

The Family Cyprinidae represents possibly the largest family of vertebrates on earth, containing many of the most species-rich genera in the Order Cypriniformes (2500 species: Nelson 1984). In Eurasia cyprinids are represented by at least 1293 species and comprise on average 44% of the species present in individiual drainage basins (Banarescu & Coad 1991). In Europe ca. 40 species are now extant, with the River Danube, the most species-rich drainage basin, containing 34 species of Cyprinidae. Over the last 2000 years (but primarily during the last 200 years) the distributions of many species have been altered by man, the most widespread being the carp *Cyprinus carpio* which has been relocated across not only Europe but most of the World (Balon 1974). These premeditated movements illustrate the value of cyprinid fishes, both as a commercial crop and due to the formation of substantial recreational fisheries. They are commonly associated with the lower reaches of rivers (Huet 1959) and eutrophic conditions (Winfield & Townsend 1991).

The 0+ life stage of cyprinids

Young fishes, particularly the young-of-the-year (i.e. fish aged 0+ years), have received considerable attention over the last two decades, owing to a recognition of their important contribution to the success of the species as a whole (Mills 1982; Mills & Mann 1985; Conover 1992; Mann 1995). It has also become apparent that many fish populations are dominated by a small number of year-classes (Mann 1976; Elliott 1995; Mann 1995), with recruitment from the 0+ year-class being the primary control upon the year-class strength (Mills & Mann 1985; Mann 1995). During the first summer of life, cyprinid fishes develop rapidly and pass through a series of developmental phases (Plate 1; Balon 1984, 1986). In the present study 0+ cyprinids were prescribed to one of four phases: young larva (hatching until the beginning of exogenous feeding), late or old larva (beginning of exogenous feeding until the less of the finfold), juvenile (loss of the finfold), and juvenile entering the first winter; see definitions in Copp (1990b) and Tong (1985), and timescales in the present study, listed in the legend of Fig. 9 (on p. 21). Previous studies have illustrated the variation in behaviour by fishes in each of these phases (Copp 1990b).

Scope of the present study

Although the fish species of the River Great Ouse (see below) are common throughout much of Europe, many species have been only rarely studied, particularly in the 0+ life stage. Several studies detail the habitat use of 0+ cyprinids in the River Great Ouse (Copp 1990a, 1992a, 1992b, 1993, Copp et al. 1994), but these studies have failed to determine the causes of species-specific habitat use and have been carried out at resolutions generally unsuitable for the production of habitat suitability models (Garner 1996b). The

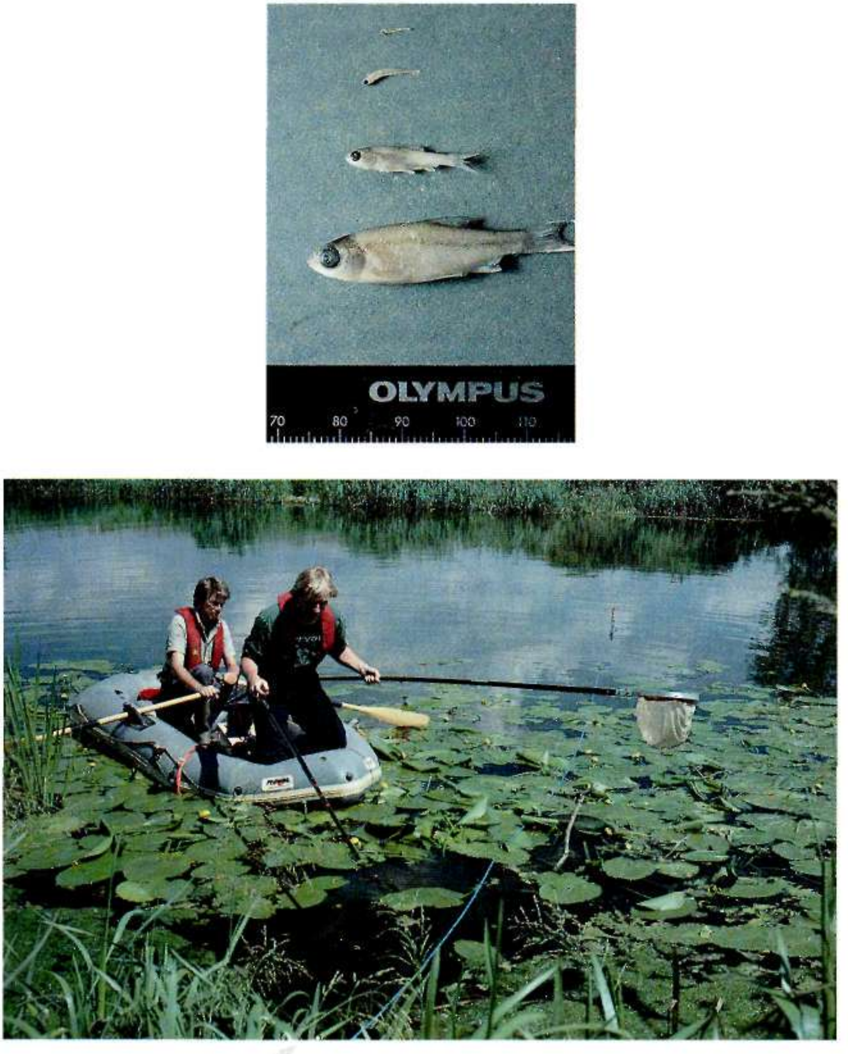

PLATE 1. *Upper picture:* Four developmental phases of cyprinid fishes aged 0+ years, used in the present study. Phases are, from the top of the picture: young larva, old larva, juvenile, and juvenile entering the first winter. The scale shown at the bottom is marked in millimetres.
Lower picture: Point sampling by electrofishing in the River Great Ouse, approaching the sampling point. Note the (blue) transect line, attached to a marker stake in mid-river and used for estimating plant cover and for sampling zooplankton.

present study was thus designed to examine the habitat use of several species of 0+ cyprinid in the regulated River Great Ouse and to determine the reasons for specific habitat use.

The River Great Ouse System

". . . the banks on one side of the river were at that time so low, . . ., that the said river was then a full mile in bredth. "

Petition from the villagers of Norfolk to Edward III (1362)

The River Great Ouse is one of the largest river systems in the United Kingdom, being ca. 152 km long and having a drainage basin of ca. 8588 km^2 (Fig. 1). It flows through the Cambridgeshire fens of East Anglia and empties into the Wash on the eastern coast of Britain. Regulation of the flow of the Ouse has occurred for almost 1000 years. During the 20th century, increasing importance has been placed upon the regulation of extreme high water events (floods) in the Ouse catchment. The most marked change in the river channel has occurred below Bedford where the river has been lined by raised flood banks that limit the laterial spread during high flows. Discharge and water temperature follow roughly seasonal cycles in the Great Ouse (Fig. 2).

The Great Ouse drainage basin has one of the most diverse fish faunas found in the United Kingdom, owing to its historic connection to mainland Europe and a number of successful introductions, most notably of the predaceous zander or pike-perch *Stizostedion lucioperca* (Family Percidae). The river is an important recreational fishery, although in recent years this appears to have declined, due to poor returns.

Sampling small fishes in large rivers

"All of the common problems of sampling error and bias must be faced by the fishery biologist. They demand of him the fullest possible understanding of habitats and habits of the fishes to be sampled, and of the construction, operation and selectivity of sampling gear."

Lagler (1968)

Few sampling techniques are suitable for capturing the early phases of fishes in large rivers. This centres on the problems imposed by trying to sample small, relatively fast-moving, contagiously-distributed organisms, which undergo considerable changes in size and behaviour during the period of interest (Prokes & Honrakova 1988; Copp 1990b). Microhabitat-based sampling techniques, such as direct observation (Krause 1993), buoyant nets (Bagenal 1974), light traps (Ponton 1994) and electric fishing frames (Bain et al. 1985) have proven most useful for investigating the behaviour of 0+ cyprinids in the wild. Microhabitat-based sampling techniques tend to have less impact upon

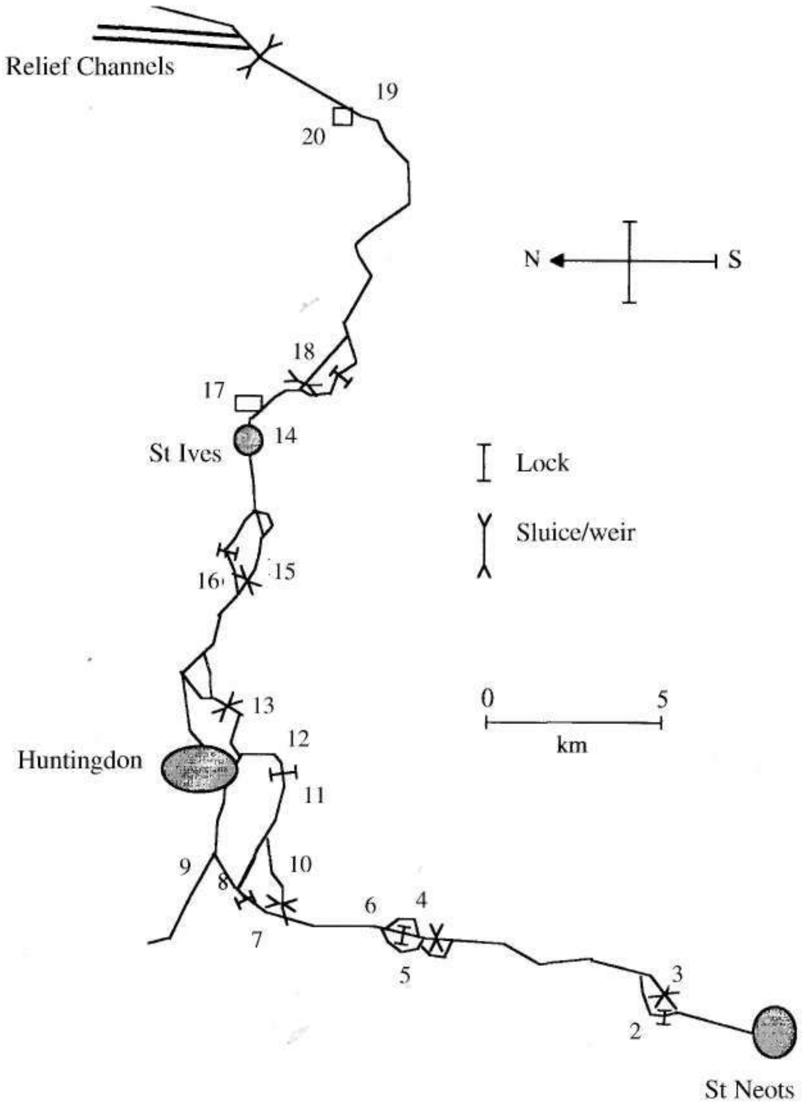

FIG. 1. Locations of the study sites in the River Great Ouse between St Neots and relief channels at Earith. Sites are numbered 2 to 20.

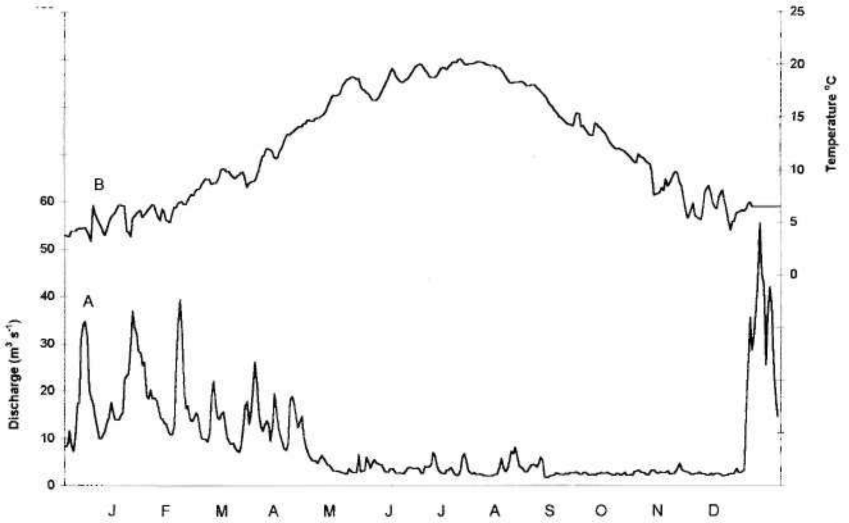

FIG. 2. Mean discharge (line A, cubic metres per second) and water temperature (line B, °C) for the lower Great Ouse at Offord (site no. 4, Fig. 1), from 1989 to 1994.

the biota and also tend to be less labour intensive, allowing a larger number of samples to be taken (Blondel et al. 1970; Blondel 1975; Downing & Anderson 1985). This greatly enhances statistical robustness and may also allow the data to be used at several spatial scales, from a single microhabitat patch to multi-basin regions (Cyr et al. 1992; Copp et al. 1994). However, the smaller number of fish captured may limit the usefulness of the technique for examination of specific traits, such as diet, where larger sample sizes are beneficial, owing to high intra-individual variability.

Of all the sampling techniques currently in use, electrofishing is one of the most popular for shallow-water situations. Yet, few studies have used electrofishing for capturing small fish because of the difficulties of sampling short fish. As a result it has been necessary to adapt current electrofishing equipment to increase the efficiency of capture of small fish. This has led to the development of the point sampling by electrofishing (PSE) methodology (Persat & Copp 1988; Copp & Garner 1995; see Plate 1, lower picture). Comparison of length-frequency relationships derived from PSE and seine netting have revealed no serial bias and provide similar estimates of mean population length and weight parameters (Fig. 3) (Garner 1997a).

In a desk-study of the suitability of sampling methods for small fish, undertaken as part of the present study, PSE was found to be the most labour-effective sampling methodology examined, offering the ability to take a large

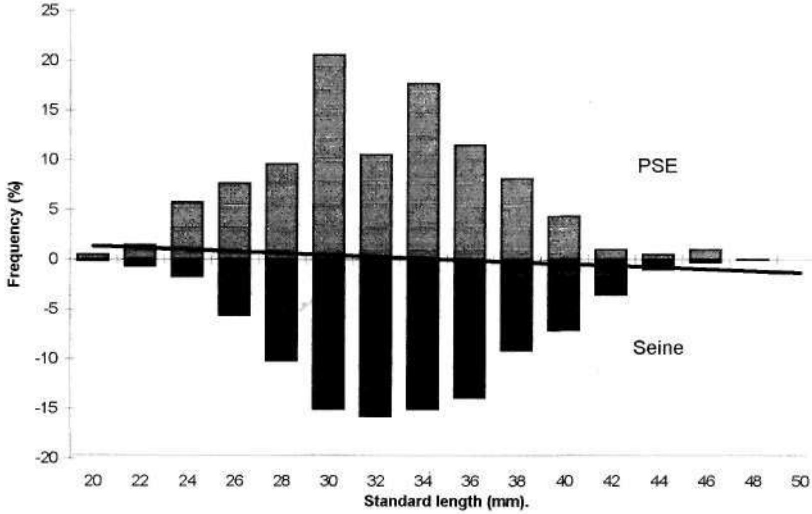

FIG. 3. Comparison of length frequency distributions for roach aged 0+ years, captured by point sampling by electrofishing (PSE) and seine netting. All fish were measured to the nearest 0.5 mm before being assigned to 2 mm length classes. Samples contained at least 40 fish for each sampling technique per visit to nineteen sampling sites. The solid line represents the best fit (linear regression, $P = 0.58$, $r^2 = 0.02$) for the relationship between PSE and seine catches. Based on Garner (1997a).

number of samples with relatively little disturbance to the habitat. On average, ca. 25 point samples can be taken per hour, including the measurement of habitat variables. Where habitat variables are not being measured this can be increased to 50 point samples per hour (Copp & Garner 1995). High flow velocities (>50 cm per second) and depths greater than 2.5 m respectively reduce the efficiency of PSE by washing the fish downstream before they can be sampled, and by being out of reach of the anode-field of the electrode. Apart from these two provisos, PSE is a reliable, easy to use technique for sampling 0+ cyprinid fishes.

Habitat use by cyprinid fish

"Individuals of different sizes in size-structured populations often differ greatly in the use of resources and/or space . . . The presence or absence of such diet or habitat segregation between different size classes can greatly affect population structure and dynamics. "

Gillam & Fraser (1988)

The description of the physical habitat preferences and diet of 0+ cyprinids has only recently been a focus of attention (Mark et al. 1989; Rincon et al. 1992; Copp 1992a, 1993; Mann & Bass 1997). The analysis of habitat use has gained prominence as one of the major areas of research for 0+ fish as the early stages are often restricted to specific habitats upon which they are reliant and for which they exhibit specific preferences (Scott 1985; Grossman et al. 1987; Greenberg 1991; Copp 1992b; Copp & Mann 1993). The habitat conditions required are often much narrower than for older (larger) individuals owing to the strict physical and energetic constraints imposed upon young fishes (Kaufmann & Weiser 1992; Schiemer & Weiser 1992). As a result, it has been proposed that the availability of suitable habitat may be one factor controlling both the species assemblage present and the numerical dominance of species within the assemblage (Gillam & Fraser 1988).

Organisms must determine their use of the environment in relation to a number of (often interrelated) habitat variables. To determine the "realised niche" for each species, habitat must be described by using a number of variables which, taken together, reflect the behavioural trade-offs faced by the organism.

Habitat use and diet of 0+ cyprinid fishes is similar for a range of common species found in lowland rivers, although there is a tendency for increasing specialisation as the fish develop (Tables 1 to 3). In general, all fish species were found associated with the marginal zone, with little diel variation in habitat use (Fig. 4; Garner 1996a). Use of shallow habitats in the presence of macrophytes correlated well with the distribution of zooplankton in the river channel, the preferred food source of 0+ cyprinids (Fig. 5; Garner et al. 1996). Initially all species fed upon rotifers and diatoms during the early larval phase and into the beginning of the late larval phase, up to a length of 10 to 14 mm. Cladocera, particularly the chydorids *Alona* spp. and *Chydorus* spp., and early instar larvae of Chironomidae, then became prevalent in the diet along with small numbers of Copepoda (Table 1; Garner 1996a). Such feeding behaviour appears to be predetermined by prey size and fish morphology (Blaxter 1986; El-Fiky et al. 1987). During mid-summer there is a "crash" in the densities of zooplankton (Garner 1996a; Garner et al. 1996). This results in a decline in prey capture by the fish and a switch by roach *Rutilus rutilus* to algal/detrital material (Garner 1996a; Mann et al. 1997). Other species appear unable to switch and remain feeding upon zooplankton and terrestrial organisms (Table 1).

The site investigated at Brampton (site no. 7, Fig. 1) was representative of ca. 90% of the lower Ouse system (66 km of river) based upon the classification proposed by Copp (1991). River form has been shifted from a meandering riffle-pool sequence with a concomitant wide floodplain to a deep homogenous pool-control-pool system with a reduced floodplain and loss of potamic waterbodies (Summers 1973), typical of lowland rivers in Europe. The

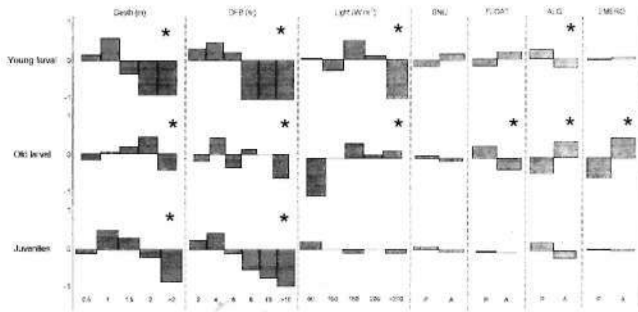

FIG. 4. Habitat use by 0+ roach in the River Great Ouse, showing the calculated electivity for each of seven recorded habitat variables. Scores on the ordinate range from 1 = always used, to –1 = never used; 0 = no selection. An asterisk indicates significant (Chi-square $P<0.01$) deviation from the habitat variables available at the nineteen sampling sites. Habitat categories are: depth (0.5 to >2.0 m); distance from bank (DFB, 2 to >10 m); light intensity (50 to >200 Watts per m^2). Plant cover categories are: SNU = submerged leaves of yellow water-lily *Nuphar lutea*; Float = floating leaves of yellow water-lily; ALG = algae; EMERG = emergent macrophytes; P = present; A = absent. Based on Garner (1996a).

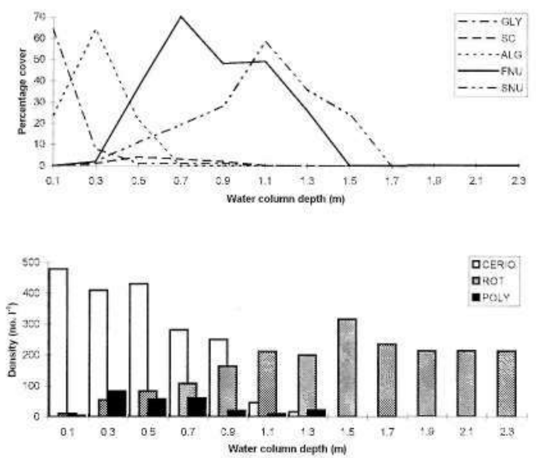

FIG. 5. Mean plant cover (%) (above) and mean zooplankton densities (numbers per litre) (below), measured along four transects in the River Great Ouse prior to the annual weed cut and a "crash" in zooplankton numbers. Plant cover categories are: floating sweet-grass *Glyceria fluitans* (GLY), common clubrush *Scirpus lacustris* (SC), filamentous algae (ALG), floating leaves of yellow water-lily *Nuphar lutea* (FNU); submerged leaves of yellow water-lily (SNU). Zooplankton categories are: cladoceran crustaceans *Ceriodaphnia quadrangula* (CERIO) and *Polyphemus pediculus* (POLY); rotifers (ROT). Adapted from Garner et al. (1996).

Table 1. A summary of ontogenetic variation in composition of the diets of four cyprinid fishes in the River Great Ouse, showing approximate mean numbers of food items per gut examined. Fish are classified as young larva (YL), old larva (OL) and juvenile (Juv): n is the number of fish examined. Food categories are: rotifers (Rot), diatoms (Dia), chironomid larvae (Chi), copepods (Cop), adult dipterans (Dip), aufwuchs (Auf), detritus (Det), *Bosmina longirostris* (Bos), *Alona* spp. (Alo), *Chydorus* spp. (Chy) and *Ceriodaphnia quadrangula* (Cer). Modified from Garner (1996a).

Fish	Phase	n	Rot	Dia	Chi	Cop	Dip	Auf	Det	Bos	Alo	Chy	Cer
Roach	YL	38	20	1	0	0	0	0	0	0	<1	<1	0
	OL	25	7	1	2	<1	0	<1	0	5	1	1	<1
	Juv	117	0	0	2	<1	<1	1	<1	<1	2	4	<1
Bream	YL	7	6	1	0	0	0	0	0	0	1	<1	0
	OL	69	0	0	<1	<1	0	<1	0	<1	1	2	7
	Juv	110	0	0	1	1	0	<1	0	<1	3	3	11
Chub	YL	50	5	4	<1	0	0	0	0	<1	<1	<1	<1
	OL	53	<1	<1	1	0	1	0	0	<1	2	<1	2
	Juv	25	0	0	1	0	3	0	0	0	<1	<1	0
Bleak	YL	41	2	1	2	<1	0	0	<1	<1	<1	<1	<1
	OL	52	3	2	<1	<1	0	0	<1	<1	<1	<1	<1
	Juv	13	0	2	2	<1	0	0	<1	0	0	0	0

Table 2. Dietary overlap of five cyprinid ecospecies in the River Great Ouse, calculated (as %) from the index of Zaret & Rand (1971). Values greater than 60% (**bold number**) indicate substantial overlap of diets for young and old larval phases (YL, OL) and juveniles (Juv). Modified from Garner (1996a).

Fish/phase		Roach OL	Juv	Bream YL	OL	Juv	Chub YL	OL	Juv	Bleak YL	OL	Juv	Gudgeon Juv
Roach	YL	30	0	**87**	5	0	**78**	14	0	53	**67**	8	0
	OL	–	**82**	34	9	**67**	35	12	6	29	33	17	5
	Juv	–	–	0	2	**64**	1	3	4	2	1	2	2
Bream	YL	–	–	–	24	3	**98**	30	**70**	**68**	**93**	37	9
	OL	–	–	–	–	**63**	34	**80**	22	37	34	35	38
	Juv	–	–	–	–	–	8	56	13	24	9	9	41
Chub	YL	–	–	–	–	–	–	37	10	**73**	**97**	49	8
	OL	–	–	–	–	–	–	–	54	55	43	39	54
	Juv	–	–	–	–	–	–	–	–	26	9	29	18
Bleak	YL	–	–	–	–	–	–	–	–	–	**79**	**65**	37
	OL	–	–	–	–	–	–	–	–	–	–	**63**	22
	Juv	–	–	–	–	–	–	–	–	–	–	–	21

Table 3. Mean similarity scores (%) for four cyprinid fishes in the River Great Ouse, calculated from percentage similarity scores (Schoener 1970) to assess potential habitat overlap between non-synchronous ecospecies. As seven habitat variables were examined, a composite similarity index has been calculated as the mean of the scores obtained for each variable. It is suggested that values greater than 75% indicate a high degree of overlap between species (**bold numbers**) and between stages of the same species (YL, OL = young and old larval phases; Juv = juveniles). Modified from Garner (1996a).

Fish/phase		Bleak OL	Bleak Juv	Roach YL	Roach OL	Roach Juv	Chub YL	Chub OL	Chub Juv	Bream OL	Bream Juv
Bleak	YL	**80**	59	75	66	**78**	**80**	**78**	74	**76**	**80**
	OL	–	69	**81**	**82**	**88**	**82**	**85**	**81**	66	**84**
	Juv	–	–	65	71	68	65	68	68	**67**	66
Roach	YL	–	–	–	74	**87**	**80**	**85**	**85**	**83**	69
	OL	–	–	–	–	**82**	**81**	**81**	75	75	**77**
	Juv	–	–	–	–	–	**83**	**91**	**82**	**81**	**80**
Chub	YL	–	–	–	–	–	–	**84**	**80**	**82**	**80**
	OL	–	–	–	–	–	–	–	**85**	**84**	**88**
	Juv	–	–	–	–	–	–	–	–	**79**	**79**
Bream	OL	–	–	–	–	–	–	–	–	–	**83**

site was dominated by roach, a generalist phyto-lithophilic spawner, whose predominance is indicative of degraded rivers (Oberdorff & Hughes 1991), indicating that conditions in the channel support only "generalist" species (Schiemer & Weiser 1992).

The causes of this lack of species diversity can be speculated. The rheophilous species (adapted to fast flows) appear to be limited by the lack of suitable spawning habitats, as adult fishes are occasionally captured from the river. The introduction of large numbers of juvenile barbel *Barbus barbus* to the river during the early 1980s resulted in localised, increased recreational catches of this species as the fish aggregated towards the most suitable habitat. Yet, in the lower, regulated river, no progeny appear to have resulted from these original stockings and the adult fishes have died of natural causes. Progeny of dace *Leuciscus leuciscus*, which appear to be able to utilise spawning gravels that have a higher silt content than the gravels used by barbel (personal observations), are abundant in the lower river, suggesting that spawning habitat may be less limiting for this species. Unfortunately little is known of the spawning requirements for rheophilic cyprinids (Mann & Mills 1986). The low abundance of potamic species (adapted to slow-flowing and relatively warm waters), particularly tench *Tinca tinca* and rudd *Scardinius erythrophthalmus*, probably reflects the lack of suitable spawning habitat as potamic waterbodies, suitable for spawning, were rare (Copp & Mann 1993).

Most species appear capable of surviving in the habitat available until the end of their first summer. Of more importance may be survival over winter (Conover 1992). Investigations on habitat use and diet were abandoned in late October owing to a decline in fish abundance. This is a common phenomenon, with few studies of 0+ fishes being carried out over winter in Europe. Although the mortality rate of roach during the summer period appeared to be constant, growth rates were significantly lower than those calculated using the optimal growth model of Mooij & Van Tongeren (1990), owing to the lack of zooplankton prey (Fig. 6; Garner et al. 1996; Mann 1997). Considering this, it can be hypothesised that other, less successful species, may fare worse than roach and so they do not reach the winter survival threshold. Unfortunately, optimal growth models similar to that developed for roach have not been developed for other cyprinid species. Evidence from populations in other inland waters suggests that growth rates of 0+ cyprinids in the River Great Ouse are depressed (Kubekja 1994). Reduced growth and survival, owing to a lack of planktonic prey, may explain the switch from a fish fauna dominated by bream *Abramis brama* to one dominated by roach, as bream appear unable to utilise alternative food sources (Garner 1996a; Garner et al. 1996).

Modelling the habitat use behaviour of cyprinid fish

The Instream Flow Incremental Methodology (IFIM; Bovee 1978) was originally developed to allow the prediction of habitat suitability and, hence, the standing stock of salmonid fishes in relatively small, high gradient North American rivers. Since that time the procedures embodied in the IFIM philosophy have been widely adopted and used to predict the effects of altered hydraulic conditions upon a whole host of target organisms, and in a range of riverine environments (Gore & Nestler 1988). IFIM adopts a microhabitat approach, consisting of three sections: the description of relationships between target species and habitats, the measurement and modelling of hydraulic conditions in the study river, and the prediction of habitat availability for the target species in relation to the hydraulic conditions that are present. In this way a value can be assigned to each habitat patch, which ultimately can be built up into a reach-level estimate of habitat availability. Then, by incorporating the discharge hydrograph into the methodology, a time-series of the quantity of habitat available to the target organism can be built up.

Several assumptions are implicit in the IFIM methodology: the target species exhibits preferences within a range of habitat conditions that it can tolerate and which can be defined numerically; the area of stream providing suitable conditions can be quantified and modelled as a function of discharge and channel structure; the target species reacts to changes in available habitat by altering its abundance in the stream (Bovee 1986). In the present study the emphasis was placed upon the first of these assumptions, i.e. that the biota are

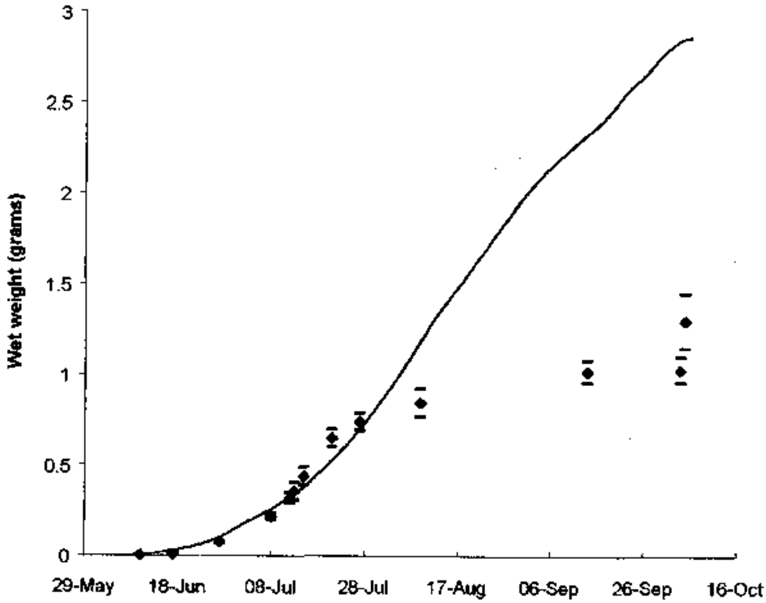

FIG. 6. Comparison of mean growth of 0+ roach at the Brampton site, with the predicted growth (solid line) calculated from the optimal growth model of Mooij & Van Tongeren (1990). All samples contained more than 40 fishes. Bars represent 95% confidence intervals. Redrawn from Garner *et al.* (1996).

responding to habitat availability in a quantifiable manner. It was the primary aim of this work to develop the ideas generated in the earlier investigation of habitat use into a suite of models that would allow the determination of habitat suitability for 0+ cyprinid fish in the River Great Ouse.

During 1994, fish were sampled on three occasions at nineteen sites, representative of the four major environments present in the lower Great Ouse river system (main river channel, sluice channels, marinas and streams) (Fig. 1). The sampling occasions coincided with the presence of young larval cyprinids (mean standard length = 8.7 mm), juvenile cyprinids (mean standard length = 34.2 mm) and winter conditions (temperature below 8°C and elevated discharges). At each site and on each visit 50 samples were taken using PSE methodology and a series of habitat variables at each point was recorded. From this data, indices of habitat suitability were developed by estimating the proportions of each habitat variable occupied by the fish, relative to the proportions of each habitat variable available in the environment. Such analysis reduces the bias resulting from unequal availability of different habitats (Bovee

1986; Thomas & Bovee 1993; Garner 1995). The habitat suitability curves developed in this study agree well with the findings of intensive studies of 0+ habitat use by cyprinids in the Great Ouse (Copp 1990a; Copp 1995; Garner 1996a), the selection of shallow, slow-flowing water, in the presence of macrophyte cover, being the preferred conditions (Fig. 7).

Owing to the low discharge of the River Great Ouse for most of the year, velocity is negligible in much of the river channel. As elevated velocities are potentially one of the most important factors influencing the habitat use by fish (Bovee 1986; Mann & Bass 1997) it was necessary to determine the response of 0+ cyprinids to currents experimentally, using a small recirculating channel (Fig. 8). Results from this experiment illustrated the importance of fish size and water temperature upon the swimming ability of 0+ fish. Such results allow a more precise model of velocity-habitat suitability to be built up, as it has been common practice to develop suitability relationships more or less independently of temperature and fish size (Mathur et al. 1985).

The compilation of habitat suitability indices for lowland fishes requires that data are collected from impacted sites (Garner 1995). In view of this limitation, it is important that spatial variation, not just at the site scale but also within the catchment and over the geographical range of the species, is taken into account. The use of experimental techniques, such as the determination of critical swimming speed presented here, represents a potential "short cut" in the determination of suitability indices. It must be remembered though, that the fish operate within strict physiological constraints (Weiser 1991) and that "maximal" and "optimal" swimming velocities will be very different (Brett 1967; Lightfoot & Jones 1979). Lightfoot & Jones (1979) concluded that preferred velocities in the River Hull tended to be up to 20% of the critical swimming speed (CSS; the maximum speed that the fish could maintain for 3 minutes). In the present study, optimal velocity was predicted as being ca. 40% of the CSS for juvenile roach (Fig. 8). The relationship between swimming speed and water temperature also allows the prediction of optimal velocity at winter temperatures. It can be predicted that the optima will be reduced to very low velocities (<5 cm per second) at winter temperatures (5 to 8°C). This is supported by field observations, which indicated an increased use of non-flowing habitats, particularly off-channel refugia such as marinas, during winter (Fig. 8).

Although the main aim of the habitat modelling project was to develop a method suitable for constructing habitat suitability relationships for 0+ cyprinids, the models developed were used to determine habitat availability in the River Great Ouse over a range of discharges, using the physical habitat simulation (PHABSIM) component of the IFIM. The results of this analysis revealed that habitat suitable for 0+ fishes comprised a relatively small percentage of the River Great Ouse main channel and generally decreased with discharge (Fig. 9). When the habitat suitability models and habitat simulation

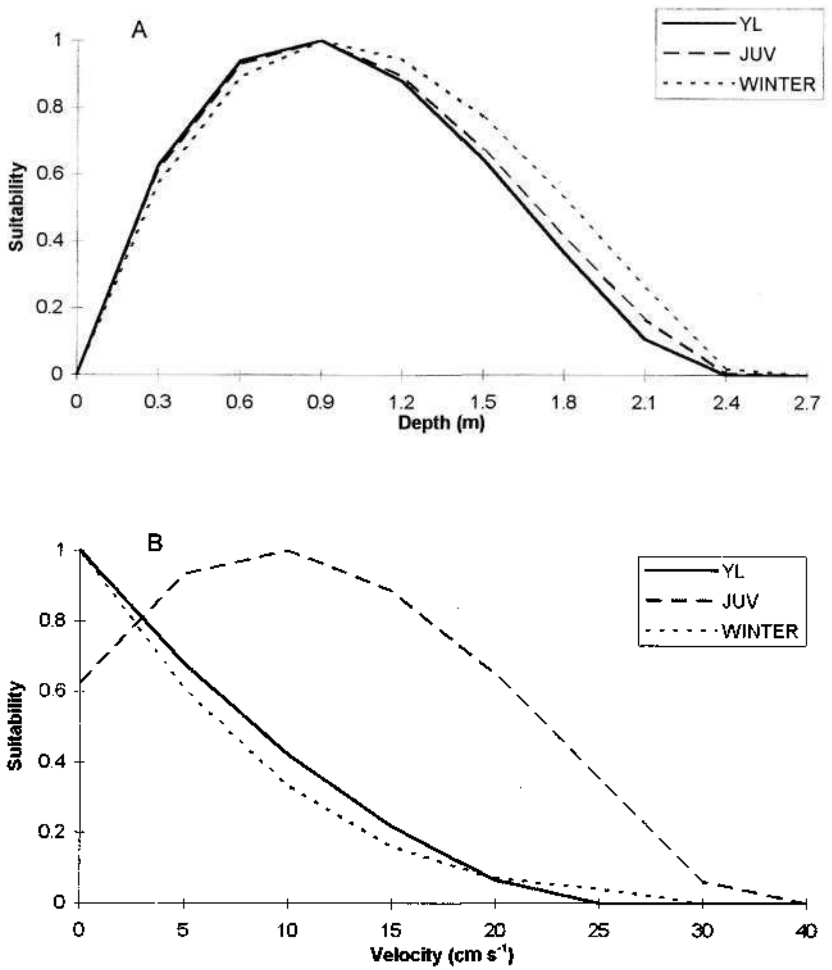

FIG. 7. Curves of habitat suitability for 0+ roach, developed from data obtained from point sampling by electrofishing. Suitability was scored between 0 = habitat never used and 1 = habitat always used by fish in relation to water depth (metres; above) and water velocity (cm per second; below). Abbreviations for phases of 0+ fish are: young larva (YL); juvenile (JUV); juveniles in winter (WINTER).

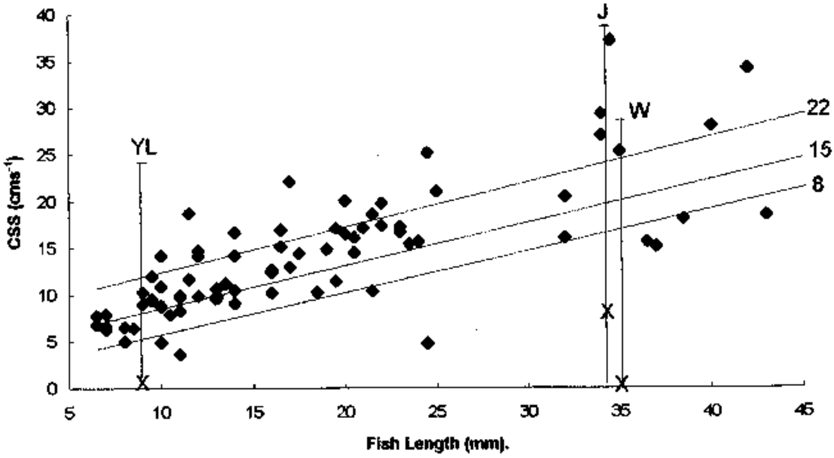

FIG. 8. Critical swimming speeds (CSS) for 0+ roach, measured in an experimental recirculating channel. Diagonal lines represent the best fit to the model: CSS = –3.49 + [0.46 x fish length) + [0.5 x water temperature]. Vertical bars indicate the ranges of swimming speeds and X indicates the optimum swimming speeds (velocities) predicted from Fig. 7 for young larva (YL), juvenile (J) and juveniles in winter (W).

model were combined with real discharge data the results indicated that habitat and availability may comprise 8% of the channel under optimal conditions and as little as *2%* under high flow, winter conditions (Fig. 9).

Large variations in discharge often occur in the River Great Ouse over relatively short time-periods (Fig. 2). Simulation of several channel types revealed that a large percentage of the channel appears to be unsuitable at all discharges and the quantity of suitable habitat available decreases as discharge increases. At low discharges, depth and cover availability control habitat suitability as velocities will be within the range suitable for habitation. As discharge increases, velocity will rapidly increase, owing to the limited spread of the channel, further reducing the availability of suitable habitat. Even at marina sites, where velocity did not increase markedly as discharge increased, the availability of suitable habitat tended to decline owing to the increase in depth of water.

Future research and management

"Compared to similar unregulated rivers . . . the Great Ouse differs by, the absence of salmonids and pelagic spawners, the reduction of. . . rheophilic and limnophilic cyprinids . . . the extreme dominance of generalists."

Copp (1990a)

Lowland regulated rivers represent a degraded habitat primarily owing to the loss of lateral habitat and the reduction of surface slope. As a result, their fish fauna often consists of high densities of a small number of generalist species and low densities of specialist species, the latter often maintained through immigration from more suitable areas (Copp 1990a, 1992b). In the River Great Ouse, regulation has led to the numerical predominance of roach in the lower river and minnow *Phoxinus phoxinus* in the smaller channels (Copp 1992b), although in all reaches the density of fish present is relatively low compared to similar lowland rivers (Anon 1994). Other species, such as the once-abundant bream, appear to be present at low densities, with localised areas of high abundance (Copp 1992b; Anon 1994). There appear to be several explanations for the current fisheries status of the river: loss of habitat diversity and fragmentation (Copp 1992b); a high proportion of habitat unsuitable for fish (particularly 0+ fish; Garner 1996a; Garner 1997b); the absence of suitable prey, resulting in slow growth (Garner et al. 1996; Mann 1997; Mann et al. 1997).

The current situation has resulted from a lack of knowledge of the requirements of fish, ignorance propagated by the view that fisheries represent a self-sustaining resource in what has slowly become a degraded habitat (Boon 1992). If the traditional practice of stocking has made little difference, what other measures can be instigated to preserve and improve the fish community of the River Great Ouse? The results of the above investigations pinpoint habitat loss as a potential cause of the decline in the distribution and populations of specialist species of fish in lowland rivers. To mitigate such impacts a more detailed knowledge of the habitat requirements for the target species at all important life-stages is required - information which is currently absent. For the less specialised species, it would appear that the relatively slow growth rates exhibited in this river may limit the recruitment to the adult population. Increasing the size of the marginal zone may increase the availability of suitable prey, allowing optimal growth (Garner et al. 1996). Perhaps it would be wise to shift the emphasis of fisheries management towards the mitigation of these problems and, in doing so, remove the cause of degraded fish populations rather than treat the symptoms through the introduction of additional fish.

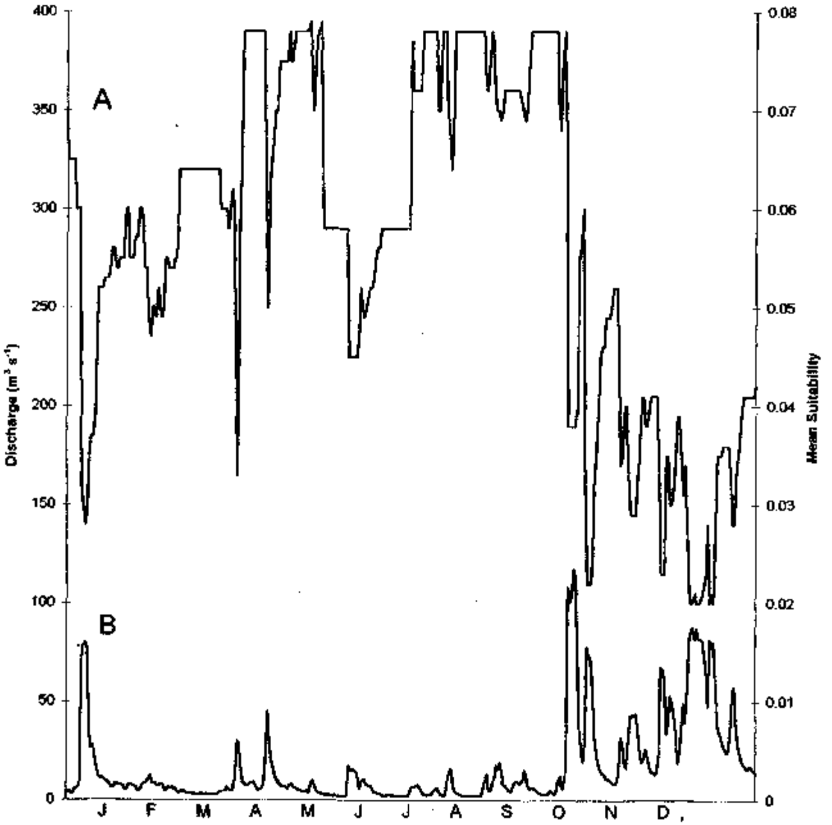

FIG. 9. Habitat availability time-series for the Needingworth main river site (No. 19 in Fig. 1) during 1992. Line A represents the mean site suitability, calculated with the models developed in Fig. 7, plus additional models for habitat suitability in relation to plant cover. The mean suitability of each site multiplied by 100 expresses the suitability of the site as a percentage of all sites studied. The appropriate models were: young larva, 15 May to 30 June; juvenile, 1 July to 30 September and 1 April to 14 May; juveniles in winter, 1 October to 14 May. Line B represents channel discharge (cubic metres per second) at the Needingworth site. (Garner 1997b).

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