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ESTIMATING SPAWNING HABITAT AVAILABILITY IN FLOODED AREAS OF THE RIVER WAAL, THE NETHERLANDS

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ABSTRACT

Fish spawning habitat availability in the river Waal is significantly influenced by seasonal and annual variations in discharge. In this paper we develop habitat suitability models, based on a literature survey of spawning preferences of the commonly occurring species roach (*Rutilus rutilus*), bream (*Abramis brama*), pikeperch (*Sander lucioperca*) and bleak (*Alburnus alburnus*). Within the resulting models water depth, flow velocity, water temperature and vegetation type were the most significant environmental parameters. Spatial data for the parameters were derived from a 2-D hydrodynamic model and detailed monitoring database. The area of suitable habitat available for spawning was calculated using the HABITAT software, based on species-specific suitability models and the environmental characteristics of two study sites on the river Waal over a 3 year period (1997–1999). The predicted available spawning area was compared with field data on the recruitment of young fish of each species for the same years and locations. There was a positive relationship between predicted available habitat and observed young of the year (YOY) densities for bream, roach and pikeperch. A negative relationship was recorded between predicted available area and observed YOY densities for bleak. The results indicate that optimal hydrological and hydraulic conditions differ even for species that are widely considered eurytopic. Moreover, annual differences in habitat availability indicate a strong influence of hydrological variability on population dynamics. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: ecohydraulics; floodplain; habitat suitability; recruitment; river; spawning

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INTRODUCTION

River floodplains are generally characterized by high biodiversity and production, but are among the most anthropogenically-impacted landscape features worldwide. Anthropogenic activities often result in habitat loss due to changes in the land use of floodplains and modification of the flow regime and flooding (Tockner and Stanford, 2002; Aarts *et al*., 2004). In some instances, expected recovery of fish populations following improvements in water quality have been limited primarily due to the lack of suitable habitat (Aarts *et al*., 2004). This is particularly important for limnophilic species that utilize shallow water with plants as spawning areas, but is also important for rheophilic species that utilize side channel habitats (de Leeuw *et al*., 2007). Many of these habitats are typically only available and accessible periodically in river systems, during the annual flood. Floodplain and backwater habitats are potentially important for fish species at all life stages as they can serve not only as spawning habitat and nursery areas for juvenile fish but also as foraging habitat for adults (Borcherding *et al*., 2002; Cucherousset *et al*., 2007; Henning *et al*., 2007; Zeug and Winemiller, 2007). A reduction in the availability of shallow and slow flowing habitat due to river management may result in the reduction of fish biodiversity and the abundance of species that use these habitats (Bain *et al*., 1988; Scheidegger and Bain, 1995; Henning *et al*., 2007).

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The availability of habitat for spawning and recruitment of juveniles is primarily determined by the magnitude, timing and duration of the annual flood (Copp, 1989; Grift *et al*., 2003; Aarts *et al*., 2004; Feyrer *et al*., 2006; Zeug and Winemiller, 2008). The geographical extent of inundation during the spawning and juvenile period has been shown to be one of the best explanatory factors for annual fish production (Feyrer *et al*., 2006; DeGrandchamp *et al*., 2007; Mingelbier *et al*., 2008). Water temperature, flow velocity, substratum composition and water depth are important parameters influencing the suitability for spawning (Fladung *et al*., 2003; Mingelbier *et al*., 2008). Hydraulic conditions may therefore be a fundamental control on the ecological response of fish and the presence/absence of vegetation (terrestrial and aquatic) (Tomsic *et al*., 2007).

An increasing number of studies have considered habitat preferences of fish in river systems (e.g. Fladung *et al*., 2003; Rosenfeld, 2003; Miranda, 2005; Blanck *et al*., 2007; Tales and Berrebi, 2007). Based on quantified habitat preferences, suitability models can be developed to link species and/or life-stage requirements to spatial data (U.S. Fish and Wildlife Service, 1980; Scholten *et al*., 2003; Mingelbier *et al*., 2008). This method can be used to help understand the positive and/or negative effect of physical modifications to riverine ecosystems and is part of an interdisciplinary field of research called eco-hydraulics. For example Mingelbier *et al*. (2008) demonstrated that dewatering of the channel margin of the St. Lawrence River (Canada) resulted in a reduction of available spawning habitat by 60% between 1960 and 2000. In other studies habitat suitability models have been used to predict the effect of dam removal on macro-invertebrates and fish (Tomsic *et al*., 2007).

In this study we develop and validate habitat suitability models for four fish species (bream (*Abramis brama*), roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*) and pikeperch (*Sander lucioperca*)) occurring in the heavily regulated river Waal, a branch of the river Rhine, in the Netherlands. These species usilize the annually flooded areas of the river for spawning and nursery and are widely considered eurytopic. They are also among the most common species recorded in the river.

MATERIALS AND METHODS

Study area

The location of the study area was based on the availability of both fish data and hydrological parameters. Two sites utilized in the study of Grift *et al*. (2003) to examine young of the year (YOY) fish were selected for analysis due to the availability of data over 3 years (1997–1999). At both sites only the floodplain waterbodies (and not the main channel) were considered. The first site (SC) consists of the vegetated floodplain and a sheltered groyne area that experiences moderate flow velocities throughout the year (surface area $40.3 \cdot 10^4\,\mathrm{m}^2$)(Figure 1). The second site is a perennially connected oxbow lake (COL) with its surrounding vegetated floodplain (surface area $42.4 \cdot 10^4\,\mathrm{m}^2$). The waterbody is connected to the main river at the down-stream end, and is lentic for long periods of the year (Figure 1). The upstream part of the waterbody is only connected to the main channel when the water level is above 12 m a.s.l. at Lobith (corresponding to a discharge above $3000\,\mathrm{m}^3/\mathrm{s}$ at Lobith). Lobith is a standard measurement location upstream for water quantity and quality near the border with Germany where the river Rhine enters the Netherlands.

Species suitability models

The four species considered (bream, roach, bleak and pikeperch) are common in the river Waal and were recorded by Grift *et al*. (2003). The habitat characteristics of areas used for spawning for these eurytopic species were determined based on a detailed literature review. This survey indicated that water depth, water temperature, flow velocity and substrate for attaching eggs were the most important factors determining spawning habitat suitability (Table I). For each parameter considered the range of values for which spawning occurred was recorded from published sources (Table I). Values within the range are considered suitable for spawning, and parameters not within the range unsuitable. Intermediate values of suitability were not used, because data to discriminate between optimal and suboptimal spawning conditions were not available.

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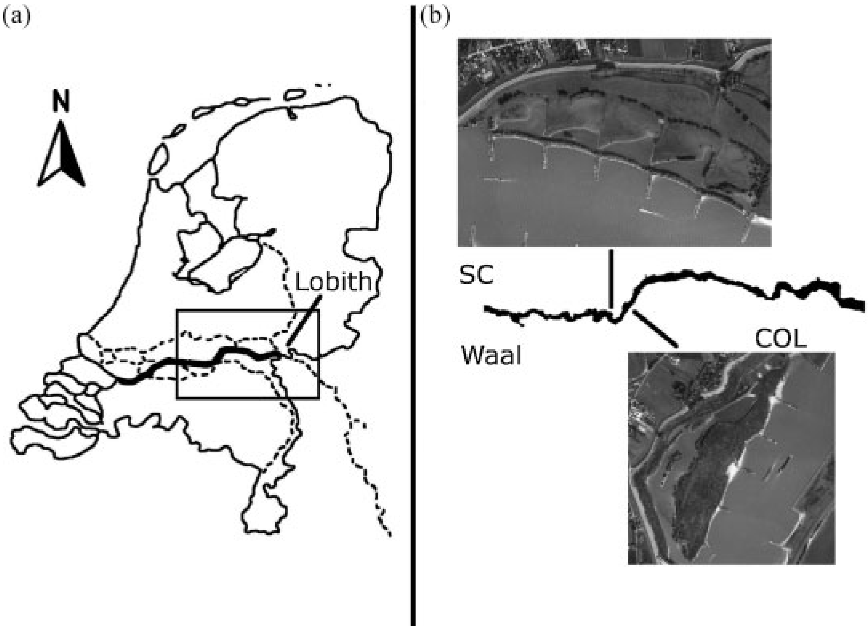

Figure 1. (a) Location map of the river Waal (solid line), and other main rivers (dashes line) and indicating the location of Lobith and (b) Location of the study sites SC and COL on the river Waal. The rivers flows from east to west

Input parameters

The spatial data on water depth and flow velocity were generated using a 2-D hydrodynamic model for the river Waal (WAQUA, developed for the Dutch Ministry of Transport, Public Works and Water Management (RWS))(Van de Pas, 2005; RWS, 2007). The model was run for a series of stationary discharges between 1000 and 14000 m^3/s at Lobith, providing spatial information on water depth and flow velocity for each discharge.

A detailed habitat (ecotope) map developed by the Dutch Institute for Inland Water Management and Waste Water Treatment was used to delineate spawning substrate. This map provided spatial (geo-referenced) information on the presence and distribution of individual habitats which could then be defined in relation to other parameters, such as land use (Rademakers and Wolfert, 1994). Due to the limited spatial coverage of water temperature and discharge, the long term record from Lobith was used as a proxy to determine the water depth and flow velocity at the two study sites for the spawning period (Figure 2). As a result three different conditions were tested corresponding to water level and flow velocities coinciding with:

- minimum water temperature recorded during spawning
- optimum water temperature for spawning
- mean spawning period.

For pikeperch the minimum water temperature was not used since this had not been exceeded during the recorded series. An alternative third measure, the relationship between spawning date and latitude was used as proxy for spawning (Lappalainen *et al*., 2003). For the Netherlands this predicts April 10 as the spawning date for pikeperch.

Modelling

The species models and the geo-referenced habitat maps were combined within a spatial analysis tool for grid calculations (HABITAT, Haasnoot and Van de Wolfshaar, in press). The maps have grid cells of 5 m $*$ 5 m and the suitability of each parameter for every grid cell is evaluated based on the species models (Figure 3). Based on its parameter value a grid cell is either suitable or unsuitable. Once this process had been undertaken for each

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Table I. Spawning habitat environmental parameter values recorded in literature and values used in habitat suitability models for bream, bleak, roach and pikeperch. Note: Parameter values outside the range reported in literature were considered unsuitable. Water temperature range is not used in the models due to the lack of spatial information, instead the minimum, optimum and general spawning period are used. For pikeperch the minimum temperature is not used because the water temperature does not drop below this value in several years. Instead the spawning date, April 10, based on Lappalainen *et al.* (2003) is used

Species	Parameter	Value	Reference	Model value used
Bream	Depth (m)	0.25–0.5	(Poncin *et al.*, 1996)	0.2–3
		0.2–0.8	(Bakiel and Zawisza, 1968)	
		0.1–0.6	(Pollux *et al.*, 2006)	
		<3	(Pinder, 2001)	
	Flow vel. (m/s)	0.1–0.5	(Pollux *et al.*, 2006)	<0.05
		<0.04	(Grift *et al.*, 2003)	
		'Very low'	(Bakiel and Zawisza, 1968)	
	Temp. (°C)	14	(Poncin *et al.*, 1996)	Min 12; opt 18
		12–20	(Bakiel and Zawisza, 1968)	
			(Mann, 1996)	
		14–16	(Quak *et al.*, 1996)	
		16; <24	(Diamond, 1985)	
	Period (month)	4–5	(Poncin *et al.*, 1996)	5–6
		5–6	Fishbase (May 2008) www.fishbase.org	
		5–6	(Mann, 1996)	
	Substratum	ph	(Copp, 1989)	ph-li
			(Pinder, 2001)	
			(Poncin *et al.*, 1996)	
		li	(Breder and Rosen, 1966)	
			(Copp, 1989)	
			(Pinder, 2001)	
			(Pollux *et al.*, 2006)	
Bleak	Depth (m)	0–1	(Vriese *et al.*, 1994)	<1
		<0.2	(Grift *et al.*, 2003)	
		0.2–0.5	(Copp, 1992)	
	Flow vel. (m/s)	<0.2	(Vriese *et al.*, 1994)	<0.2
			(Mann, 1996) and references therein	
		'Weak-strong'	(Copp, 1989)	
	Temp. (°C)	'Cool'	(Copp, 1989)	Min 14; opt 18
		13–14	(Hladík and Kubečka, 2003)	
		'as bream'	(Rinchard and Kestemont, 1996)	
	Period (month)	5–6	(Rinchard and Kestemont, 1996)	5–6
		4–5	(Hladík and Kubečka, 2003)	
		2–4	(Vriese *et al.*, 1994)	
	Substratum	ph	(Vriese *et al.*, 1994)	ph-li
		li	(Copp, 1989)	
			(Vriese *et al.*, 1994)	
Roach	Depth (m)	'Shallow'	(Van Emmerik, 2003)	0.1–1
		1.7; <5	(Copp, 1989)	
		0.1–0.3	(Diamond, 1985)	
		0.2–0.9	(Grift *et al.*, 2003)	
		0.1–0.6	(Pollux *et al.*, 2006)	
	Flow vel. (m/s)	'Stagnant'	(Goldspink, 1979)	<0.3
			(Lappalainen and Tarkan, 2007)	
			(Tarkan, 2006)	
		0.1–0.5	(Pollux *et al.*, 2006)	
		>0.2	(Mann, 1996)	
		'No relation'	(Copp, 1989)	
	Temp. (°C)	>14	(Rinchard and Kestemont, 1996)	Min 10; opt 14

(*Continues*)

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Table I. (Continued)

Species	Parameter	Value	Reference	Model value used
			(Goldspink, 1979)	
		Max 17–20	(Goldspink, 1997)	
		7–19	(Lappalainen and Tarkan, 2007)	
		12	(Mann, 1973)	
		14–17.4	(Diamond, 1985)	
		13–18	(Tarkan, 2006)	
		19; 10–20	(Gillet and Quétin, 2006)	
	Period (month)	5	(Goldspink, 1979)	4–5
		4–5	(Mann, 1973)	
		5	(Diamond, 1985)	
		4–5	(Tarkan, 2006)	
	Substratum	po	(Aarts *et al*., 2004)	po
			(Copp, 1989)	
			(Lappalainen and Tarkan, 2007)	
			(Pollux *et al*., 2006)	
			(Gillet and Quétin, 2006)	
		ph	(Goldspink, 1997)	
			(Diamond, 1985)	
Pikeperch	Depth (m)	1–8	(Lappalainen *et al*., 2003) and references therein	0.5–8
			(Lehtonen *et al*., 2006)	
		>0.5	(Vriese *et al*., 1994)	
	Flow vel. (m/s)	0.05–0.2	(Vriese *et al*., 1994)	<0.3
		<0.3	(Grift *et al*., 2003)	
	Temp. (°C)	4–20	(Lappalainen *et al*., 2003)	Opt 12
		'No relation'	(Raikova-Petrova and Zivkov, 1998)	
	Period (month)	4–5	Fishbase (May 2008)	4–5
		4–6	(Breder and Rosen, 1966)	
			(Mann, 1996) and references therein	
	Substratum	po	(Vriese *et al*., 1994)	po
			(Lappalainen *et al*., 2003)	
			(Lehtonen *et al*., 2006)	
		ph	(Aarts *et al*., 2004)	

ph: phytophil, li: lithophil and po: polyphil.

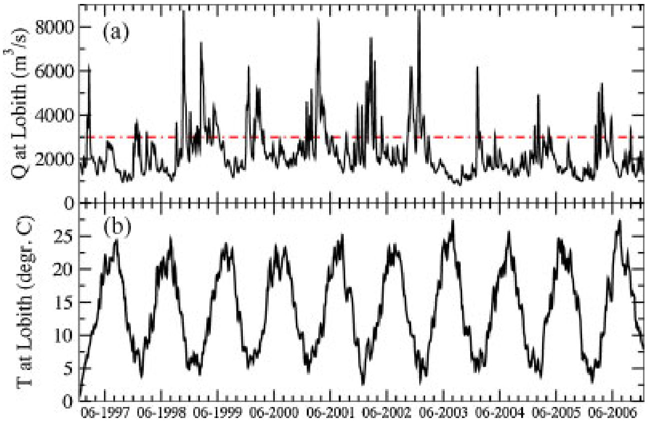

Figure 2. (a) Five-day running average of discharge at Lobith 1997–2006. Dash-dotted line denotes the discharge above which COL becomes connected at the upstream end and (b) Five-day running average of water temperature at Lobith 1997–2006. This figure is available in colour online at www.interscience.wiley.com/journal/rra

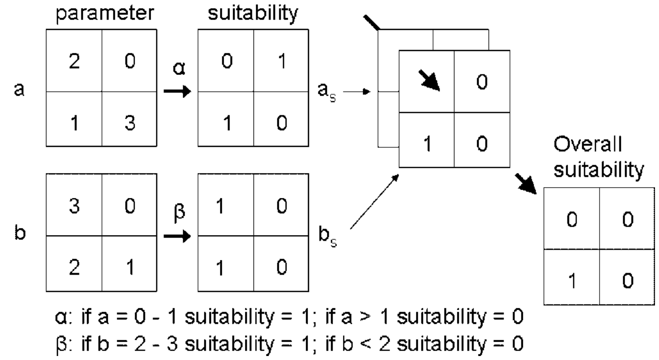

Figure 3. Schematic of the grid-based modelling of habitat suitability. Information per grid cell of parameter maps *a* and *b* are translated into suitability maps using the parameter specific rules α and β. The resulting suitability maps a_s and b_s are combined within an overall suitability map

parameter, the maps were combined to produce a single suitability map for each species (Figure 3). If all of the parameters for an individual grid cell were suitable on the individual maps the grid cell was considered suitable on the composite map (Figure 3). This approach assumes that one parameter can limit the overall suitability of the habitat for the species.

Field data

The rules developed for spawning habitat availability were validated with the YOY densities from Grift *et al.* (2003) as a proxy for available spawning habitat. The data from Grift *et al.* (2003) are not spatially explicit for each sample point and as a result it is only possible to compare the total area of available habitat at each site with the observed densities of fish for each year. The densities of YOY reported in this study were calculated from catch efforts from April to September. The sites were sampled every 3 weeks from April to September in 1997 and 1998, and weekly from April through June and every 3 weeks after june in 1999 (Grift *et al.*, 2003). Field data on the presence and distribution of fish eggs, larvae and YOY of any of the species (to determine point spawning conditions) are scarce due to difficulties of working in these habitats, especially those species that usually inhabit deeper waters. It should be noted that the suitability of spawning habitat and the presence of YOY do not necessarily coincide, particularly during the summer months due to elevated water temperatures and the drift of larval fish. However, because the larvae of the species used in this study occupy the same habitat where they hatched, it is assumed that larval densities can be used to represent the availability of spawning habitat (Feyrer *et al.*, 2006; DeGrandchamp *et al.*, 2007; Mingelbier *et al.*, 2008).

RESULTS

The relationship between discharge and available spawning habitat varied between species (Figure 4). The model for bream (Figure 4a) indicated that maximum spawning habitat availability occurred at an average discharge (Q) of 4000 m^3/s at both sites, with a maximum of $15 \cdot 10^4$ m^2 at COL and $10 \cdot 10^4$ m^2 at SC. At discharges less than 2500 m^3/s there was no suitable spawning area available at SC because only sandy substrates between the groynes remained submerged, although there was still $1.5 \cdot 10^4$ m^2 available at COL. The overall available spawning habitat declined at $Q > 5000$ m^3/s and both sites were unsuitable at $Q > 7000$ m^3/s due to increased depth and flow velocity. There was less spawning habitat available for roach compared to bream, although the maximum availability of spawning habitat occurred at similar discharge ($9.7 \cdot 10^4$ m^2 at SC and $9.3 \cdot 10^4$ m^2 at COL)(Figure 4c). The differences between the model primarily reflects the fact that bream can spawn in deeper areas than roach. At discharges below 2500 m^3/s no spawning habitat was available at SC and only $0.5 \cdot 10^4$ m^2 was present at COL.

The relationship between habitat and discharge for bleak was similar to roach, with maximum availability at SC and COL at $Q = 5000$ m^3/s and $Q = 3500$ m^3/s, respectively (Figure 4b).

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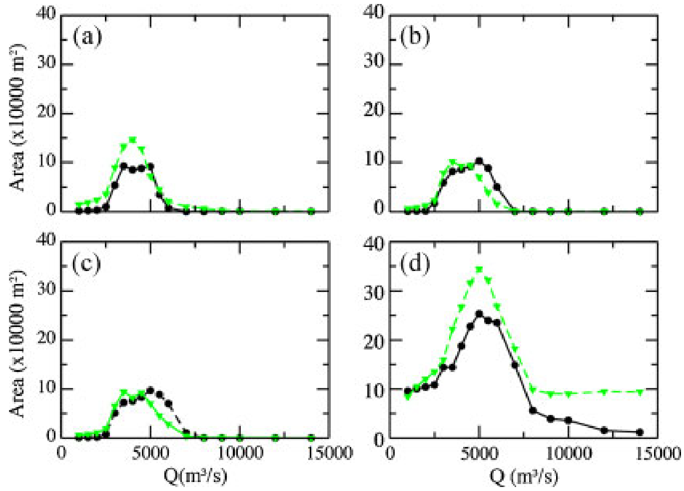

Figure 4. The available spawning habitat (area) as a function of the discharge at Lobith for the different species models based on water depth, current velocity and substrate. (a) bream, (b) bleak, (c) roach and (d) pikeperch. Black circles denote SC and grey triangles COL. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Pikeperch appeared to be the most tolerant species in relation to flow velocity and depth. This is reflected in the large area available even at higher discharges (Figure 4d). The maximum available habitat was recorded at $Q = 5000\,\mathrm{m^3/s}$ at SC $25 \cdot 10^4\,\mathrm{m^2}$ and COL $35 \cdot 10^4\,\mathrm{m^2}$. Even at low discharges ($Q < 2500\,\mathrm{m^3/s}$) there was still a large amount of available habitat for pikeperch spawning ($9.5 \cdot 10^4\,\mathrm{m^2}$ at SC and $8.5 \cdot 10^4\,\mathrm{m^2}$ at COL). At discharges above $8000\,\mathrm{m^3/s}$ the availability remains high at COL ($10 \cdot 10^4\,\mathrm{m^2}$), while availability at SC gradually decreases due to increasing flow velocities.

For each species and each environmental condition the corresponding discharge was used to calculate the available spawning habitat at each site for each year. The densities of the YOY recorded for each species for 1997–1999 are presented in Table II (data from (Grift *et al*., 2003)). To allow the relative differences between years to be considered directly (rather than absolute changes) fish density and available habitat were standardized using the Z-score ($(x - x_{\mathrm{avg}})/SD$). These standardized variables were then used to determine the correlation coefficients for the minimum, optimum and average spawning period for each species (Table III). For bream an increase in available habitat corresponded with an increase in catch regardless of the condition (Table III and Figure 5a and e, for the minimum temperature as condition). However, the model for bleak indicated an increase in available spawning habitat, but reduced densities were caught (Table III and Figure 5b and f). For roach an increase in available spawning habitat coincided with an increase in density (Table II and Figure 5c and g), with the strongest correlation at the optimum spawning temperature of 14°C (Table III). For pikeperch the correlation between predicted spawning habitat and density was not as strong as for bream or roach, although there was a consistent positive association between density and available spawning habitat (Table III and Figure 5d and h). The strongest correlation between available spawning habitat and density for pikeperch occurred when April 10 was used (Table III, Figure 5d and h).

The individual species suitability models were used to determine the total area of spawning habitat available annually for the period 1997–2006. The annual variation in modeled available spawning habitat for each species was marked (Figure 6). For bream the model indicated that 1999, 2001 and 2006 were most favourable for spawning at a water temperature of 12°C (Figure 6a). For bleak the model indicated that a large amount of spawning habitat was available during 1999 when the average discharge during April and May was used (Figure 6b). For roach 2001, 2005 and 2006 were predicted to be favourable for spawning (Figure 6c), at a water temperature of 14°C. Pikeperch had a large spawning habitat available for all years, with exceptionally good years in 1999, 2001 and 2006, based on the model predictions using April 10 as the key condition for the spawning period (Figure 6d). Even years with low discharges during spring such as 1997, 2003 and 2004 still resulted in around $10 \cdot 10^4\,\mathrm{m^2}$ of available spawning habitat at both sites. During the 10 year study period the model indicated that significant areas

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Table II. Densities of YOY fish caught at the two study sites during 1997–1999 (numbers per 1000 m^2). Density is the fraction of non-zero catches multiplied by mean density per non-zero catch (data taken from Grift *et al*., 2003)

Year	SC	COL	Year	SC	COL
Bream			Pikeperch		
1997	5	14	1997	7	35
1998	16	35	1998	10	55
1999	143	279	1999	10	53
Bleak			Roach		
1997	11	28	1997	24	23
1998	17	41	1998	50	47
1999	2	6	1999	50	48

Table III. Correlation coefficients between standardized density (Grift *et al*., 2003) and standardized available area for water levels and flow velocities corresponding to water temperatures coinciding with: minimum spawning temperature, optimum spawning temperature and the average spawning period. Note: For pikeperch the minimum spawning temperature was met on a limited number of occasions and was therefore not used. An alternative measure of habitat availability on April 10th was used, which results from the equation of (Lappalainen *et al*., 2003) as the spawning date. Standardization was achieved using $(x - x_{\mathrm{avg}})/SD$. Correlation coefficients are given per location ($N = 3$) and for both locations ($N = 6$)

Criterion	SC	COL	SC+COL
Bream			
12°C	0.9970	0.9974	0.9972
18°C	0.9957	0.9962	0.9916
May–June	0.9963	0.9968	0.9949
Bleak			
14°C	−0.1147	−0.1468	−0.1308
18°C	−0.9175	−0.9437	−0.9306
April–May	−0.9177	−0.9149	−0.9163
Roach			
10°C	0.4949	0.5020	0.4984
14°C	1	0.9994	0.9997
April–May	0.5050	0.5579	0.5315
Pikeperch			
12°C	0.5	0.4193	0.4597
April–May	0.5718	0.5245	0.5481
April 10	0.5794	0.7203	0.6498

of favourable spawning habitat were only recorded during 3 years for bream and roach and 1 year for bleak. These favourable conditions coincide with discharges greater than 2500 m^3/s. During all of the other years little to no suitable spawning habitat was available for these three species although there was abundant pikeperch spawning habitat throughout the study period.

DISCUSSION

This study compared results of modeled suitable spawning habitat availability with field catches of YOY fish during spring and summer over a 3 year period (1997–1999). Data on the presence of fish eggs would have been preferred for field-validation; although these data were not available. The use of larval data could be problematic if spawning and nursery areas did not overlap. The presence of YOY in catches in the field is a result of multiple factors

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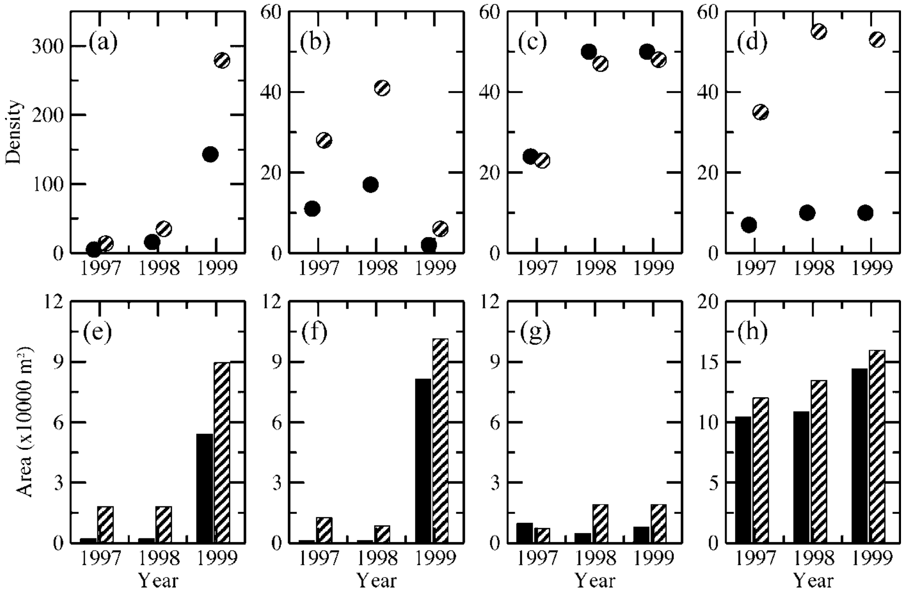

Figure 5. Catch densities for 1997–1999 (a–d) (Grift *et al.*, 2003) and area of suitable spawning habitat as a function of the discharge of the river at Lobith for the different species models based on water depth, current velocity and substrate (e–h). For each species the temperature condition giving the best fit was used—a and e: bream (12°C); b and f: bleak (18°C); c and g: roach (14°C) and d and h: pikeperch (April 10). Closed circles: SC; Hatched circles: COL; Closed bars: SC and Hatched bars: COL. Note that the scale on the *Y*-axis for the bream field data (a) and the pikeperch model result (h) differ from other graphs

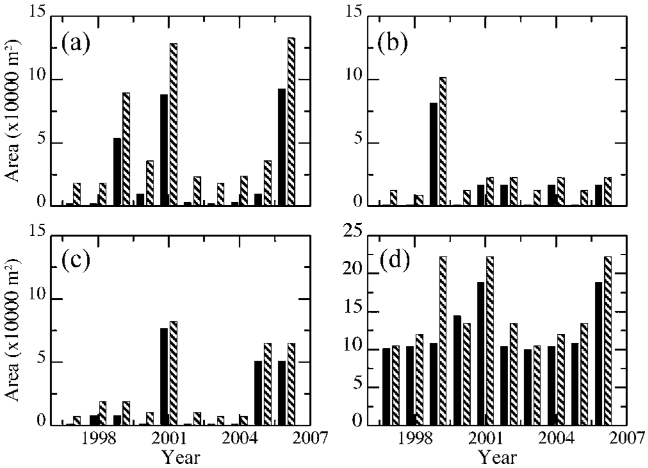

Figure 6. The predicted available area of suitable spawning habitat for 1997–2006 per species. For each species the temperature condition giving the best fit was used: (a) bream (12°C); (b) bleak (18°C); (c) roach (14°C) and (d) pikeperch (April 10). Closed bars denote SC and hatched bars COL. Note that the scale on the *Y*-axis for pikeperch (d) differs from the others

including the presence of suitable spawning habitat, mortality of egg and larvae, passive or active migration of the YOY and catchability in the field (personal experience of J.J de Leeuw). Low numbers of a YOY cohort could be due to any of these factors. However, with a high number of YOY it is reasonable to assume that the availability of suitable spawning habitat was adequate. Therefore, we assume that for species with spawning and nursery areas not strongly spatially separated, spawning conditions and larval densities are positively correlated.

Three out of four species models predicted the trends between the area of suitable habitat and density accurately. However, the models only included four parameters (water depth, flow velocity, water temperature and substrate)

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and did not consider any interactions between species or population dynamics. For bleak the model did not appear to produce a reliable result for 1999. Modifying the spawning period by using different months within the period found in literature did not improve the model and a re-evaluation of the species model based on available literature did not suggest any errors in the parameters used. This mismatch could therefore be due to reasons other than availability of suitable habitat. For instance, water level during 1999 was elevated resulting in the connection of COL to the main channel at the upstream side, thereby creating a strong flow through the lake resulting in washout of bleak larvae. Unlike the other species, bleak larvae prefer deeper water with an inevitable increased risk of larval drift (Copp, 1992).

River and floodplain restoration has received increased attention in the past decade and the focus has shifted from water quality to habitat availability. In this study habitat availability is considered to be a function of both ecology and hydrology. Aarts *et al*. (2004) argue that the availability of suitable habitat can be considered the most likely factor limiting the recovery of fish populations after improvements in water quality. Pretty *et al*. (2003) argue that improvements of marginal and riparian habitats may be more successful and beneficial than improvements of in-channel habitats. There is increasing evidence to support this based on research centred on the role floodplains play in fish life histories (Vriese *et al*., 1994; King *et al*., 2003; Lytle and Poff, 2004; Hohausova and Jurajda, 2005; Henning *et al*., 2007). The models developed in this study clearly indicate that even when common eurytopic fish species are concidered the optimal spawning conditions differ significantly between species. If a combined species model were to be developed without acknowledging species and functional differences, river restoration measures undertaken based on it could result in the destruction/degradation of habitat of some taxa rather than enhancement/restoration. However, if appropriate species level models are developed, the use of habitat suitability models form an effective guide for river restoration projects.

As a result of differences in the requirements of species, heterogeneity in the river landscape (Amoros and Bornette, 2002; Fladung *et al*., 2003; Grift *et al*., 2003; Aarts *et al*., 2004; Hohausova and Jurajda, 2005; Tales and Berrebi, 2007; Zeug and Winemiller, 2008) and the flow regime (magnitude, frequency, duration and timing of hydrological events) may ultimately promote fish community diversity (Cattanéo, 2005; Miranda, 2005). The species models developed in this study show that for eurytopic species the maximum availability of suitable habitat at the two sites occurred at discharges around 4000 m^3/s at Lobith. Analysis of the hydrograph indicated that during the last decade only a limited number of years had a discharge of this magnitude or greater than 2500 m^3/s during the spawning season (3 years for bream, roach and pikeperch, and 1 year for bleak). This clearly indicates that higher discharges during spring result in an increased availability of suitable spawning and nursery habitat. Differences between species in the timing of spawning may favour individual species in any given year. The low number of years with favourable conditions, based on spawning habitat availability, demonstrates the relatively limited potential for population recruitment. The results also clearly demonstrate that channel hydraulics may have a significant impact on population dynamics.

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REFERENCES

Aarts BGW, van den Brink FWB, Nienhuis PH. 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Research and Applications* **20**: 3–23.

Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47**: 761–776.

Bain MB, Finn JT, Booke HE. 1988. Streamflow regulation and fish community structure. *Ecology* **69**(2): 382–392.

Bakiel T, Zawisza J. 1968. *Synopsis of Biological Data on the Bream Abramis brama*. FAO Fisheries Synopsis No. 36.

Blanck A, Tedesco PA, Lamouroux N. 2007. Relationships between life-history strategies of European freshwater fish species and their habitat preferences. *Freshwater Biology* **52**: 843–859.

Borcherding J, Bauerfeld M, Hintzen D, Neumann D. 2002. Lateral migration of fishes between floodplain lakes and their drainage channels at the lower Rhine: diel and seasonal aspects. *Journal of Fish Biology* **61**: 1154–1170.

Breder CM, Rosen DE. 1966. *Modes of Reproduction in Fishes*. T.F.H. Publications: Neptune City, New Jersey.

Cattanéo F. 2005. Does hydrology constrain the structure of fish assemblages in French streams? *Archiv fur Hydrobiologie* **164**(3): 345–365.

Copp GH. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes* **26**: 1–27.

Copp GH. 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. *Environmental Biology of Fishes* **33**: 181–193.

Cucherousset J, Carpentier A, Pailisson JM. 2007. How do fish exploit temporary waters throughout a flooding episode? *Fisheries Management and Ecology* **14**: 269–276.

de Leeuw JJ, Buijse AD, Haidvogel G, Lapinska M, Noble R, Repecka R, Virbickas T, Wisniewolski W, Wolter C. 2007. Challenges in developing fish-based ecological assessment methods for large floodplain rivers. *Fisheries Management and Ecology* **14**: 483–494.

DeGrandchamp KL, Garvey JE, Csoboth LA. 2007. Linking adult reproduction and larval density of invasive carp in a large river. *Transactions of the American Fisheries Society* **136**: 1327–1334.

Diamond M. 1985. Some observations of spawning by roach, *Rutilus rutilus*, and bream, *Abramis brama*, and their implications for management. *Aquaculture and Fisheries Management* **16**: 359–367.

Feyrer F, Sommer T, Harrell W. 2006. Managing floodplain inundation for native fish: production dynamics of age-0 splittail (*Pohonichthys macrolepidotus*) in California's Yolo Bypass. *Hydrobiologia* **573**: 213–226.

Fladung E, Scholten M, Thiel R. 2003. Modelling the habitat preferences of preadult and adult fishes on the shoreline of the large, lowland Elbe river. *Journal of Applied Ichtyology* **19**: 303–314.

Gillet C, Quétin P. 2006. Effect of temperature changes on the reproductive cycle of roach in Lake Geneva from 1983 to 2001. *Journal of Fish Biology* **69**: 518–534.

Goldspink CR. 1979. The population density, growth rate and production of roach *Rutilus rutilus* (L.) in Tjeukemeer, The Netherlands. *Journal of Fish Biology* **15**: 473–498.

Goldspink CR. 1997. The return of the marked roach (*Rutilus rutilus* l.) to spawning grounds in Tjeukemeer, The Netherlands. *Journal of Fish Biology* **11**: 599–603.

Grift RE, Buijse AD, van Densen WLT, Machiels MAM, Kranenbarg J, Klein Breteler JGP, Backx JJGM. 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower river Rhine. *River Research and Applications* **19**: 353–374.

Haasnoot M, Van de Wolfshaar KE. (in press). Combining a conceptual framework and a spatial analysis tool, HABITAT, to support the implementation of river basin management plans. *International Journal of River Basin Management* **7**(3).

Henning JA, Gresswell RE, Fleming IA. 2007. Use of seasonal freshwater wetlands by fishes in a temperate river floodplain. *Journal of Fish Biology* **71**: 476–492.

Hladík M, Kubečka J. 2003. Fish migration between a temperate reservoir and its main tributary. *Hydrobiologia* **504**: 251–266.

Hohausova E, Jurajda P. 2005. Restoration of a river backwater and its influence on fish assemblage. *Czech Journal of Animal Science* **50**(10): 473–482.

King AJ, Humphries P, Lake PS. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 773–786.

Lappalainen J, Dorner H, Wysujack K. 2003. Reproduction biology of pikeperch (*Sander lucioperca*)—a review. *Ecology of Freshwater Fish* **12**: 95–106.

Lappalainen J, Tarkan AS. 2007. Latitudinal gradients on onset date, onset temperature and duration of spawning of roach. *Journal of Fish Biology* **70**: 441–450.

Lehtonen H, Lappalainen J, Kervinen J, Fontell E. 2006. Spatial distribution of spawning sites of pikeperch (*Sander lucioperca* (L.)) in a highly eutrophic clay-turbid lake—implications for management. *Journal of Applied Ichthyology* **22**: 540–542.

Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**(2): 94–100.

Mann RHK. 1973. Observations on the age, growth, reproduction and food of the roach *Rutilus rutilus* (L.) in two rivers in southers England. *Journal of Fish Biology* **5**: 707–736.

Mann RHK. 1996. Environmental requirements of European non-salmonid fish in rivers. *Hydrobiologia* **323**: 223–235.

Mingelbier M, Brodeur P, Morin J. 2008. Spatially explicit model predicting the spawning habitat and early stage mortality of northern pike (*Esox lucius*) in a large system the St. Lawrence River between 1960 and 2000. *Hydrobiologia* **601**: 55–69.

2005. Fish assemblages in oxbow lakes relative to connectivity with the Mississippi River. *Transactions of the American Fisheries Society* **134**: 1480–1489.

Pinder AC. 2001. *Keys to larval and juvenile stages of coarse fishes from fresh water in the British Isles*, Vol. 60, Freshwater Biological Association. Scientific Publication No. 60: The Ferry House, Far Fawrey, Ambleside, Cumbria, UK; 136.

Pollux BJA, Korosi A, Verberk WCEP, Pollux PMJ, van der Velde G. 2006. Reproduction, growth, and migration of fishes in a regulated lowland tributary: potential recruitment to the river Meuse. *Hydrobiologia* **565**: 105–120.

Poncin P, Phillipart JC, Ruwet JC. 1996. Territorial and non-territorial spawning behaviour in the bream. *Journal of Fish Biology* **49**: 622–626.

Pretty JL, Harrison SSC, Shepherd DJ, Smith C, Hildrew AG, Hey RD. 2003. River rehabilitation and fish populations: assessing the benefit of instream structures. *Journal of Applied Ecology* **40**: 251–265.

Quak J, Riemersma P, Goeting GCWM, Scheepers PACA. 1996. *Onderzoek visstandwatersysteem Mark en Vliet. Hoofdrapport*. Organisatie ter Verbetering van de Binnenvisserij, Nieuwegein, The Netherlands. In Dutch.

DOI: 10.1002/rra

Rademakers JGM, Wolfert HP. 1994. Het rivier-ecotopen-stelsel. een indeling van ecologisch relevante ruimtelijke eenheden ten behoeve van ontwerp- en beleidsstudies in het buitendijkse rivierengebied. *Technical Report*, 61-1994, Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterbehandeling Lelystad, The Netherlands. In dutch. Publicaties en rapporten van het project 'Ecologisch Herstel Rijn en Maas' 61-1994. In Dutch.

Raikova-Petrova G, Zivkov M. 1998. Maturity, spawning and sex ratio of pike perch, *Stizostedion lucioperca* (L.), in two Bulgarian reservoirs as compared to other European habitats. *Journal of Applied Ichtiology* **14**: 31–35.

Rinchard J, Kestemont P. 1996. Comparative study of reproductive biology in single- and multiple-spawner cyprinid fish. I. Morphological and histological features. *Journal of Fish Biology* **49**: 883–894.

Rosenfeld J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. *Transactions of the American Fisheries Society* **132**: 953–968.

RWS. 2007. *Users Guide WAQUA: Technical Report SIMONA 92–10*. National Institute for Coastal and Marine Management, The Hague, Online documentation, http://www.waqua.nl/systeem/documentatie/usedoc/slib3d/ug-slib3d.pdf, Accessed on 13-02-2008.

Scheidegger KJ, Bain MB. 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia* **1**: 125–155.

Scholten M, Wirtz C, Fladung E, Thiel R. 2003. The modular habitat model (MHM) for the ide, *Leuciscus idus* (L.)—a new method to predict the suitability of inshore habitats for fish. *Journal of Applied Ichtyology* **19**: 315–329.

Tales E, Berrebi T. 2007. Controls of local young-of-the-year fish species richness in flood plain water bodies: potential effects of habitat heterogeity, productivity and colonisation-extinction events. *Ecology of Freshwater Fish* **16**(2): 144–154.

Tarkan AS. 2006. Reproductive ecology of two cyprinid fishes in an oligotrophic lake near the southern limits of their distribution. *Ecology of Freshwater Fish* **15**: 131–138.

Tockner K, Stanford JA. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation* **29**(3): 308–330.

Tomsic CA, Granata TC, Murphy RP, Livchak CJ. 2007. Using a coupled eco-hydrodynamic model to predict habitat for target species following dam removal. *Ecological Engineering* **30**: 215–230.

U.S. Fish and Wildlife Service. 1980. *Habitat Evaluation Procedures (HEP)*. U.S. Department of Interior Fish and Wildlife Service, Division Ecological Services Manual 102. Washington, D.C. USA.

Van de Pas B. 2005. *Users guide WAQUA: Technical Report SIMONA 92–10*. RIZA, Arnhem, The Netherlands, werkversie pr843.30 edition. Baseline data protocol, baseline 3.31.

Van Emmerik WAM. 2003. *Indeling van de vissoorten van de Nederlandse binnenwateren in ecologische gilden en in hoofdgroepen*. Organisatie ter Verbetering van de Binnenvisserij, Nieuwegein, The Netherlands. In Dutch.

Vriese FT, Semmekrot S, Raat AJP. 1994. Assessment of spawning and nursery area in the river Meuse. *Water Science Technology* **29**(3): 297–299.

Zeug SC, Winemiller KO. 2007. Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 1291–1301.

Zeug SC, Winemiller KO. 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Research and Applications* **24**: 90–120.

DOI: 10.1002/rra