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The interaction of low flow conditions and spawning brown trout (*Salmo trutta*) habitat availability

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ABSTRACT

Over-abstraction from surface waters is having a detrimental impact on freshwater dependant ecosystems. Spawning fish are impacted during low flow periods which can be exacerbated by over-abstraction. In this study habitat models were used to assess the impact of low flows on the habitat availability of spawning brown trout. The approach used assesses the habitat availability of spawning brown trout (*Salmo trutta*) as well as that of their biotic dependants: refugia (*Ranunculus fluitans*) and food source (*Ephemeroptera beraeidae*).

The analysis uses fuzzy logic to show how habitat availability changes for the three species over a 32 year period with detailed investigation of the role of hydrological extremes. Critical flows were determined below which habitat availability suffers. Results indicated that wet years provide increased habitat availability for spawning brown trout as an individual species, but when the results are combined with their biotic dependants it becomes clear that more habitat for these is available during drier years. The study highlights the importance of the natural flow regime to the dependent freshwater ecosystem components and understanding different species requirements.

1. Introduction

Low flows in rivers, caused by anthropogenic pressures, impact freshwater dependant ecosystems which are of great importance for human wellbeing due to the services they provide (MEA, 2005; Pander and Geist, 2013). Over-abstraction of freshwater is one of the main anthropogenic threats these ecosystem services face, disrupting the natural flow regime upon which species and habitats depend (Poff et al., 1997). During dry periods, the negative environmental impacts of low flows in rivers are exacerbated by abstraction which leads to a reduction in wetted area, modified water velocities and lower flow depths along the river. These conditions can have a particularly devastating effect on fish populations, increasing fish density and reducing food resources. This affects survival rates, the reproduction and emigration of fish and ultimately creates a loss in fish habitats (Armstrong et al., 2003; Benejam et al., 2009). The basic water quantity requirements for salmonid fish are well researched and include adequate: flows (at appropriate times of the year), water depths, and flow velocities for spawning fish (Hendry et al., 2003). A reduction in the numbers of spawning fish has been identified during low flow years (Jonsson and Jonsson, 2009). This has been attributed to low flows causing increased sediment deposition smothering vital spawning grounds and limiting macrophyte growth, a vital source of food and refugia (Hendry et al., 2003; S&TA, 2014). Knowing how low flows impact habitat availability is a key challenge as a change in the natural flow regime does not only directly impact upon fish but can indirectly affect the species which interact with them such as the predators, competitors and prey (Armstrong et al., 2003). Many studies have aimed to quantify the habitat requirements of brown trout (*Salmo trutta*) and their flow requirements are relatively well understood due to their economic importance (Acreman et al., 2008). However with the increasing threats of over-abstraction, investigating and understanding habitat availability for brown trout and its biotic dependents during periods of hydrological drought is important.

Using physical habitat models to predict how changes in flow affects habitat availability is a well-established and successful technique (Dunbar et al., 2007). Habitat models provide structure to investigate interacting hydraulic processes and their influence on habitat distribution (Dunbar et al., 2012). A main assumption used in this type of modelling is that physical habitat such as velocity and depth is the limiting factor determining species distribution (Milhouse and Waddle, 2012). In reality more factors affect the species and related habitat. This has led to criticism of such approaches as the results represent an incomplete analysis of potential impacts to species of flow changes (Orth, 1987). For

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example, shade is important to brown trout, but may lead to a reduction in benthic macro-invertebrates and thus food availability (Armstrong et al., 2003; Booker et al., 2004). Therefore good habitat predicted by a habitat model for one species may not be a preferred environment due to the lack of available food sources. A key challenge for the future and development of habitat modelling is to understand, and integrate the numerous spatial and temporal, abiotic and biotic factors affecting fish (Fig. 1) and then translate these into models (Maddock, 1999).

Brown trout in the UK most commonly spawn between October and December (Armstrong et al., 2003), which is a key time in their lifecycle. During this time ideal hydraulic conditions include relatively low depths and low velocities. Studies have shown however that a range of depths and velocities exist which encourage spawning but that minimum flows exist, below which spawning does not occur (Armstrong et al., 2003). Bagenal (1969) discovered from lab based experiments that better fed brown trout contained significantly more eggs and that a reduced diet lead to a lower fecundity. Other studies have shown significant correlations between trout abundance and invertebrate biomass and Weighted Usable Area (WUA) (i.e. hydraulic habitat availability). Invertebrate biomass was found to be the single most important factor in determining brown trout abundance (Jowett, 1992) with suitable living space, including cover, the second most important factor (Jowett, 1992). Consequently adequate food and refugia are of great importance alongside appropriate hydraulic conditions.

The aim of this study was to determine the impacts that low flow has on spawning brown trout habitat availability. The method presented investigates the wider biotic controls on brown trout habitat, alongside the standard abiotic. The work uses results from the physical habitat model CASiMiR (Mouton et al., 2007) to show how low flows affect spawning brown trout habitat availability in conjunction with habitat models investigating refugia (macrophytes: *Ranunculus fluitans*) and food source (Macro-invertebrates: Mayfly: *Ephemeroptera beraeidae*) habitat availability. For the purposes of this paper it is assumed refugia and food sources have equal weighting with regards to brown trout habitat availability. By linking best available habitat (temporally and spatially) for all three species, the conditions which result in the optimum habitat availability for spawning brown trout can be analysed and some of the complex interactions between fish, their food source (*E. beraeidae*) and refugia (*Ranunculus*) can be understood.

2. Methods

2.1. Study area

The study focussed on the River Nar, a chalk stream in Norfolk in the South-East of England. Its distinctive progression from a chalk to fen stretch of the river gives the river a Site of Special Scientific Interest (SSSI) designation, with the chalk reach being particularly sensitive to low flows. Despite its status of high conservation value, it has been historically modified along most of its length. Abstraction, diffuse pollution and the legacy of channel modifications all contribute to pressures on the ecology of the river. Abstraction is a significant problem in the river Nar; the lower river (downstream of Narborough) is classified as 'over-licensed', whilst the upper river is classified as 'over-abstracted' by the Environment Agency (EA) (EA, 2005). During the most extreme hydrological drought year on record (1991) at Marham the river failed its flow targets as set for the water framework directive (WFD) to reflect the sensitivity of ecology in the river (Norfolk Rivers Trust, 2013). The river is approximately 42 km in length with one gauging station at Marham, situated at around the dividing point between chalk and fen sections (Fig. 2). The mean flow at Marham is 1.14 m^3/s. The highest and lowest recorded flows between 1953 and 2014 are 7.8 m^3/s and 0.14 m^3/s, respectively. High (Q_{10}) and low (Q_{90}) flow parameters for this period are 2.02 m^3/s and 0.47 m^3/s, respectively. Due to the underlying chalk, the river has a high Base flow index (BFI), which is typical of pure chalk streams (Norfolk Rivers Trust, 2013). The river is host to a diverse range of aquatic species. Brown trout (*S. Trutta*) are of particular importance in the river and are considered highly valuable by the local fisherman. The river provides good habitat for a large range of benthic-macroinvertebrate and a rich abundance of chalk stream macrophytes such as water

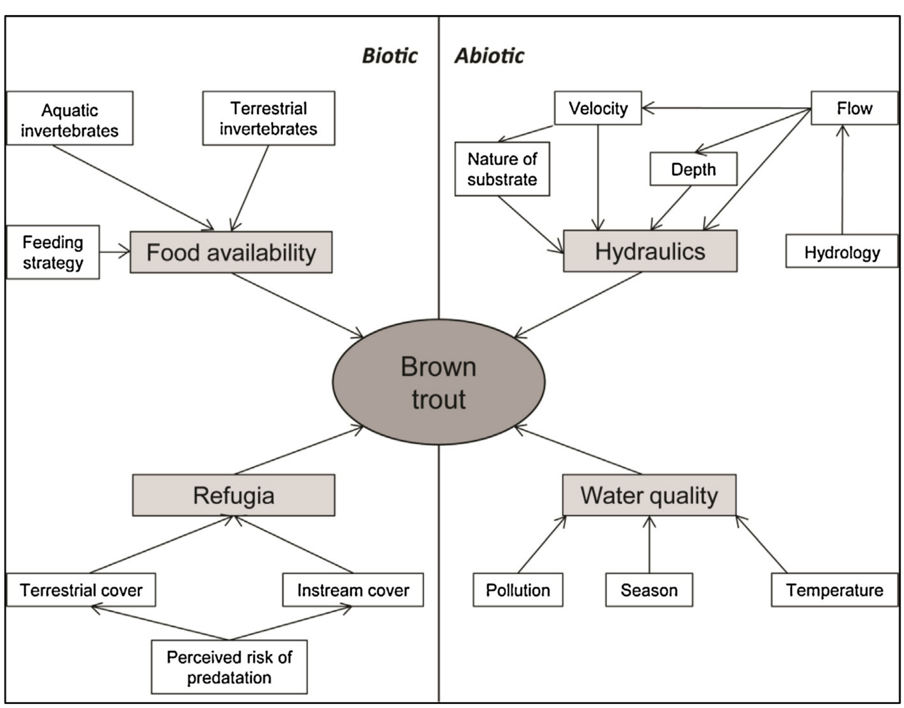

Fig. 1. Factors affecting brown trout habitat availability.

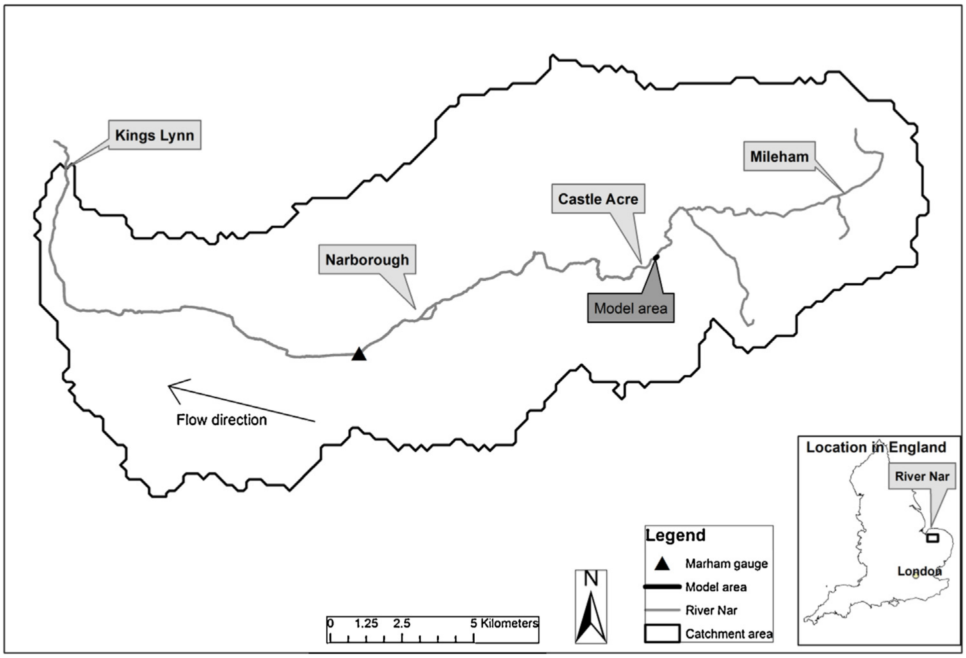

Fig. 2. River Nar catchment, model area and location in England.

crowfoot (*Ranunculus*). A study reach of 500 m was chosen for the research given its importance for spawning fish (Fig. 2).

2.2. Data collection

Data collection was undertaken in May 2013 for cross-section, velocity and flow data. To measure these, an M9 RiverSurveyor was used which uses laser beams to measure the bathymetry of the channel and subsequently water levels and velocities. Further data collection occurred in May 2014 for substrate and cover values as well as vegetation mapping following British Standard EN 14184; 'Water quality—Guidance for surveying of aquatic macrophytes in running waters' (European Standard, 2003). This recorded the occurrence and abundance of *Ranunculus*. The substrate values used are based on the Wentworth scale and the cover values were as specified in CASiMiR (Bovee, 1986) (Table 1). Light Detection and Ranging (LiDAR) data used for riparian topography was available from the Geomatics Group (Environment Agency) from 2012.

Table 1
Substrate and cover values used.

Substrate types	Index (–)	Cover types	Index (–)
Organic material, detritus	0	No cover	0
Silt, clay, loam	1	Aquatic plants	1
Sand <2 mm	2	Stones/detritus	2
Fine gravel 2–6 mm	3	Roots	3
Medium gravel 6–20 mm	4	Deadwood	4
Large gravel 2–6 cm	5	Wet branches	5
Small stones 6–12 cm	6	Dry branches	6
Large stones 12–20 cm	7	Floating macrophytes	7
Boulders >20 cm	8	Turbulence	8
Rock	9	Undercut banks	9
		Overhanging grass	10

2.3. Hydraulic model

The one-dimensional (1D) hydrodynamic software Flood Modeller provided hydraulic input (depth, velocity and flow) to CASiMiR. Flood Modeller solves the one-dimensional Saint Venant equations to predict flows in open channels in both steady and unsteady state (CH2M Hill, 2015). The model extends from upstream of Castle Acre to Narborough (Fig. 2). A 1D, rather than 2D model was employed as the focus of the study was in the upper reaches of the river. This area is morphologically uniform and therefore a 1D model was representative of the channel.

The model was built using river channel bathymetry data surveyed in May 2013 and LiDAR data (2012) covering the floodplain. Forty cross sections were measured and in addition to main channel geometry these captured water depth (m) and velocity (m/s). Model calibration for in-channel flows (May 2013) was undertaken using measured water level data and a Mannings *n* of 0.05 estimated which resulted in water levels within $\pm$ 0.25 m. Gauged flows from Marham (1980–2011) were used to determine the upstream flow conditions. The model provided hydraulic output for the habitat model which concentrated on average and normal flow conditions; consequently calibration for in-bank flows only was sufficient for this study.

2.4. Habitat model

CASiMiR 1D (Schneider et al., 2010) was used to build a habitat model of the site for the modelled period (1980–2011). The 32 year modelled period captured a variety of historical hydrological regimes from hydrological drought periods to higher flow periods. Habitat preferences were determined by expert knowledge and set using fuzzy rules (Schneider et al., 2010). Geometry data from the May 2013 survey and in-stream vegetation, cover and substrate data from the May 2014 survey were used to construct the model. Water surface profiles were extracted from the hydraulic model for the site.

For habitat suitability data, fuzzy logic rules were used to expresses non-linear relationships between ecological variables in a transparent manner (Muñoz-Mas et al., 2012). The biotic variables used were; water depth, velocity, substrate and cover (i.e. in-stream vegetation). These variables are generally considered the most important microhabitat variables in determining habitat selection (Louhi et al., 2008). Fuzzy rule and set determination for each species is described below, final fuzzy rules and sets are presented in Appendices A and B, respectively.

Two main outputs from CASiMiR were used for analysis:

- Spatial distributions of suitability Index (SI) (m^2). This provides information on the area available for each different habitat value on a scale from 0 (no habitat availability) to 1 (maximum habitat availability).
- Hydraulic Habitat Suitability (HHS) (–). This is determined by dividing WUA (the reaches total habitat suitability related to a flow rate obtained by multiplying the area of each mesh cell by the SI value) by the wetted area. This eliminates the effect of changing discharges and allows comparisons between different sites as wetted areas are negligible (Schneider et al., 2010).

*2.4.1. Spawning brown trout (*Salmo trutta*)*

The relationship between spawning brown trout and flow conditions has been well researched, therefore fuzzy rules and sets were derived based on those available in the literature. Generally low velocities (0.2–0.55 m/s) and low depths (0.15–0.45 m) are preferred (Witzel and Maccrimmon, 1983; Louhi et al., 2008). Whilst cover is important for spawning brown trout (Armstrong et al., 2003), cover was not included as a variable in the fuzzy rules as it is considered for brown trout using refugia (Section 2.4.2). Substrate is known to be an important factor for spawning brown trout (Armstrong et al., 2003), the substrate must be sufficiently unconsolidated for the fish to penetrate in order to make the redd. Crisp and Carling (1989) determined that brown trout used gravel and sand for spawning but mostly pebbles with a median grain size of 20–30 mm therefore medium gravel was considered the preferable substrate.

*2.4.2. Refugia (*Ranunculus fluitans*)*

Fuzzy rules for refugia (*R. fluitans*) were provided by CASiMiR and validated to the river based on field observations and available literature. A high velocity with a medium depth was determined as preferential based on literature (Dawson, 1973; Spink, 1992). *R. fluitans* requires stable substrate of coarse gravel and pebbles and moreover silt provides the least preferable habitat conditions for the species (Cranston and Darby, 2004). Therefore a preferential substrate of gravel was chosen rather than silt and sand, based on literature.

The field survey results used for validation of the fuzzy rules to the river conditions indicated most *R. fluitans* is found in medium substrates and none was found in silt or sand. Most *R. fluitans* was found in depths of 0.4–0.8 m and in velocities of 0.1 to 0.3 m/s. This therefore corresponded well to literature findings.

*2.4.3. Food source (*Ephemeroptera beraeidae*)*

The food source data for Mayfly (*E. beraeidae*) were developed based on fuzzy rules for the family of Mayfly and then validated to the River Nar based on collected data. Within CASiMiR velocity, substrate and FST hemisphere curves define the mayfly habitat (Kopecki, 2008). FST values (number depicting hydraulic stress acting on Benthos species, Kopecki, 2008) were provided by CASiMiR. The FST fuzzy set is demonstrated in Appendix B, this shows how the FST curve corresponds to the fuzzy sets.

Two depths were specified; medium and low. Medium (<1 m) was established as preferred. The highest abundances of Mayfly were found in depths of 0.6–1 m in the collected data from the River Nar and therefore the findings correspond well to the environmental conditions in the river. It is commonly understood that a reduction in flow causes a reduction in water levels and velocities, this in turn decreases available habitat and reduces habitat diversity, therefore neither low depths are low velocities were preferred (Dewson et al., 2007). Literature determined that Mayfly have a preference for velocities over 0.75 m/s and 0.56 m/s (Jowett, 1990; Kopecki, 2008), the highest abundances of Mayfly found in the river were however found at around 0.2 m/s, the fuzzy rules were therefore adapted to represent this. Medium substrate (under an index of 4—Table 1) provide poor habitat, and high substrate (over an index of 4—Table 1) provides good habitat (Jowett, 1990). FST numbers were supplied by CASiMiR for *E. beraeidae*. These are shown in the FST fuzzy set in Appendix 2. 'Low' FST was given medium suitability, 'medium' FST was given very high suitability, 'high' FST was given medium suitability and 'very high' FST was given low suitability.

Table 2
Suitability scales for HHS total habitat availability. .

Suitability scale	Corresponding HHS values (–)
Very good suitability	0.81–1
Good suitability	0.61–0.8
Moderate suitability	0.41–0.6
Poor suitability	0.21–0.4
Very poor suitability	0–0.2

2.5. Data analysis

Four main areas of analysis took place as described below, which used SI values and HHS scores.

2.5.1. Habitat availability and critical flows

Results were analysed on the HHS scale to determine the quality of the habitat availability in the study reach. The average HHS for each species was calculated and a corresponding HHS suitability scale was determined (Table 2). The range of results over the 32 year period were then analysed by categorising the results into three even bins (upper, middle and lower) to inform the understanding of the spread of predicted habitat suitability. For example if a species had a total range of results between HHS 0.3 and 0.6 i.e. varying between poor suitability and moderate suitability, this was binned into:

- Upper habitat category (0.5–0.6),
- Middle habitat category (0.4–0.49),
- Lower habitat category (0.3–0.39).

This therefore showed what percentage of the total habitat suitability was in the upper, middle and lower regions of the total HHS suitability. Finally critical flows below which habitat availability became compromised for all three species were determined based on the flow at which 'low' habitat occurs.

2.5.2. Seasonal habitat

The binned results were analysed to understand the interaction between the habitat for the three species to determine the time spent in each of the 27 (Table 3) different combinations (upper, middle and lower bin) of habitat availability for different hydrological years and seasons (wettest, driest and average). For example, one scenario would be 'upper' availability for spawning brown trout, 'lower' availability for food sources and 'middle' availability for refugia. The wettest and driest seasons and years were determined based on number of days above Q_{10} and below Q_{90}. Average years have a mean flow close to the 32 year Q_{50} (0.49 m^3/s). Table 4 records the years used for each season. Of the 27 combinations, only seven (highlighted in grey in Table 3) revealed results; the

Table 3
Combination of binned results. Grey highlights indicate scenarios which occurred for this site, all values not highlighted did not occur.

Scenario	Spawning brown trout	Refugia (*Ranunculus fluitans*)	Food (*Ephemeroptera beraeidae*)
1	Upper	Upper	Upper
2	Upper	Upper	Middle
3	Upper	Upper	Lower
4	Upper	Middle	Upper
5	Upper	Middle	Middle
6	Upper	Middle	Lower
7	Upper	Lower	Upper
8	Upper	Lower	Middle
9	Upper	Lower	Lower
10	Middle	Upper	Upper
11	Middle	Upper	Middle
12	Middle	Upper	Lower
13	Middle	Middle	Upper
14	Middle	Middle	Middle
15	Middle	Middle	Lower
16	Middle	Lower	Upper
17	Middle	Lower	Middle
18	Middle	Lower	Lower
19	Lower	Upper	Upper
20	Lower	Upper	Middle
21	Lower	Upper	Lower
22	Lower	Middle	Upper
23	Lower	Middle	Middle
24	Lower	Middle	Lower
25	Lower	Lower	Upper
26	Lower	Lower	Middle
27	Lower	Lower	Lower

remaining 20 combinations resulted in 0 days per year under those conditions.

2.5.3. Extreme years

In order to understand the distribution of habitat availability spatially, the distributions of SI values, rather than HHS values, were used to investigate the influence of low flows on habitat availability by comparing wet and dry years. The SI values were categorised as shown in Table 5 into: highly unsuitable, unsuitable, moderate, suitable and highly unsuitable. Then per wet and dry year the percentage of time in each of these categories was derived.

Mann- Whitney statistical tests compared habitat availability between years to investigate whether there were statistically significant differences between wet and dry years and seasons. Table 4 shows the years used for each wet, dry and average condition.

2.5.4. Spatial distribution

Spatial analysis showed how the habitat availability varied spatially for the Q_{50} flow for each species. The habitat availability maps were output for each species and discussed.

3. Results

The results (Fig. 3) indicate that for the study site spawning brown trout have 'good suitability' habitat classification availability (mean = 0.64, SD = 0.03) whilst refugia (*R. fluitans*) (mean = 0.53, SD = 0.05) and food (*E. beraeidae*) (mean = 0.48, SD = 0.01) both have only 'moderate suitability' habitat availability (Table 2) throughout the 32 year period (1980–2011). The driest flow on record, 1991, shows the habitat availability for refugia (*R. fluitans*) and food (*E. beraeidae*) significantly drop in this year. The available habitat for spawning brown trout however remains fairly high during this period, which is related to their preference for lower flows (Louhi et al., 2008). Habitat availability for all three species are generally negatively skewed towards the upper bin, with fish, food (*E. beraeidae*) and refugia (*R. fluitans*) reporting 98.3%, 84.3%, 71.1% of the time in the 'upper' category (Fig. 4). The results for the critical flow analysis are demonstrated in Fig. 5 and are based on the binned data. These results show that the critical flows for spawning brown trout and their biotic dependents are 0.18 m^3/s and 2 m^3/s, this is further discussed in Section 4.

The results of the seasonal analysis are presented in Fig. 6. Scenario 1, where all three species record good habitat availability is dominant during wet winters and average/wet springs. Overall scenario 1 (upper, upper, upper) and 2 (upper, upper, middle) occurs most frequently during average flow years and scenario 23 (lower, middle, middle) occurs most frequently during wet winters.

The results of the extreme year analysis are shown in Fig. 7. As can be seen each species responds differently to the wet and dry years often with large differences. The Mann–Whitney tests revealed that for spring and summer seasons the predicted habitat availability was statistically similar ($p > 0.05$) between hydrologically similar years and statistically different ($p < 0.05$) between dry and wet years.

For the spatial distribution analysis, the results (Fig. 8) showed that the middle of the reach tends to provide the best availability for all species (SI = 0.8/0.9), while the downstream reaches provide SI's of around 0.3/0.4 for food (*E. beraeidae*) and refugia (*R. fluitans*) however slightly higher availability for spawning brown trout.

Table 5
Suitability scales for spatial habitat availability (SI values).

Suitability scale	Corresponding SI values (–)
Highly suitable	0.81–1
Suitable	0.61–0.8
Moderate suitability	0.41–0.6
Unsuitable	0.21–0.4
Highly unsuitable	0–0.2

4. Discussion

This paper aimed to illustrate the importance of modelling the three species individually to show the overall habitat availability of spawning brown trout. It is key to model the three species separately to show the complexity and the seasonality of each species.

The results from the habitat availability show that the flow at which the habitat availability falls into the lower bin for brown trout, food (*E. beraeidae*) and refugia (*R. fluitans*) is 0.1 m^3/s, 0.13 m^3/s and 0.18 m^3/s, respectively (Fig. 5). Using these flows it

Table 4
Years used for hydrological seasons. These were based on most number of days at or above Q_{10} for wet years and at or above Q_{90} for dry years. Average seasons were determined based on most days closest to the mean flow.

Winter			Spring			Summer			Autumn		
Dry	Wet	Average	Dry	Wet	Average	Dry	Wet	Average	Dry	Wet	Average
1990	1988	1986	1990	1981	1984	1990	1980	1982	1989	1987	1983
1991	1994	1987	1991	1988	2002	1991	1981	1994	1990	1993	1985
1992	1995	1993	1992	1994	2003	1992	1987	2000	1991	1998	1988
1996	2001	1998	1996	1998	2007	1996	2001	2004	2009	2000	1999
2006	2003	2005	2011	2001	2010	2011	2007	2008	2011	2002	2010

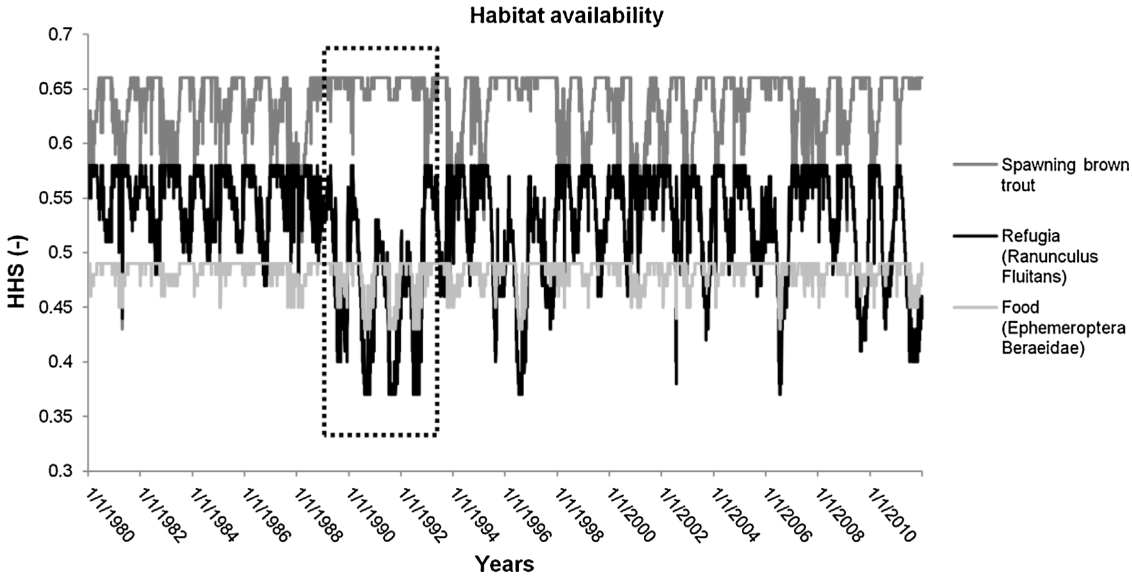

Fig. 3. Habitat availability (HHS (−)) for all 3 indicator species from 1980 to 2011.

is possible to identify that a critical flow for this section of the river is in the order of 0.18 m^3/s to protect overall habitat for spawning brown trout. The upper flow limit which resulted in reduced habitat availability is 2 m^3/s, 3.7 m^3/s and 4.3 m^3/s, (for fish, refugia and food respectively). Thus flows over 2 m^3/s results in less habitat availability for spawning brown trout and its biotic dependents. Low flow policies (the hands-off-flow (HOF)) limit water abstractions based on a Q_{33} at Marham. The HOF corresponds to a flow

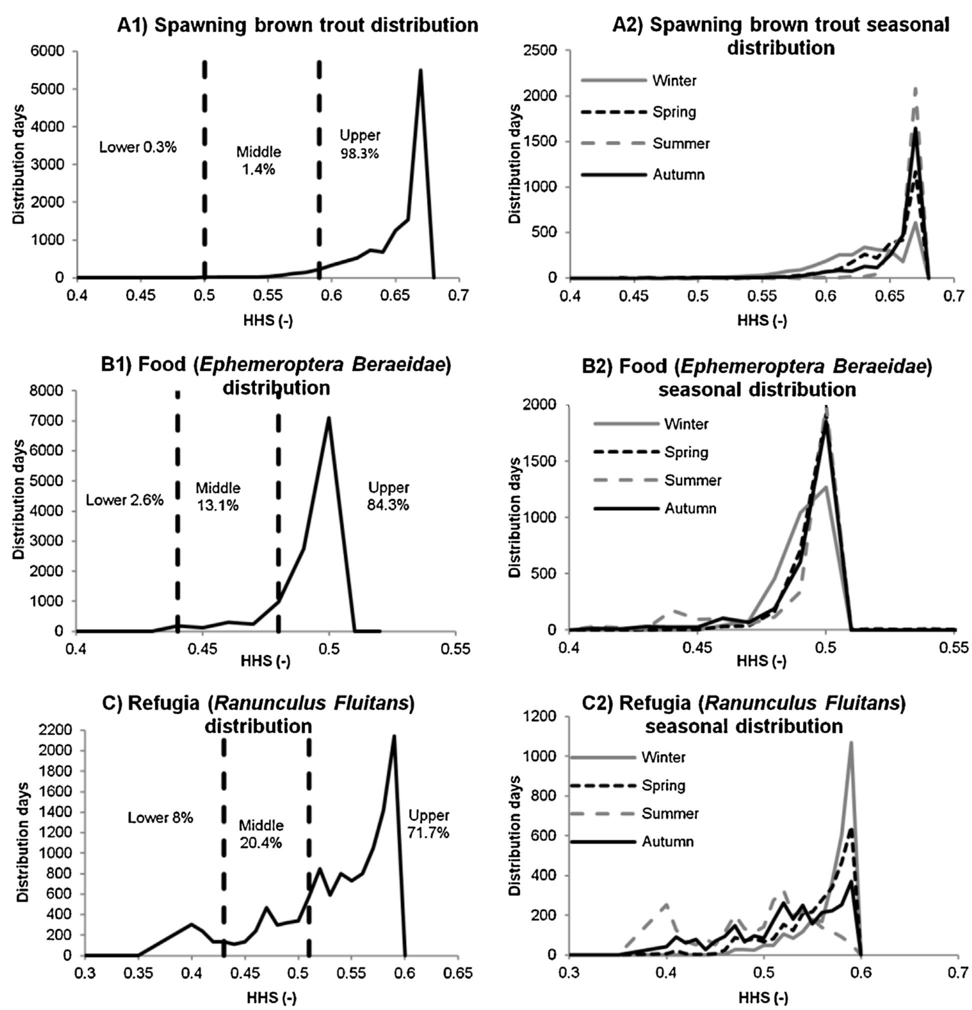

Fig. 4. Seasonal habitat distribution throughout the 32 year period (1980–2011). Compartmentalised into 'lower', 'middle', and 'upper' bins.

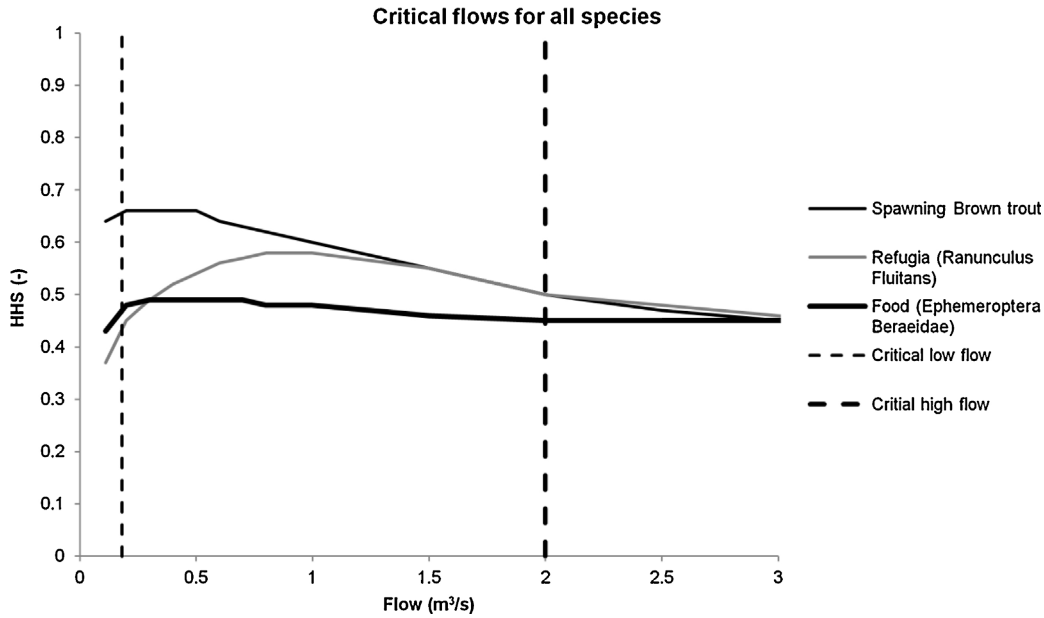

Fig. 5. Critical flows for spawning brown trout based on point at which habitat availability becomes 'low' for spawning brown trout and its biotic dependants.

of 0.63 m^3/s at this section of the river. Thus this limit does adequately protect spawning brown trout and its biotic dependents. The spawning brown trout results are therefore the limiting factor for the upper flow and the refugia are the limiting factor the lower flows, this demonstrates the importance of including more biotic parameters when determining low flow policies.

For the seasonal analysis, the results indicated that wet winters provide the worst habitat availability for all species combined. By looking at more detail at different seasons, this allows greater appreciation of the complexity. It is clear that dry winter/spring seasons impact on food (*E. beraeidae*) habitat availability, with these being more sensitive to flow changes than the other species. Wet summer and autumn periods provide good habitat for all three species, however if these periods are dry then habitat availability for both refugia (*R. fluitans*) and food (*E. beraeidae*) become compromised.

For the extreme year analysis, generally for all species the Mann–Whitney test revealed that for spring and summer seasons the predicted habitat availability was statistically similar ($p < 0.05$) between hydrologically similar years and statistically different ($p < 0.05$) between dry and wet years. Consequently for spring and summer season habitat availability in wet and dry years provide

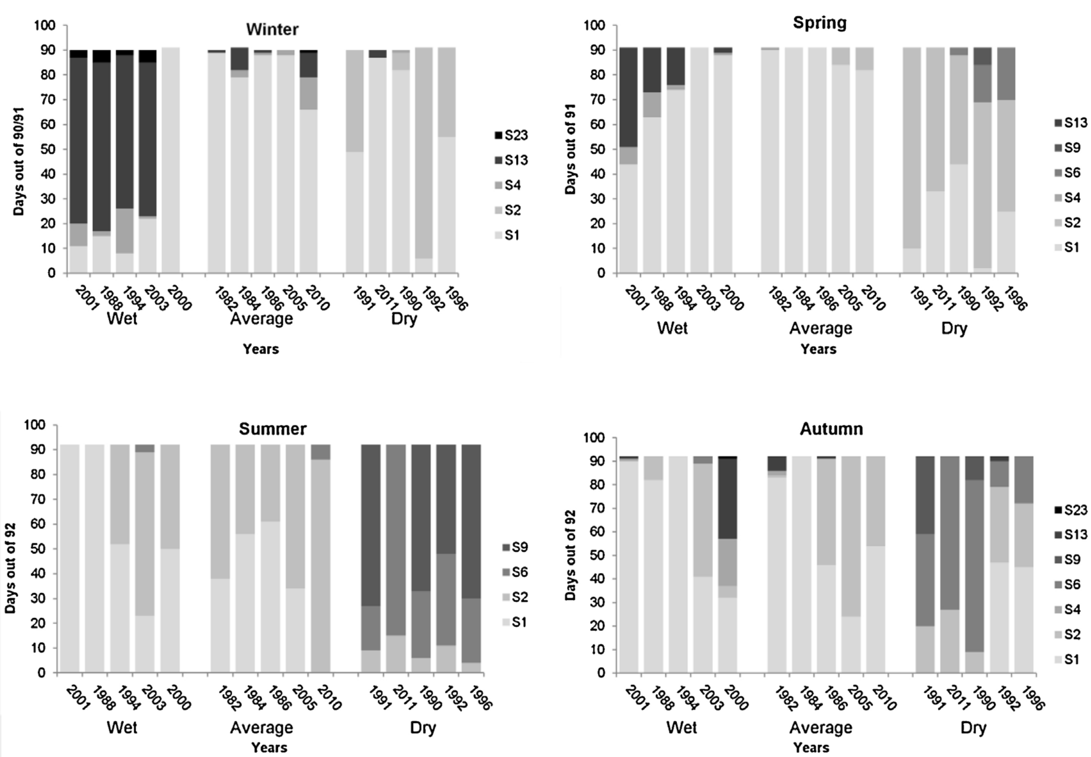

Fig. 6. Seasonal analysis showing number of days in each year (wet, dry and average) in each category (for categories see Table 3).

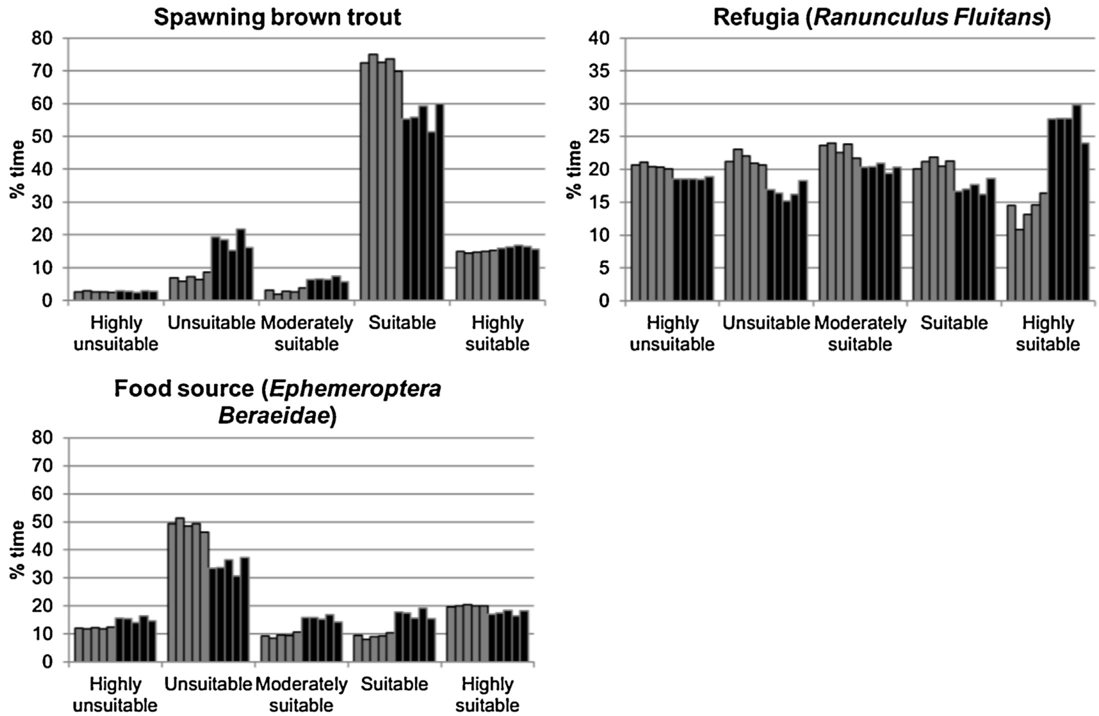

Fig. 7. Habitat suitability (based on SI values) in wet and dry years: grey = dry (1990, 1991, 1992, 1996, 2011), black = wet (1988, 1994, 2000, 2001, 2003).

statistically different habitats. For fish this difference is specifically seen for the unsuitable, suitable and highly suitable categories. During wet years a higher proportion of time is spent in the unsuitable category and during drier years, the results tended towards suitable or highly suitable habitat suitability.

Looking at the habitat suitability for refugia (*R. fluitans*), during dry years the results tended to lower classes while wetter years had a greater proportion of highly suitable habitat. It must be noted that the difference between different hydrological years was particularly pronounced during the summer

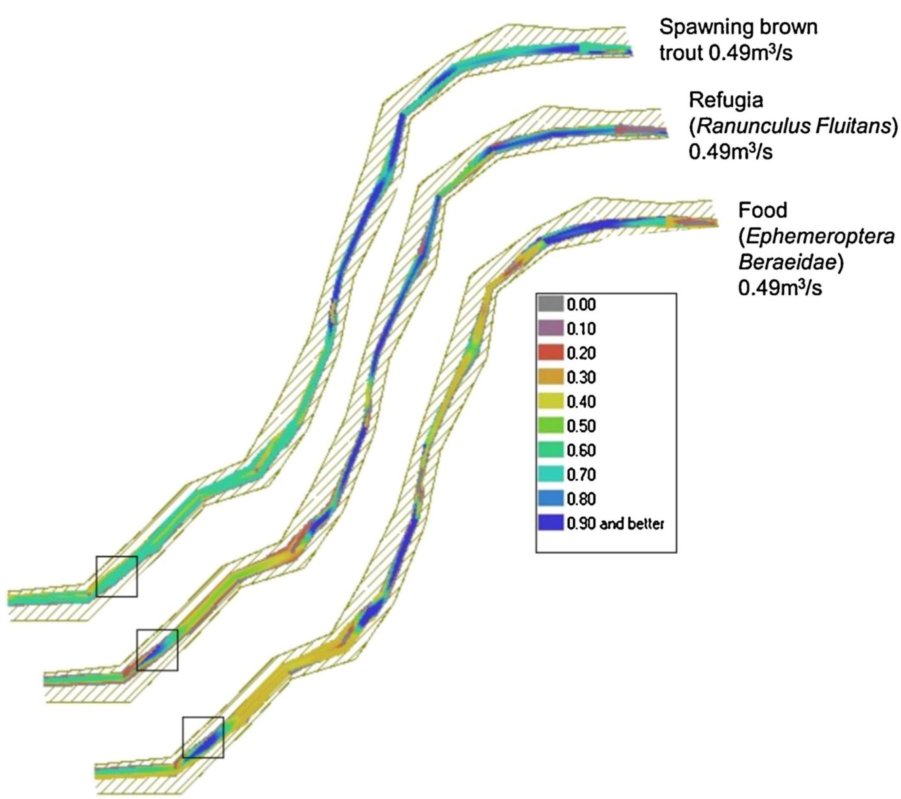

Fig. 8. Spatial distribution of habitat availability for Q_{50}. Box showing area where suitability of brown trout would be higher than the model predicts based on availability of its biotic dependants.

season for this species, whilst the trend was much weaker during spring.

Finally for food (*E. beraeidae*), the habitat suitability tended to be poorer (unsuitable) during dry years, whilst wet years offered better (suitable) habitat. These results indicate that for spring/summer seasons while wet years favour food (*E. beraeidae*) and refugia (*R. fluitans*) habitat, drier years are preferred by spawning fish. Additionally it is clear that a dry year has statistically different habitat suitability to a wet year (habitat is statistically similar between hydrologically similar years).

However, for autumn and winter seasons the predicted habitat availability was statistically different between hydrologically similar years according to the Mann–Whitney tests. Consequently there were no clear differences resulting from dry or wet conditions during these seasons.

Overall this analysis suggests that different conditions are preferred by different species and that low flows during dry years are good for spawning fish however these conditions provide less habitat availability for refugia (*R. fluitans*) and food (*E. beraeidae*). The Mann–Whitney tests reveal that these observations are robust for spring and summer results however are less evident for winter and autumn.

The spatial distribution analysis was important to show if the habitat availability for spawning brown trout would in reality be higher or lower in certain areas than the model predicts. There is a small area towards the bottom of the reach (shown in the black box) where the SI increases to 0.9 for food (*E. beraeidae*) and refugia (*R. fluitans*) indicating a hotspot for these species, but interestingly not for spawning brown trout. This is due to a combination of hydraulic conditions (depth and velocity) being present which is preferred by food (*E. beraeidae*) and refugia (*R. fluitans*) but not by spawning brown trout. This hotspot is of importance as whilst the habitat model for spawning fish predicts that area to have low suitability, the fish are still likely to use the area in a transient manner due the presence of the biotic variables. Analysis of the spatial distribution of habitat varies for reach flow conditions as a function of the species requirements. However what is important to note is that an overlap of hotspots for habitat for all three species does occur within the reach.

5. Conclusions

This paper has investigated the interplay between spawning brown trout and its dependents (refugia and food) and found that understanding the habitat availability of spawning brown trout in isolation does not provide a full picture of the potential interactions associated with its resilience to low flow periods. Consequently, the work has highlighted the importance of combining the biotic dependents of particular species in any investigation, as where there is high available habitat for one species there may be low availability for its dependents, and it is understanding these that allows scientists to appreciate the flow requirements of any river reach.

Overall this section of river provided reasonable habitat for spawning brown trout including their biotic dependants of food (*E. beraeidae*) and refugia (*R. fluitans*). Flow has been shown as an important factor in habitat availability for spawning brown trout; this was demonstrated particularly during the hydrological drought of 1991–1992 where availability for spawning brown trout remained relatively high whilst availability for food (*E. beraeidae*) and refugia (*R. fluitans*) decreased.

Ultimately low flow conditions do have an impact on habitat availability for spawning brown trout, as whilst habitat models may predict the available habitat for spawning brown trout to remain relatively stable, the habitat availability for their biotic dependants reduces, indicating that the overall available habitat would decrease. This highlights the importance of protecting flows for a wide range of species rather than only one species.

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Appendix A.

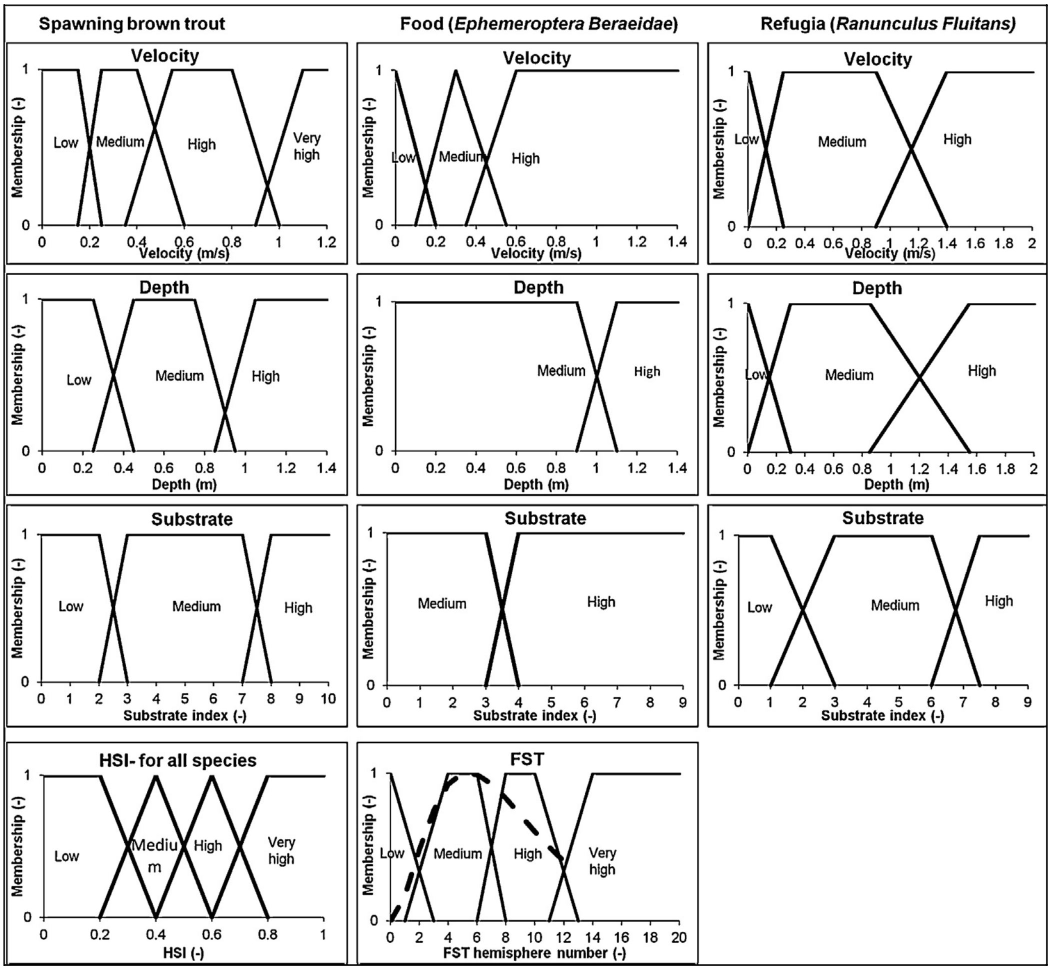
Fuzzy rule base describing habitat suitability for the three different species: spawning brown trout, Refugia (*Ranunculus Fluitans*) and Food (*Ephemeroptera Beraeidae*).

Parameter			Species		Parameter				
V	*D*	Sub	*S* spawning BT	*S* Ran no cover	*V*	*D*	Sub	FST	*S* EB
H	H	H	L	L	L	M	M	L	L
H	H	M	M	M	L	M	M	M	M
H	H	L	L	L	L	M	M	H	L
H	M	H	L	M	L	M	M	VH	L
H	M	M	VH	H	L	M	H	L	M
H	M	L	H	L	L	M	H	M	H
H	L	H	L	L	L	M	H	H	M
H	L	M	VH	M	L	M	H	VH	L
H	L	L	H	L	L	H	M	L	L
M	H	H	L	L	L	H	M	M	L
M	H	M	M	M	L	H	M	H	L
M	H	L	L	L	L	H	M	VH	L
M	M	H	L	M	L	H	H	L	L
M	M	M	H	VH	L	H	H	M	M
M	M	L	H	M	L	H	H	H	L
M	L	H	L	L	L	H	H	VH	L
M	L	M	H	M	M	M	M	L	L
M	L	L	H	L	M	M	M	M	H
L	H	H	L	L	M	M	M	H	M
L	H	M	M	L	M	M	M	VH	L
L	H	L	L	L	M	M	H	L	M
L	M	H	L	L	M	M	H	M	VH
L	M	M	H	L	M	M	H	H	H
L	M	L	M	L	M	M	H	VH	L
L	L	H	L	L	M	H	M	L	L
L	L	M	H	L	M	H	M	M	L
L	L	L	M	L	M	H	M	H	L
VH	H	H	L	n/a	M	H	M	VH	L
VH	H	M	L	n/a	M	H	H	L	L
VH	H	L	L	n/a	M	H	H	M	H
VH	L	H	L	n/a	M	H	H	H	M
VH	L	M	M	n/a	M	H	H	VH	L
VH	L	L	L	n/a	H	M	M	L	M
VH	M	H	L	n/a	H	M	M	M	H
VH	M	M	M	n/a	H	M	M	H	M
VH	M	L	L	n/a	H	M	M	VH	L
					H	M	H	L	M
					H	M	H	M	VH
					H	M	H	H	H
					H	M	H	VH	L
					H	H	M	L	L
					H	H	M	M	M
					H	H	M	H	L
					H	H	M	VH	L
					H	H	H	L	M
					H	H	H	M	H
					H	H	H	H	M
					H	H	H	VH	L

V = velocity, *D* = depth, Sub = substrate, *S* = suitability, BT = brown trout, Ran = Ranunculus, EB = *Ephemeroptera Beraeidae*, H = high, M = Medium, L = Low, VH = Very high.

Appendix B.

Membership functions of the input variables flow velocity, depth, substrate and FST and the output variable Habitat Suitability Index for all species: spawning brown trout, Refugia (*Ranunculus fluitans*) and Food source (*Ephemeroptera beraeidae).* The curve in the FST fuzzy set for food represents the FST curve to demonstrate how the fuzzy sets correspond to it.



References

Acreman, M.C., Dunbar, M.J., Hannaford, J., Mountford, O., Wood, P.J., Holmes, N., Cowx, I., Noble, R., Extence, C., Aldrick, J., King, J., Black, A., Crookall, D., 2008. Developing environmental standards for abstractions from UK rivers to implement the EU water framework directive. Hydrol. Sci. 53 (6), 1105–1118.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., Milner, N.J., 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. 62 (2), 143–170.

Bagenal, T., 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. J. Fish Biol. 1, 167–182.

Benejam, L., Angermeier, P., Munne, A., Garcia-Berthou, E., 2009. Assessing effects of water abstraction on fish assemblages in Mediterranean streams. Freshwater Biol. 55, 628–642.

Booker, D.J., Dunbar, M.J., Acreman, M.C., Akande, K., Declerck, C., 2004. Habitat assessment at the catchment scale; application to the River Itchen, UK. In: Hydrology: Science & Practice for the 21st Century. Volume II. British Hydrological Society.

Bovee, K., 1986. Development and Evaluation of Habitat Suitability Criteria for use in the Instream Flow Incremental Methodology, Instream Flow Information Paper No. 21. Biological Report, vol. 89, 7.

CH2M Hill, 2015. ISIS 1D, ⟨https://www.floodmodeller.com/en-gb/products/desktop/r/legacy-software/2/isis-1d/⟩ (accessed on 15/1/15), (Online).

Cranston, E., Darby, E., 2004. Ranunculus in Chalk Rivers Phase 2. Environment Agency, Bristol (accessed on).

Crisp, D., Carling, P., 1989. Observations on siting, dimensions and structure of salmonoid redds. J. Fish Biol. 34, 119–134.

Dawson, F., 1973. Macrophyte production in chalk streams. In: Seminar on the Ecology of Chalk Streams.

Dewson, Z., James, A., Death, R., 2007. A review of the consequences of a decreased flow for instream habitat and macroinvertebrates. J. North Am. Benthol. Soc. 26 (3), 401–415.

Dunbar, M.J., Acreman, M.C., Kirk, S., 2007. Environmental flow setting in England and Wales: strategies for managing abstraction in catchments. Water Environ. 18 (1), 6–10.

Dunbar, M.J., Alfredsen, K., Harby, A., 2012. Hydraulic-habitat modelling for setting environmental flow needs for solmonids. Fish. Manage. Ecol. 10 (5), 500–517.

EA, 2005. The North West Norfolk Catchment Abstraction Management Strategy, ⟨http://publications.environment-agency.gov.uk/PDF/GEAN0305BQYU-E-E.pdf⟩ (accessed on 11/07/12).

European Standard, 2003. Water quality—guidance for surveying of aquatic macrophytes in running waters. In: British Standard EN 14184 (accessed on 14/3/13).

Hendry, K., Cragg-Hine, D., O'Grady, M., Sambrook, H., Stephen, A., 2003. Management of habitat for rehabilitation and enhancement of salmonid stocks. Fish. Res. 62 (2), 171–192.

Jonsson, B., Jonsson, N., 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trour *Salmo trutta*, with particular reference to water temperature and flow. J. Fish Biol. 75, 2381–2447.

Jowett, I.G., 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. N.Z. J. Mar. Freshwater Res. 24, 19–30.

Jowett, I.G., 1992. Models of the abundance of large brown trout in New Zealand rivers. North Am. J. Fish. Manage. 12, 417–432.

Kopecki, I., 2008. Calculational Approach to FST-Hemispheres for Multiparametrical Benthos Habitat Modelling. University of Stuttgart, Stuttgart.

Louhi, P., Maki-Petays, A., Erkinaro, J., 2008. Spawning habitat of Atlantic Salmon and Brown trout: general criteria and intragravel factors. River Res. Appl. 24, 330–339.
Maddock, I., 1999. The importance of physical habitat assessment for evaluating river health. Freshwater Biol. 41, 373–391.
MEA, 2005. Ecosystems and human well-being. In: Synthesis. Island Press, Washington, DC.
Milhouse, R.T., Waddle, T.J., 2012. Physical Habitat Simulation (PHABSIM) Software for Windows (v.1.52). Fort Collins Science Centre, Fort Collins, CO.
Mouton, A.M., Schneider, M., Depestele, J., Goethals, P.L.M., De Pauw, N., 2007. Fish habitat modelling as a tool for river management. Ecol. Eng. 29 (3), 305–315.
Muñoz-Mas, R., Martinez-Capel, F., Schneider, M., Mouton, A.M., 2012. Assessment of brown trout habitat suitability in the Jucar river basin (Spain): comparison of data-driven approaches with fuzzy-logic models and univariate suitability curves. Sci. Total Environ. 440, 123–131.
Norfolk Rivers Trust, 2013. The River Nar, a Water Framework Directive Local Catchment Plan, ⟨http://www.norfolkriverstrust.org/wp-content/uploads/2014/09/River-Nar-Catchment-Plan-Sept-2014.pdf⟩ (accessed on 14/3/14).
Orth, D., 1987. Ecological considerations in the development and application of instream flow-habitat models. Regul. Rivers: Res. Manage. 1, 171–181.
Pander, J., Geist, J., 2013. Ecological indicators for stream restoration success. Ecol. Indic. 30, 106–118.
Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. BioScience 47 (11), 769–784.
S&TA, 2014. Salmon and Trout Association: Abstraction, ⟨http://www.salmon-trout.org/c/over-abstraction/⟩ (accessed on 2/3/13), (Online).
Schneider, M., Noack, M., Gebler, T., Kopecki, I., 2010. Handbook for the Habitat Simulation Model CASiMiR, ⟨http://www.casimir-software.de/ENG/download_eng.html⟩ (accessed on 2/5/14).
Spink, A.J., 1992. The Ecological Strategies of Aquatic Ranunculus Species Faculty of Science. University of Glasgow, Glasgow.
Witzel, L., Maccrimmon, H., 1983. Redd site selection by brook trout and brown trout in southwestern Ontario streams. Trans. Am. Fish. Soc. 112, 760–771.