

Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary

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Abstract – The population behaviours associated with the migrations of fishes in lowland river ecosystems are amongst the most poorly-understood dispersal mechanisms of temperate freshwater organisms. This study evaluated the influence of four environmental variables (light levels, river discharge, water temperature and water velocity) on the timing, intensity and direction of fish movements between the River Avon (Hampshire, England) and a small floodplain tributary, Ibsley Brook, over a 12-month period. Using canonical correspondence analysis (CCA) to identify patterns of movement (by groups of species) and the relative strengths of explanatory variables in the data, the probability of fishes migrating between the river and tributary was determined using Bayesian modelling. The intensity and direction of fish movements between the river and tributary varied temporally, both on a diel and seasonal basis, and there were species- and age-specific patterns in behaviour. Diel movements appeared to be triggered by changes in light intensity and brook water velocity, whereas seasonal movements were mostly driven by changes in river discharge and water temperature, particularly those associated with floods. This study emphasises the importance of connectivity in river systems, as fishes migrated in all conditions, but especially during rapidly-rising discharge.

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Key words: ecosystem function; habitat connectivity; habitat fragmentation; habitat use; river discharge; water velocity

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Introduction

The population behaviours associated with the migrations of fishes in lowland rivers are amongst the most poorly-understood dispersal mechanisms in temperate freshwater ecosystems. This contrasts with upland systems, which are invariably dominated by salmonid fishes, and for which knowledge is far superior compared with cyprinid-dominated lowland rivers. It is only relatively recently that the prevalence and magnitude of migrations by non-salmonid fishes have begun to become appreciated. A number of sturgeon species (Acipenseridae), for example, may migrate more than 3000 km in unobstructed rivers, and considerable distances can be covered by a range of fish species, including some previously considered to be sedentary, even in comparatively small water-

courses (see Baras & Lucas 2001). The increase in understanding of migrations in recent years has led to concerns over the possible impacts of barriers on the distribution, population structures, spawning success and recruitment of many species (Ponton et al. 2000; Nunn et al. 2008). Indeed, migration barriers are now recognised as one of the key threats to freshwater fishes world-wide (Baras & Lucas 2001), particularly for the recovery of impacted populations (Albanese et al. 2009).

Although the importance of longitudinal, and lateral, migrations of fishes for spawning purposes is becoming increasingly recognised, much less is known about non-spawning migrations and the significance of tributaries to riverine fish populations. A number of studies have reported migrations of fish between rivers and their tributaries, such as

movements of riffle minnow *Leuciscus souffia agaszii* between the River Argen (Germany) and a tributary (Wocher & Rösch 2006), and those of barbel *Barbus barbus* between the rivers Ouse and Nidd, England (Lucas & Batley 1996). Moreover, tributaries and floodplain annexes can be important for the recruitment of fish populations in the main channel, particularly in regulated river systems (Cattaneo et al. 2001; Pollux et al. 2006; Nunn et al. 2007a), yet few studies have examined the intensity (Hohausová et al. 2003) and/or probability of fishes moving into off-channel habitats. Indeed, literature concerning seasonal and diel non-spawning migrations is relatively scarce, and little is known of the year-round movements of multiple fish species between lowland rivers and their tributaries. The aim of the study was thus to examine the timing, intensity and direction of fish movements during day and night between the main stem and a tributary of the River Avon (Hampshire, England). The specific objectives were to: (i) determine the probability of diel fish movements in different seasons and (ii) identify the explanatory variables of diel and seasonal migration patterns. Given that hydrology and seasonal variability form a complex driver of fish recruitment success in river systems (Cattaneo et al. 2001; Nunn et al. 2003, 2007b), it was predicted that species-specific differences in diel and seasonal migration patterns (i.e., in the probabilities of movement) between the River Avon and its tributary are triggered by specific combinations of environmental conditions.

Study area, material and methods

The River Avon is a groundwater-dominated river that originates from chalk springs near Burbage, Wiltshire, and flows south for ~100 km before discharging into the English Channel at Christchurch. The majority of the Avon is designated a Site of Special Scientific Interest, as well as a Special Area of Conservation, a Special Protection Area and a Ramsar site, but the system is nonetheless impacted by a variety of factors (Wheeldon 2003). The present study focuses on the confluence of a small tributary, Ibsley Brook, with the middle reaches of the River Avon. The brook (also known locally as Northend Stream) is a narrow (1–5 m), relatively short (about 1.5 km) water course that drains a small tributary catchment (49 ha) that lies almost entirely within the flood plain of the River Avon (50:54:13:N, 01:47:17:W). Near its confluence with the Avon, the brook's channel is generally trapezoidal (mean width = 4 m, mean depth = 0.6 m) with predominantly silt, sand and gravel substratum and variable water velocities, from null to fast (10–15 cm s⁻¹). The brook's discharge is variable, depending upon season and the discharge of the Avon

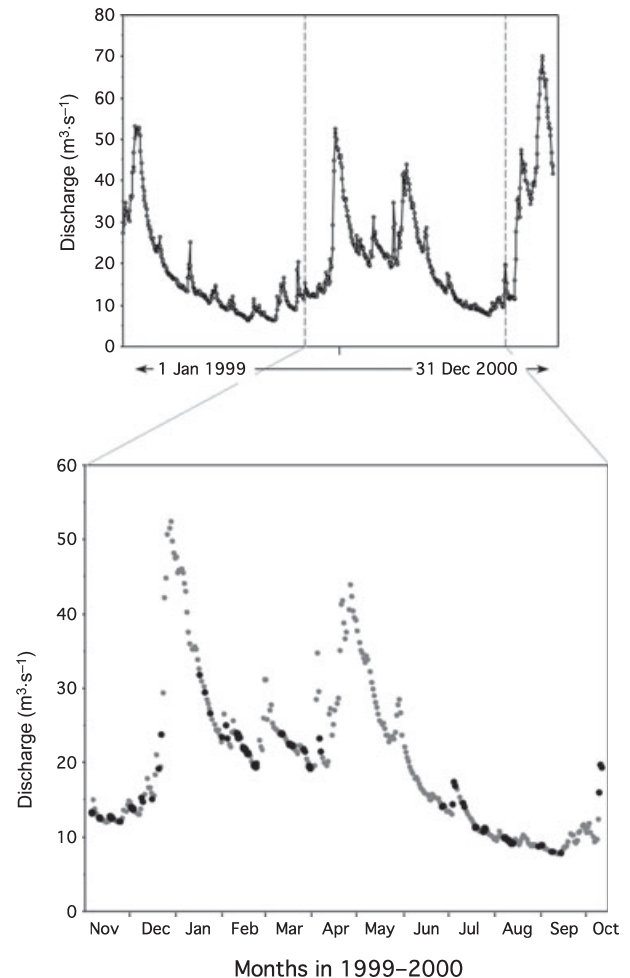


Fig. 1. Discharge regime of the River Avon (Hampshire, England). Fish traps were exposed over 24-h on dates indicated by large black dots.

(Fig. 1), which influences subterranean flows that feed the brook. Fish species in Ibsley Brook and the River Avon are mainly native species (Carter et al. 2004), including European bullhead *Cottus gobio*, stone loach *Barbatula barbatula*, threespine stickleback *Gasterosteus aculeatus*, gudgeon *Gobio gobio*, dace *Leuciscus leuciscus*, chub *L. cephalus*, roach *Rutilus rutilus*, common bream *Abramis brama*, Atlantic salmon *Salmo salar*, brown trout *S. trutta*, European eel *Anguilla anguilla*, northern pike *Esox lucius*, Eurasian perch *Perca fluviatilis*, barbel, tench *Tinca tinca*, European minnow *Phoxinus phoxinus*, rudd *Scardinius erythrophthalmus*, ninespine stickleback *Pungitius pungitius* and introduced common carp *Cyprinus carpio*. Brook lamprey *Lampetra planeri* are also present in both the river and brook.

Field sampling

Fish migrations between the River Avon and Ibsley Brook were assessed over forty-seven 24-h periods

from November 1999 to October 2000 using traps of a design similar to fyke nets, whereby a square opening (51 cm × 51 cm) led into a conical 'fyke' section that itself led to a 7-cm diameter entrance. The overall length of the traps was 92 cm, and two traps were deployed at the river–brook confluence. The leader net (210 × 100 cm, 5 mm mesh) of the entrance trap (immigration: river to brook) was set flush with the Avon's banks and the exit trap (emigration: brook to river) spanned the entire width of the confluence. Setting the traps in this way, as opposed to in the river and tributary, ensured that migrating, rather than resident, fishes were captured. The traps were exposed in a manner similar to Bunt et al. (2002), with the nets emptied in the morning (as soon after dawn as possible) and in the evening (at dusk). As the traps spanned the entire width of the small confluence, their efficiency was assumed to be high. All fishes were measured (nearest mm) for either fork length (FL) or total length (TL), depending upon the species' caudal-fin morphology, and scale samples were collected for ageing purposes. Immigrating fishes were released in the brook 5 m upstream of the exit trap, and emigrating fishes were released in the river 5 m downstream of the entrance trap.

Each time the traps were set and emptied, four variables were recorded: time of day; water temperature (to nearest 0.5 °C); brook water level (in cm) at 10 and 100 m from its confluence with the Avon; and brook water velocity, which was categorised using a wooden pole positioned in the water column perpendicular to the brook bed (as described in Carter et al. 2004): 1 = absent (no movement of water past pole), 2 = negligible (minimal movement of water past pole: >0 but <5 cm·s⁻¹), 3 = slow (water movement but no rippled effect around pole: 5–10 cm·s⁻¹), 4 = moderate (rippled effect around pole: >10 cm·s⁻¹ but ≤15 cm·s⁻¹), 5 = fast (pressure wave upstream of pole: >15 cm·s⁻¹). A preliminary study (Copp et al. 2000) revealed a linear relationship between the water level (stage) in Ibsley Brook and the discharge (Q , in m³·s⁻¹) of the Avon (Stage = 2.534 Q + 34.01, r^2 = 0.893, F = 349.19, d.f. = 42, P = 0.0001), so brook stage was used as a surrogate of river discharge (Fig. 1).

Data analyses

Fishes were aged by scale reading and with reference to published information on lengths-at-age (e.g., Britton 2007). Analyses were restricted to 0+ and 1+ fishes as these dominated the catches. Numbers of fishes captured were standardised as numbers per 10 h of trapping (i.e., catch per unit effort) to remove bias due to differences in day and night length. The samples collected overnight from 31 August to 1 September were grouped with the August samples.

Probabilities of diel fish movement (i.e., day/night, immigration/emigration) were estimated according to both season and age class using Bayesian inference (Gelman et al. 2004). The use of Bayesian inference over classical/frequentist techniques has been discussed extensively on the grounds of both philosophy and pragmatism (Clark 2005). In this study, it was considered that analysing fish movements in terms of probabilities, rather than null hypotheses, improved the presentation and interpretation of the results, thereby facilitating comparisons by future studies. For seasonal movements, due to the presence of zero values in the sample × species data matrix, fishes were grouped *a priori* by subjecting the data for all dates combined to canonical correspondence analysis (CCA), as per ter Braak (1986), using the ADE software library (Thioulouse et al. 1997; Chessel & Thioulouse 1998). Analysis of the data matrices (samples-by-species, samples-by-environmental trends) was used to reveal the best synthetic gradients that maximise species/age-class separation (ter Braak & Verdonschot 1995). In addition, triplots were produced (ter Braak 1986) that combined the ordinations of samples, species/age classes and environmental vectors (trends) for relevant ordination axes (dimensions), and which revealed associations between species/age groups for axis 1 versus axis 2 and versus axis 3 (Fig. 2). The groups were (Table 1 for codes): cyprinids (Ab0, Ab1, Cc0, Gg0, Gg1, Lc0, Lc1, Ll0, Ll1, Pp0, Rr0, Rr1), benthic non-cyprinids (Cg0, Cg1, Nb0, Nb1), sticklebacks (Ga0, Pu0) or potential piscivores ('predators': An0, An1, El0, El1, Pf0, Pf1) ('0' = 0+ age class, '1' = 1+ age class). For eel (An0, An1), the suffix indicates the number of years spent in fresh water, rather than the age of the fish *per se*. Seasons were defined as spring (March–May), summer (June–August), autumn (September–November) or winter (December–February). For both seasonal and age-class movements, the number of individuals of each group/species immigrating and emigrating was then summed over all sampling events. This resulted, for each group × season × time of day (seasonal movements) and species × age × time of day (age-class movements) combination, in the simple binomial mode:

$$p(y|\theta) = \text{Bin}(y|n, \theta)$$

where y is the number of fish immigrating, n the total number of fish captured, and θ the proportion of fish immigrating. To perform Bayesian inference a uniform prior distribution for θ in the interval [0, 1] (i.e., with individual fish having the same probability of either immigrating or emigrating) was deemed reasonable, in which case the posterior distribution is Beta($\theta|\alpha + y, \beta + n - y$). As per Gelman et al. (2004), 1000 draws were first obtained from the beta distribution (S-Plus[®]

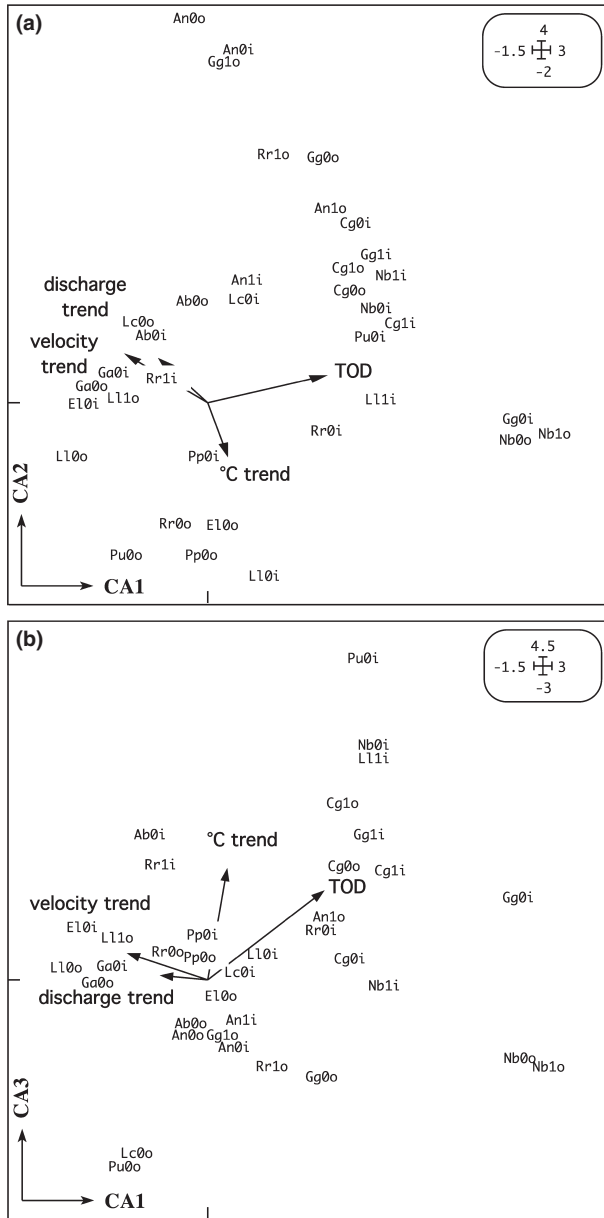


Fig. 2. Canonical correspondence analysis triplots of movements (suffix 'i' = from the River Avon to Ibsley Brook; suffix 'o' = from Ibsley Brook to the River Avon) by fish species/age classes (codes as in Table 1) relative to the time of day (TOD = day, night) and environmental trends (see Methods): river stage (fast falling = decreases of $>0.4 \text{ cm}\cdot\text{h}^{-1}$; slow falling = -0.4 to $-0.01 \text{ cm}\cdot\text{h}^{-1}$; no change; slow rising = 0.01 to $0.4 \text{ cm}\cdot\text{h}^{-1}$; fast rising = increases of $>0.4 \text{ cm}\cdot\text{h}^{-1}$); brook water velocity (decreasing, $< 0 \text{ cm}\cdot\text{s}^{-1}$; no change = 0 ; increasing, $> 0 \text{ cm}\cdot\text{s}^{-1}$); water temperature (fast falling = mean decreases of $>0.02 \text{ }^\circ\text{C}$ per 10 h; slow falling = mean decreases of 0.01 to $0.02 \text{ }^\circ\text{C}$; no change; slow rising = mean increases of 0.01 to $0.02 \text{ }^\circ\text{C}$; fast rising = mean increases of $>0.02 \text{ }^\circ\text{C}$). The length of the trend vector indicates the relative importance of that variable in the ordination (ter Braak & Verdonschot 1995).

2000 Professional Release 2 for Windows TIBCO Software, Palo, Alto, California, USA), the logit transform $\log(\theta/1 - \theta)$ was then applied to each draw

Table 1. Species name, common name, species code, and numbers of fishes trapped in the confluence of the River Avon and Ibsley Brook, November 1999–October 2000.

Species name	Common name	Code	No.	Group
<i>Abramis brama</i>	Common bream	Ab	34	Cy
<i>Anguilla anguilla</i>	European eel	An	25	Pred
<i>Barbatula barbatula</i>	Stone loach	Nb	245	Ben
<i>Cottus gobio</i>	European bullhead	Cg	197	Ben
<i>Cyprinus carpio</i>	Common carp	Cc	1	Cy
<i>Esox lucius</i>	Northern pike	El	12	Pred
<i>Gasterosteus aculeatus</i>	Threespine stickleback	Ga	382	Stic
<i>Gobio gobio</i>	Gudgeon	Gg	22	Cy
<i>Leuciscus cephalus</i>	Chub	Lc	284	Cy
<i>Leuciscus leuciscus</i>	Dace	Ll	158	Cy
<i>Perca fluviatilis</i>	Eurasian perch	Pf	32	Pred
<i>Phoxinus phoxinus</i>	European minnow	Pp	241	Cy
<i>Pungitius pungitius</i>	Ninespine stickleback	Pu	9	Stic
<i>Rutilus rutilus</i>	Roach	Rr	126	Cy
<i>Salmo salar</i>	Atlantic salmon	Ss	1	—
<i>Scardinius erythrophthalmus</i>	Rudd	Se	1	—
<i>Tinca tinca</i>	Tench	Tt	1	—

Group codes: Cy = cyprinids, Ben = benthic non-cyprinids, Stic = sticklebacks, Pred = potential piscivores.

and, finally, the 95% interval on the logit scale was inverted to obtain a normal approximation for θ including the median (Microsoft Excel[®] 2007 for Windows).

For analysis of environmental triggers of fish movements, abiotic variables were converted to semi-quantitative categories that reflected trends. This was because trends in environmental conditions are widely regarded as more influential than absolute conditions *per se* (e.g., Bischoff & Wolter 2001). This approach did not prevent a systematic analysis of the environmental triggers of fish movements, however, as all possible combinations of abiotic conditions were encountered during the study. River-stage trends ($\Delta \text{ cm}\cdot\text{h}^{-1}$, over a 10-h sampling period) were classed as: fast falling (decreases of $>0.4 \text{ cm}\cdot\text{h}^{-1}$), slow falling (-0.4 to $-0.01 \text{ cm}\cdot\text{h}^{-1}$), no change, slow rising (0.01 to $0.4 \text{ cm}\cdot\text{h}^{-1}$), and fast rising (increases of $>0.4 \text{ cm}\cdot\text{h}^{-1}$). Trends in brook water velocity were determined as the difference between the greater and lesser values (scale: -4 = maximum decrease to $+4$ = maximum increase) and classed as: decreasing (< 0), no change (0), increasing (> 0). Water-temperature trends ($\Delta \text{ }^\circ\text{C}$ per 10-h sampling) were classed as: fast falling (mean decreases of $>0.02 \text{ }^\circ\text{C}$ per 10 h), slow falling (mean decreases of 0.01 to $0.02 \text{ }^\circ\text{C}$), no change, slow rising (mean increases of 0.01 to $0.02 \text{ }^\circ\text{C}$), and fast rising (mean increases of $>0.02 \text{ }^\circ\text{C}$). Samples were also coded by the time of day (TOD) of collection: daytime (the traps were set as soon as possible after sunrise until as close as possible to sunset), night-time (the interval outside of 'day-time'). To provide a synthesis of the movement

Fish migrations between a river and tributary

patterns of the groups of fish species defined above (cyprinids, benthic non-cyprinids, sticklebacks, predators) relative to environmental trends, CCA (ter Braak 1986) was performed on the samples-by-species groups and samples-by-environmental trends matrices. For illustrative purposes, the 90% confidence intervals for samples by seasons (defined above) are presented in the CCA triplot as ellipses (Green 1971).

Results

A total of 1770 specimens of 17 fish species was captured during the study (Table 1), the majority of which were 0+ individuals (i.e., <1-year-old). The most abundant species were European bullhead, bream, chub, dace, European minnow, roach, stone loach and threespine stickleback. Other species captured in smaller numbers were European eel, gudgeon, Eurasian perch, northern pike, ninespine stickleback, and single specimens of common carp (64 mm FL), rudd (87 mm FL), Atlantic salmon (86 mm FL) and tench (425 mm FL). The CCA triplots, of all sampling dates combined, revealed a relatively clear distinction between day (lower left half of plots a and b in Fig. 2) and night-time samples (upper right half of plots a and b in Fig. 2). Simultaneous interpretation of the 1 × 2 (Fig. 2a) and 1 × 3 (Fig. 2b) plots revealed that cyprinid age classes were associated with each other during both day and night, as were those of benthic non-cyprinids and potential predators (most notably in Fig. 2b). Similarly, all stickleback movement occurred during the daytime except the movements of ninespine stickleback into Ibsley Brook, which occurred at night.

The intensity and direction of fish movements between the River Avon and Ibsley Brook varied temporally, both on a diel and seasonal basis, and there were species- and age-specific differences in behaviour (Tables 2 and 3). The movements of bullhead, stone loach, gudgeon and eel were mostly nocturnal, whereas pike, perch, minnow and threespine stickleback were mainly diurnal; dace, bream, chub and roach showed less diel variation in behaviour (Table 2). The direction of movements also differed between fish species (Fig. 3). Regardless of time of day/night, 0+ bream, dace and minnow always had a higher probability of moving into the brook than the river, whereas bullhead, pike, threespine stickleback and stone loach always had a higher probability of moving into the river. By contrast, 0+ chub and ninespine stickleback generally moved into the river in daylight and into the brook at night, whereas the opposite behaviour was observed in perch. Amongst 1+ fishes, bullhead and pike always had higher probabilities of emigrating (similar to 0+ individuals), and chub of immigrating, whereas different day–night behaviours were displayed by eel (immigration in

Table 2. Numbers (CPUE: standardised as mean numbers per 10 h) and fork length ranges in mm (total length for An, Cg, Ga, Nb, Pu) of fishes trapped in the confluence of the River Avon and Ibsley Brook grouped according to time of day and age. Immigrating (into the brook from the river); Emigrating (into the river from the brook). Codes as in Table 1.

Age	Code	Length range	Day		Night	
			Immigrating	Emigrating	Immigrating	Emigrating
0+	Ab	<70	0.21	0.06	0.23	0.07
	An*	<100	0	0	0.05	0.12
	Cc	64	0	0	0	0.01
	Cg	≤50	0	0.07	0.11	0.90
	El	<150	0.06	0.11	0.01	0.04
	Ga	<55	2.50	3.63	1.11	1.21
	Gg	<45	0	0	0.03	0.05
	Lc	≤50	0.87	1.37	1.85	0.78
	Li	≤70	1.27	0.94	0.52	0.12
	Nb	<68	0	0.04	0.14	0.74
	Pf	<60	0.71	0	0	0.04
	Pp	<60	1.94	1.64	1.08	0.50
	Pu	24–44	0	0.21	0.04	0
Rr	≤70	0.27	0.77	0.50	0.20	
Ss	86	0	0	0	0.01	
1+	Ab	70–75	0.03	0	0	0
	An*	100–550	0.03	0	0.07	0.08
	Cg	50–90	0	0.02	0.12	1.37
	El	150–320	0	0.03	0	0.01
	Gg	45–85	0	0	0.05	0.16
	Lc	50–142	0.02	0	0.06	0
	Li	71–116	0.03	0.11	0.16	0.05
	Nb	68–104	0	0	0.01	2.39
	Pf	60–165	0	0.02	0.01	0.01
	Rr	70–105	0.04	0.04	0.04	0.38
	Se	87	0	0	0	0.01

*number of years in fresh water

Table 3. Numbers of fishes (CPUE: standardised as mean numbers per 10 h) trapped in the confluence of the River Avon and Ibsley Brook grouped according to season and time of day (TOD). Immigrating (fish moving into the brook from the river); Emigrating (fish moving into the river from the brook). Codes as in Table 1.

Season/TOD	Immigration				Emigration			
	Cy	Ben	Stic	Pred	Cy	Ben	Stic	Pred
Autumn/day	3.3	0	1.1	0	3.6	0.1	1.6	0.1
Autumn/night	8.0	0.0	0.8	0	2.5	0.1	0.4	0.0
Spring/day	0.2	0	0.2	0	11.9	0.2	1.6	0.2
Spring/night	3.4	0.0	0.1	0	1.4	36.7	2.9	0.3
Summer/day	12.7	0	8.3	3.1	5.9	0	12.1	0.3
Summer/night	3.1	0	3.4	0.6	4.5	0.1	3.0	1.1
Winter/day	1.4	0	0.2	0	3.3	0.2	0.5	0.1
Winter/night	3.2	1.0	0.4	0	1.1	3.8	0.2	0.0

daylight, emigration at night) and by dace, perch and roach (emigration in daylight, immigration at night).

Amongst the four main groups of fishes, cyprinids displayed the most diverse seasonal behaviours (Figs 4 and 5). In spring and winter they emigrated (brook to river) in daylight and immigrated (river to brook) at night, whereas in summer the opposite behaviour was observed; autumn movements were

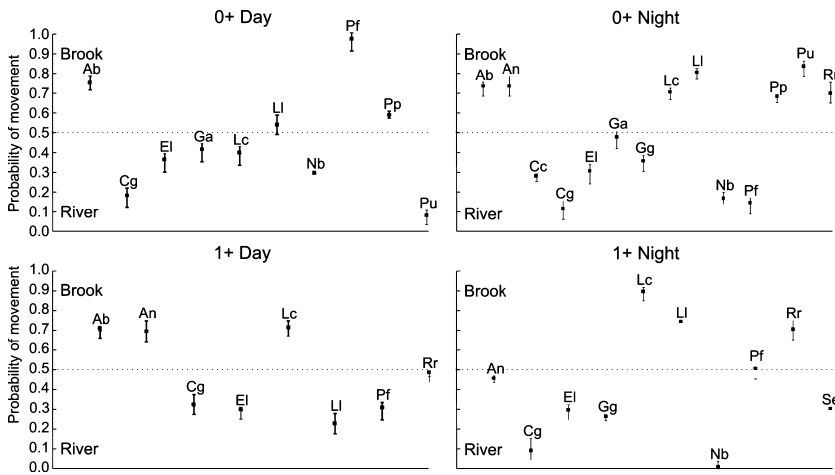


Fig. 3. Bayesian posterior medians and 95% intervals for the probabilities of diel movement of 0+ and 1+ fishes between the River Avon and Ibsley Brook (seasons combined). Brook: immigration (into the brook); River: emigration (into the river).

always into the brook. By contrast, benthic non-cyprinids always migrated out of the brook, regardless of season and time of day, except during daylight in summer when no migration was observed. Sticklebacks always emigrated during daylight, regardless of season, and showed a preference for immigration at night (summer, autumn and winter), except in spring. Finally, potential piscivores (predators) always emigrated, except during daylight in summer when they immigrated (Figs 4 and 5).

The environmental factors affecting the direction of fish movements differed across groups (Fig. 5). Thus, immigrations of cyprinids were influenced by increasing river stage and brook water velocity, whereas benthic non-cyprinids emigrated with increasing velocity. By contrast, sticklebacks always emigrated during daylight and immigrated at night with increasing temperature, whereas potential piscivores emigrated according to stage and time of day (Fig. 5).

Discussion

Hydrological connectivity between rivers and their tributaries and flood plains is essential for the natural functioning of river ecosystems (Amoros & Bravard 1985; Amoros & Roux 1988; Copp 1989; Junk et al. 1989; Ward & Stanford 1995). For fishes, the significance of connectivity between rivers and their flood plains as spawning and nursery habitats is well known (e.g., Welcomme 1985; Hohnausová et al. 2003). In some river systems, tributaries can serve similar functions as refuge and spawning or nursery habitats. For example, a range of fish species have been observed to use a tributary of the River Meuse, the Netherlands, as spawning, nursery and adult habitats (Pollux et al. 2006). Similarly, a number of tributaries of the River Ouse (Yorkshire, England) are important spawning and nursery habitats for lampreys (Petromyzontidae), with little if any spawning occur-

ring in the Ouse itself (Nunn et al. 2008). Notwithstanding, the migratory behaviour of fishes in lowland river ecosystems, particularly of non-spawning migrations between rivers and tributaries, remains poorly understood.

The most extensive migrations in the majority of temperate riverine fishes occur in late spring and early summer, when most species congregate to spawn, and a number of studies have demonstrated that water temperature and photoperiod are influential factors (see Baras & Lucas 2001). By contrast, surprisingly few studies have identified the key environmental correlates for non-spawning migrations, which appear to vary between seasons as a function of a combination of variables. Knowledge of how riverine fishes respond to environmental stimuli in dynamic ecosystems is fundamental to understanding the small-scale migrations often associated with foraging or predator evasion. The present study revealed diel and seasonal variations in the composition of fishes migrating between a main river channel and a small tributary. Cyprinids displayed the most diverse behaviours. In spring and winter, they emigrated (brook to river) in daylight and immigrated (river to brook) at night, whereas in summer the opposite behaviour was observed; autumn movements were always into the brook. Seasonal movements were mostly driven by changes in river discharge and water temperature, particularly those associated with floods. Specifically, cyprinids migrated from river to tributary with increasing river discharge and tributary water velocity, whereas bullhead and stone loach moved into the river. Similar to the use of floodplain water bodies by fishes during floods (e.g., Hohnausová et al. 2003), it is possible that increasing river discharge and water velocity stimulated the fishes to seek shelter, either in the tributary or the margins of the Avon. This may be particularly the case for young or small fishes, as studied here, due to their poor swimming ability

Fish migrations between a river and tributary

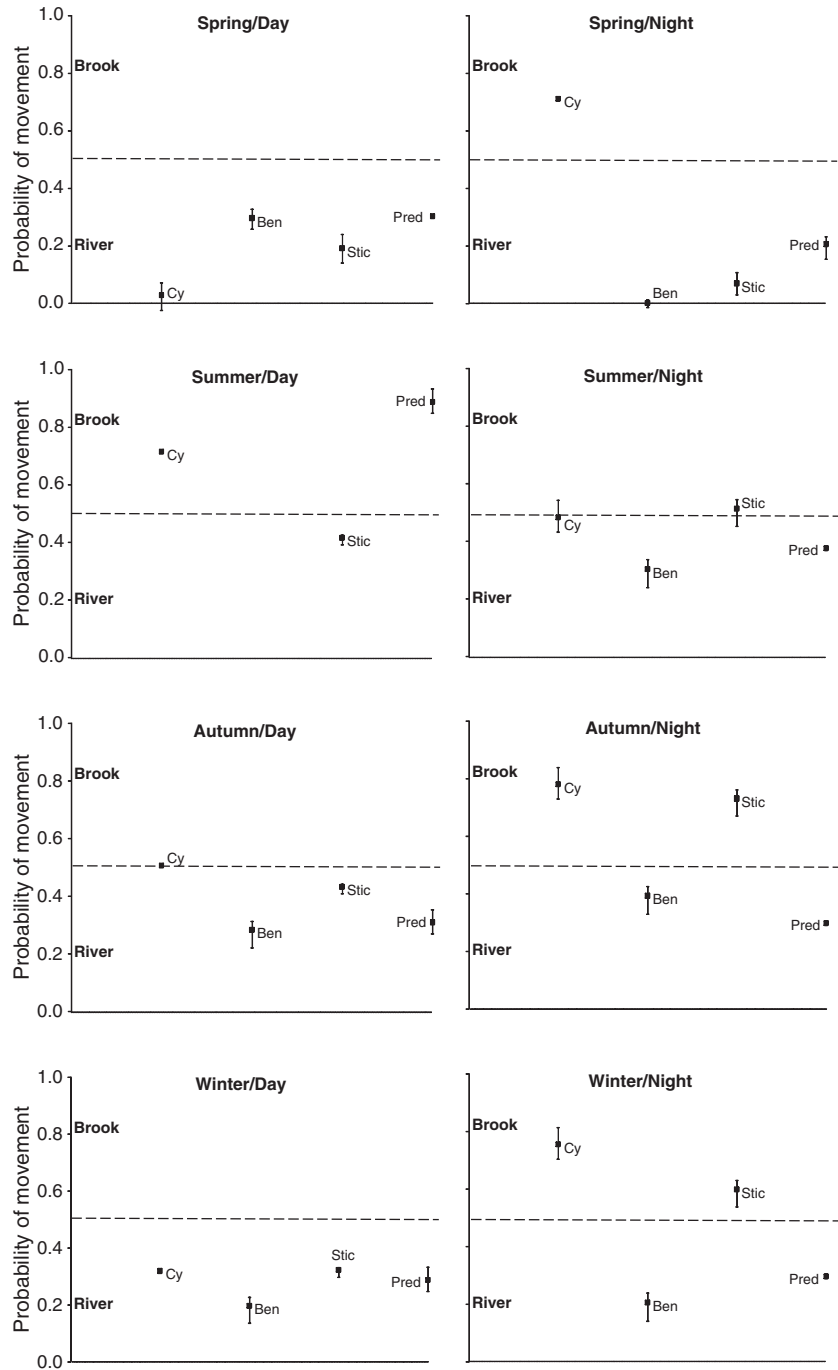


Fig. 4. Bayesian posterior medians and 95% intervals for the probabilities of diel movement of fish groups (codes as in Table 1) between the River Avon and Ibsley Brook according to season and time of day. Brook: immigration (into the brook); River: emigration (into the river).

compared with larger individuals. Alternatively, increasing discharge and water velocity may have stimulated mid-water species, such as most of the cyprinids, to move upstream to compensate for downstream displacement, whereas benthic species, such as bullhead and stone loach, may have moved downstream in response to increased bed load. Changes in water temperature have also been correlated with shifts in the behaviour and habitat use of fishes (Alabaster & Robertson 1961; Hohausová et al. 2003; Heermann & Borchering 2006).

Movements of fishes may occur with or without changes in river level or temperature (Hohausová et al. 2003), indicating that other factors can have an influence on migration behaviours. For example, habitat shifts in stream fishes are often elevated at dusk and night in small streams (Copp & Jurajda 1993; Bischoff & Scholten 1996), irrespective of discharge conditions (Copp et al. 2005a,b). In larger European water courses, such as the Danube, fish densities in side-channels tend to peak during daylight (Copp et al. 2005b), whereas in water

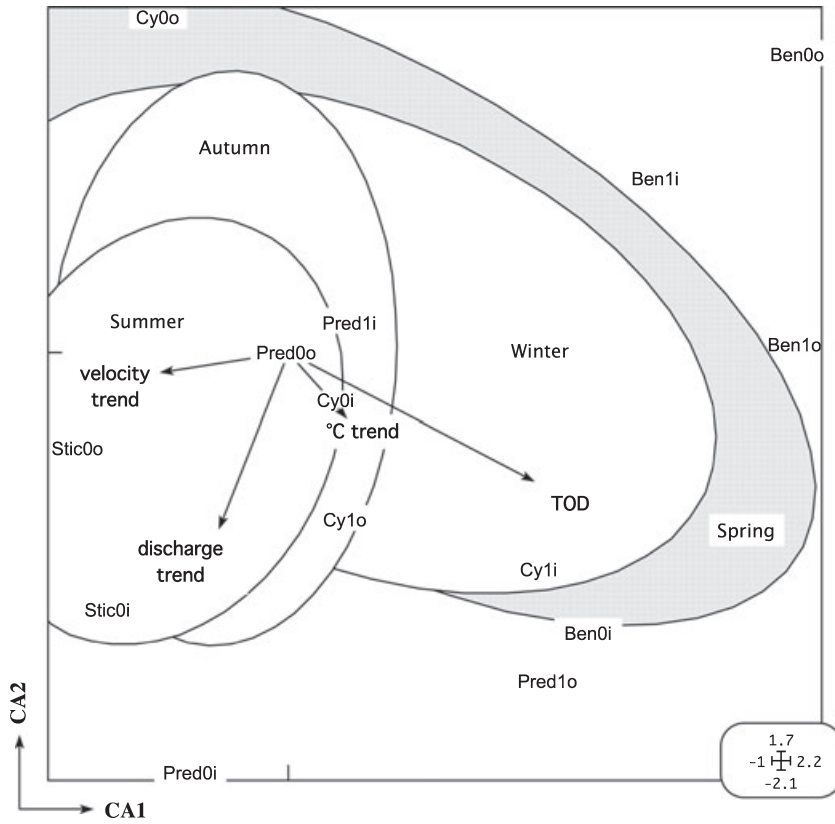


Fig. 5. Canonical correspondence analysis triplot of movements (suffix 'i' = from the River Avon to Ibsley Brook; suffix 'o' = from Ibsley Brook to the River Avon) by groups of fish species (codes as in Table 1) relative to the time of day (TOD = day, night) and environmental trends (river stage; brook water velocity; water temperature). See Fig. 2 caption for details and explanation. Samples by season are represented by 90% confidence ellipses (Green 1971).

courses of small-to-medium width (e.g., rivers Lee, Morava and Sieg) fish densities generally peak at night (Copp & Jurajda 1993, 1999; Bischoff & Scholten 1996; Copp 2004; G.H. Copp unpublished data). This general pattern appears to apply to the River Garonne (Mastrorillo & Copp 2005), a relatively large river in southwestern France, where peak numbers of 0+ fishes would be expected during daylight. In the River Avon, a medium-sized river, diel movements appeared to be triggered by changes in light intensity and brook water velocity, with the numbers of migrating fishes generally being greatest at night in some species and during daylight in others. Notably, the movements of bullhead, stone loach, gudgeon and eel were mostly nocturnal, whereas pike, perch, minnow and threespine stickleback were mainly diurnal; dace, bream, chub and roach showed less diel variation in behaviour. Furthermore, although some species consistently moved from river to brook, others migrated from brook to river. Inter-specific differences in the migration of adult fishes has been observed in the River Derwent (Yorkshire, England), with chub migrating at night, whereas other species migrated over a wide range of light conditions (Lucas 2000). By contrast, stocked juvenile cyprinids migrated mostly during daylight. The decline in daytime movement between early winter and early spring

observed in this study has also been reported in the River Rhine, with light suggested as the most important stimulus for the migration of most fishes into backwaters and floodplain lakes at twilight (Borcherding et al. 2002).

Other factors that may influence fish movements include the risk of predation. Diurnal species seek refuge from predation at night and move to profitable foraging habitats during daylight, while the opposite behaviour is characteristic of nocturnal species. In the present study, bullhead, stone loach and gudgeon were mostly nocturnal, whereas minnow and threespine stickleback were mainly diurnal, and it is possible that this was associated with directed movements to foraging habitats. Explorative behaviour, which is often undirected and stochastic, will also contribute to observed fish distributions (Vilizzi & Copp 2005). However, that there were consistent inter-specific differences in the timing, intensity and direction of movements suggests that explorative movements were relatively unimportant at the population level. The activity of predators can also vary on a diel basis (Copp & Jurajda 1993, 1999). As anticipated, perch and pike, which are principally sight predators, were most active during daylight, whereas the eel, a mainly nocturnal predator, was most active at night. Notwithstanding, the patterns in the probabilities of predator migration did not closely follow those of the prey

species, and there was no evidence that predators adjusted their behaviour according to the movements of particular prey species.

The impacts of habitat fragmentation on biodiversity have become increasingly recognised in recent years (Saunders et al. 1991; Fahrig 2003). In rivers, reduced hydrological connectivity may impede or eliminate access by fishes to key habitats, and modifications to sediment dynamics may alter the quality of potential spawning areas. Furthermore, tributary confluences represent one of the most heterogeneous and biologically diverse freshwater habitats (Benda et al. 2004). Maintaining connectivity between rivers and their tributaries is essential given the importance of tributaries in the diel and seasonal cycles of fishes, as well as a corridor for nutrient exchange (Junk et al. 1989; Ward & Stanford 1995). Any modification to hydrological regimes may, temporarily or permanently, reduce or eliminate the connectivity between rivers and tributaries, with inherent implications for both resident and migratory biota. This study emphasises the importance of connectivity in river systems, as fishes migrated in all flow conditions, but especially during rapidly rising discharge.

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