Autumnal habitat use of non-native pumpkinseed *Lepomis gibbosus* and associations with native fish species in small English streams

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A b s t r a c t. Habitat use of introduced pumpkinseed *Lepomis gibbosus* in small European streams has received little study despite the species' potential associations to native fauna of conservation and angling amenity, e.g. brook lamprey *Lampetra planeri*, European bullhead *Cottus gobio,* brown trout *Salmo trutta*. We examined body size, relative body condition, habitat use and species-species associations of pumpkinseed with accompanying fishes in two small streams in southern England during August 2001. Pumpkinseed body condition decreased with pumpkinseed density; the latter correlated with % clay and % riparian grasses in fish < 63 mm FL, with % riparian shrubs in fish 83–92 mm FL and with water depth in fish > 92 mm FL. Most pumpkinseed size classes occurred more often than expected in stretches with conspecifics and with brown trout >300 mm FL; densities of the latter did not correlate with any habitat variables. Indeed, correlations between trout densities and habitat variables were observed mainly in smaller size classes. Habitat associations in other species corresponded to known levels of rheophily; substratum, channel slope, channel width and riparian trees were also important habitat variables. Pumpkinseed dispersal and establishment under conditions of climatic change, which could have ecological and management ramifications, are discussed.

Key words: electivities, canonical correspondence analysis, invasiveness, lag-phase, establishment, condition index, Sussex Ouse

Introduction

An important aspect of invasion success in fishes is their adaptation to habitats outside their native range (F a u s c h et al. 2001). The pumpkinseed sunfish *Lepomis gibbosus* (L.) was introduced into European waters during the late 19th century and is now widely established in Europe (C o p p et al. 2002). Despite having been intentionally introduced in some areas (K ü n s t l e r 1908), the pumpkinseed was relatively quickly claimed to be detrimental to native species, in particular the Eurasian perch *Perca fluviatilis* (R o u l e 1931) although this remains unsubstantiated. Indeed, evidence from dietary and other studies remains equivocal with regards to the detrimental impacts by pumpkinseed on native European species (G o d i n h o & F e r r e i r a 1998, C o p p et al. 2002, D e c l e r c k et al. 2002). The most compelling evidence has been reported for Iberia (e.g. G o d i n h o et al. 1997, G u t i é r r e z - E s t r a d a et al. 2000). Aside from general studies of pumpkinseed biology and distribution (e.g. N e o p h y t o u & G i a p i s 1994, V i l a - G i s p e r t & M o r e n o - A m i c h 1998), habitat use of European pumpkinseed has received little study except for the microhabitat of larvae and juveniles in large river flood plains (C o p p 1993b, N i c o l a s & P o n t 1995, G r e n o u i l l e t & P o n t 2001, Č e r n ý et al. 2003).

Following its introduction to the British Isles in the late 19th century as an ornamental fish for estate ponds, the pumpkinseed remained unstudied until the 1999s (Copp et al. 2002), perhaps because its distribution was limited to ponds of southern England and because it was rarely encountered in UK rivers. More recently (late 1990s), the frequency and number of pumpkinseed observed in the River Ouse (Sussex) has increased, with the highest densities observed in stream sections downstream of on-line still waters at the top of two small tributaries, Sheffield Stream and Batts Bridge Stream (EA 2002). These stream populations of pumpkinseed appear to be maintained by inputs of escapee fish from on-line lakes rather than by in-stream recruitment, as no evidence yet exists to suggest that reproduction takes place in UK streams despite the presence of ripe fish (G.H. Copp, M.G. Fox & R. Horsfield, unpublished data). Regardless, the presence throughout the year of pumpkinseed in streams of the Sussex Ouse (R. Horsfield, unpublished data) poses potential risks to the native fishes of the catchment.

Therefore, as part of Environment Agency's duty to protect the aquatic environment, studies of pumpkinseed habitat use and diet are being undertaken in the Sussex Ouse to determine whether this non-native species is associated with habitat and food resources

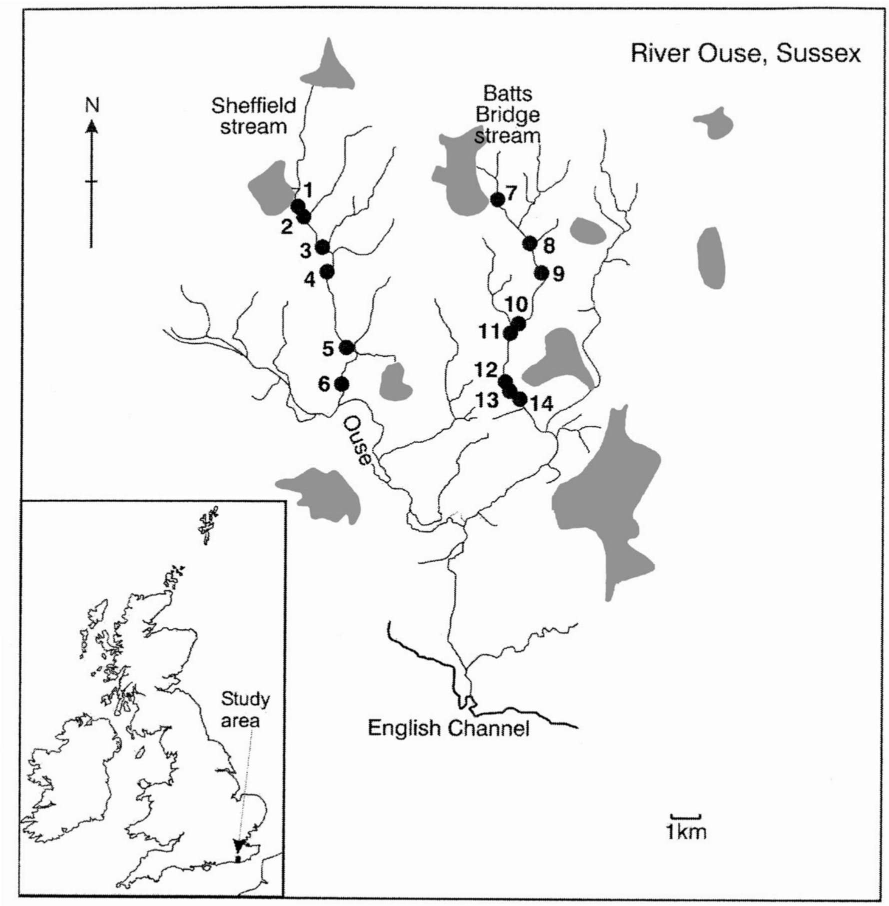

Fig. 1. Map of the Sussex Ouse with the location of study stretches indicated.

normally exploited by native fish species. The aim of the present study was to examine habitat use and potential associations of fish species in tributary streams of the Sussex Ouse, with the following specific objectives to: 1) determine fish distribution and density (catch per unit effort), 2) examine the size and condition of the pumpkinseed and test for any relationships between body condition and environmental factors, 3) test for relationships between species/size classes and habitat variables, and 4) test for associations that might suggest interactions between pumpkinseed and native fish species.

Study Site, Material and Methods

The River Ouse catchment (Sussex, England) arises from springs at Tunbridge Wells Sands about 90 m above sea level, has an area of about 664 km^2 and an approximately length of 62 km of which 21 km is tidal, and discharges into the English channel east of Brighton (NGR: TQ4513000095). The streams flow through rural areas and a number of large villages and towns, with the headwaters cutting deeply into the agricultural landscape, and the lowland stretches being of typical pool and riffle type topography. Study stretches were in the Sheffield and Batts Bridge streams (Fig. 1), two small tributaries of the Sussex Ouse. Sheffield Stream rises from springs near Nutley (NGR: TQ4425927551), flows southward for about 7.5 km, passing through or adjacent to a number of on-line lakes. For example, in the upper part of the Sheffield catchment, pumpkinseed are known to be established in a fishery (Tanyards) that consists of eight spring-fed, interconnected lakes, the last of which drains into Sheffield Stream via a 7 cm diameter pipe. Batts Bridge Stream, which rises from springs just east of Nutley (NGR: TQ4425927551), also flows southward (for about10.5 km) through a number of on-line fishing lakes and is joined by a number of smaller, spring-fed tributaries before entering the River Ouse at Sharpsbridge (NGR: TQ4430420663). For example, near the stream's source, pumpkinseed are known to be established in a trout fishery (Boringwheel Lake), which discharges directly into Batts Bridge Stream via a gated culvert.

Fish sampling and analysis

Sampling was undertaken in August 2001 by electrofishing (36 cm dia. aluminium ring anode, 1.9 kVa Honda generator, average voltage = 230 V, operating on average at 1 A, 50 Hz pulsed D.C.). Using upstream and downstream stop-nets of 12 mm mesh, the one-removal (Zalewski 1983) or 'strip sampling' (EA 2001) catch-per-unit effort (fish per m of stretch sampled) sampling strategy was employed. All captured fishes were measured for fork length and, except pumpkinseed, categorized by standard size class (0–100 mm, 101–200 mm, 201–300 mm, >301 mm FL). All native fishes were returned immediately to the water. All pumpkinseed were killed with an overdose of benzocaine or 2-phenoxyethanol and subsequently fixed in 10% formaldehyde solution.

Stream habitat was evaluated using an adapted form of the HABSCORE assessment method (Milner et al. 1998), which recognises stream depth, current and substrate as being the three most important variables in determining stream fish diversity and distribution (Gorman & Karr 1978). Each study site was divided into a series of 10 m sections in which measurements were made of channel width (m), depth (in cm, at the 1/4, 2/4 and 3/4 distance across each transect), substratum composition (in % of section area estimated visually: clay, < 0.06 cm; silty sand, < 0.2 cm; gravel, 0.2–6.4 cm; coarse alluvia, > 6.5 cm), submerged and emergent aquatic vegetation (% of section area), riparian trees, shrubs and grasses (all as % of bank length). Water velocity was determined using a flat ruler placed perpendicular to the substratum and categorized as: 1 = slack shallow, 2 = slack deep, 3 = glide/run shallow, 4 = glide/run deep, 5 = turbulent/broken shallow, 6 = turbulent/broken deep, 7 = cascade/torrential (slack water = no ripple effect around the ruler; glide = a ripple or whirl effect around the ruler; turbulent = noisy turbulent flow around the ruler; shallow refers to < 30 cm and deep to ≥ 30 cm).

In the laboratory, pumpkinseed length and weight were measured to the nearest mm and g, respectively. To account for variations in body condition due to size differences, relative body condition was calculated using Le Cren's (1951) formula (see Copp 2003), which requires populations to be sampled at same time of year: $K = w/w'$, where w is the observed weight of each individual and w' is the expected weight using the

Table 1. List of fish species, codes and corresponding size classes (mm fork length) observed at 14 study stretches of the Sussex Ouse catchment, southern England, in July and August 2002. Species without a code occurred at too few sites to be included in the analyses.

Latin name	Common name	code	Size class
Abramis brama	bream	—	—
Anguilla anguilla	eel	An1	0–100
		An2	101–200
		An3	201–300
		An4	> 300
Barbatula barbatula	stone loach	Nb+	all sizes
Carassius auratus	brown goldfish	—	—
Cottus gobio	bullhead	Cg+	all sizes
Cyprinus carpio	common carp	—	—
Esox lucius	pike	El+	101–400
Gasterosteus aculeatus	three-spine stickleback	Ga+	all sizes
Gogio gobio	gudgeon	Gg1	0–100
		Gg+	> 100
Lampetra planeri	brook lamprey	Lp1	0–100
		Lp2	101–200
Lepomis gibbosus	pumpkinseed	Lg1	< 63
		Lg2	63–72
		Lg3	73–82
		Lg4	83–92
		Lg5	> 92
Leuciscus cephalus	chub	Lc2	0–200
		Lc4	> 200
Leuciscus leuciscus	dace	—	—
Oncorhynchus mykiss	rainbow trout	—	—
Perca fluviatilis	perch	Pf1	0–100
		Pf+	101–300
Phoxinus phoxinus	minnow	—	—
Rutilus rutilus	roach	Rr1	0–100
		Rr2	101–200
		Rr3	201–300
Salmo trutta	brown trout	St1	0–100
		St2	101–200
		St3	201–300
		St4	> 300
Scardinius erythrophthalmus	rudd	Se+	all sizes
Tinca tinca	tench	Tt+	all sizes

Table 2. Mean values for environmental variables measured at numerous sections (n) within 14 stretches of stream/river of the Sussex Ouse catchment (u/s = upstream, m/s = mid-stream, d/s = downstream) in southern England (July and August 2002): distance from source (in km), channel width (in m), water depth (in cm), channel slope (mid-channel depth ÷ 1/2 of channel width), % substratum types (clay: < 0.06 cm; silty sand: < 0.2 cm; gravel: 0.2–6.4 cm; coarse alluvia: > 6.5 cm), water velocity mode (vm: 1 = slow to moderate, 2 = moderate fast, 3 = faster, 4 = very fast), water velocity range (vr: 1 = moderate, 2 = elevated, 3 = very variable), % aquatic vegetation (aquat. = submerged and emergent), % of bank containing trees, shrubs and overhanging grasses. Variables with which pumpkinseed density in $\log_{10}$ (^{D}) and body condition (^{K} = Le Cren) are significantly ($P < 0.05$) related (regression: width, depth, slope; Spearman's Rank correlation: all others), with underline indicating $P = 0.10$.

site no.	site name	Nat. Grid Reference	dist. source	n	channel width	water depth^{K,D}	channel slope^{K,D}	Substratum clay	sand	gravel	coarse alluvia^{K,D}	Velocity mode	range	aquat.	Vegetation trees	shrubs	grasses
1	Tanyard u/s	TQ 409 272	3.0	9	1.49	21.7	0.33	38.9	59.4	1.7	0	1	1	0	20.0	21.1	3.3
2	Tanyard m/s	TQ 410 269	3.5	4	1.64	25.9	0.34	5.3	41.2	49.2	4.3	1	1	0.3	18.2	19.6	6.8
3	Tanyard d/s	TQ 414 263	4.3	19	1.75	25.7	0.31	5.4	57.1	34.5	2.9	1	1	0.3	18.4	13.4	6.8
4	Sheffield Mill	TQ 415 257	4.9	18	2.40	15.8	0.15	5.6	23.9	41.9	29.2	1	1	0	30.2	5.5	0.1
5	Sheffield Park u/s	TQ 420 243	6.9	18	2.36	32.9	0.33	22.5	69.7	7.5	0.3	1	1	7.5	19.4	21.1	0.8
6	Sheffield Park	TQ 418 234	7.9	20	3.39	30.4	0.21	6.0	69.3	18.8	6.3	3	2	1.4	17.3	20.5	0.6
7	Chestnut Farm	TQ 450 273	1.3	19	1.41	16.7	0.26	8.3	20.3	24.9	46.6	3	3	0	29.2	14.8	4.3
8	Cackle Street	TQ 457 263	2.3	17	2.31	29.2	0.25	4.2	18.8	72.3	4.9	2	1	0	38.8	5.7	9.6
9	Old Forge Lane	TQ 459 258	3.0	15	2.33	15.6	0.15	8.5	16.7	34.7	42.5	3	2	0	33.0	18.7	1.0
10	Cavewood u/s	TQ 455 248	4.2	8	3.62	26.9	0.20	25.0	20.6	38.1	12.5	2	2	0.3	4.4	31.3	1.3
11	Cavewood d/s	TQ 452 246	4.5	9	3.30	28.8	0.20	7.2	66.1	21.1	5.6	1	1	0.6	26.7	7.4	0.8
12	Batts Upper	TQ 452 234	6.0	20	2.32	22.0	0.19	7.0	15.4	76.8	0.9	3	1	0.3	30.3	17.0	2.9
13	Batts Middle	TQ 453 234	6.1	19	2.86	21.7	0.18	12.9	8.1	67.1	12.2	4	2	0.8	27.6	11.2	0
14	Batts Lower†	TQ 454 233	6.3	10	2.25	16.5	0.15	24.8	7.3	65.5	2.1	4	3	1.0	33.5	7.3	4.9

† a UK Environment Agency National Monitoring Programme site

length-weight relationship (W=aL^b, where in this case a = -5.54 and b = 3.449) for all pumpkinseed captured in August 2001. K values > 1 or < 1 indicate that the individual is in better or worse condition, respectively, than the average individual of same length range. Scale samples were taken from a sub-sample of pumpkinseed to determine age. Following length-frequency analysis, pumpkinseed were classed as < 63, 63–72, 73–82, 83–92, > 92 mm FL. Size classes of some species occurred at too few sites for analysis and these were either combined with contiguous size classes or the species was excluded from analysis entirely (Table 1). Relative fish density was calculated as the number of fish per 100 m of river stretch.

From the environmental data (Table 2), mean values were calculated for each study stretch (distance from source was measured from the mid-point of the stretch). For water

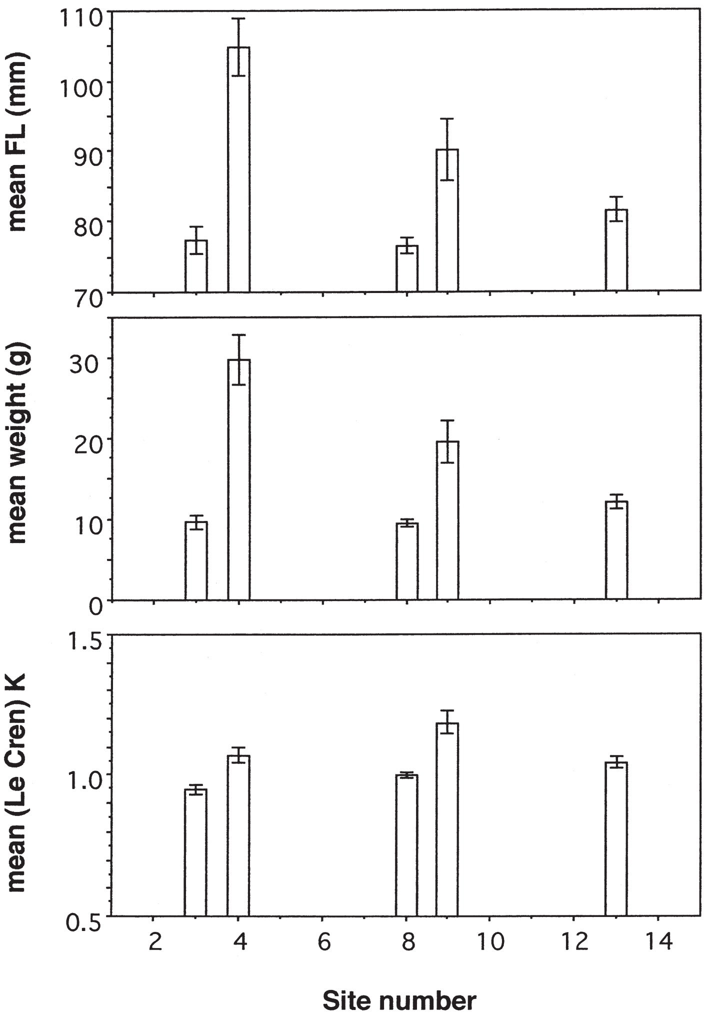

Fig. 2. Mean FL (in mm), body weight (in g) and Le Cren's condition index (K = observed weight ÷ expected weight) of pumpkinseed at sites in the Sussex Ouse catchment, August 2001 (see Table 2 for site names and locations).

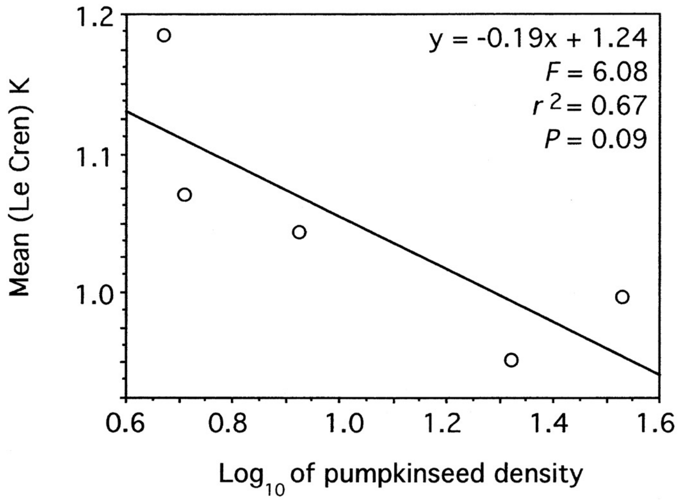

Fig. 3. Decreasing trend in Le Cren's condition index (*K* = observed weight ÷ expected weight) with increasing density of pumpkinseed (fish per 100 m stretch) at sites in the Sussex Ouse catchment, August 2001 (see Table 2 for site names and locations).

velocity categories, the modal value was used as a surrogate of the mean (except if two contiguous categories occurred in equal or nearly equal frequency, when the numerical mid-point between two categories was used [e.g. the mid-point between categories 4 and 5 = 4.5], or when the frequency was bi-modal, when the numerically intermediate category was used). The original seven velocity categories were then recoded as: 1 = slow to moderate, 2 = moderate-to-fast, 3 = fast, 4 = very fast. Because the frequency distributions of the 7 water velocity categories were contiguous and unimodal, the range of categories encountered at a given site could be used as a surrogate of variance. For this, the number of original velocity categories encountered at a given site was counted and categorized as: 1 = low (4 of the 7 velocity categories were encountered), 2 = moderate (5 of 7 categories were encountered), 3 = high (≥ 6 categories were encountered). Channel slope was calculated using mid-channel water depth divided by one half of stream width.

Associations between fish size classes (data $\log_{10}$ transformed to reduce influence of occasional high values) and environmental variables (raw quantitative, categorized qualitative) were tested using Spearman's correlation. Relationships between fish condition and environmental variables were tested using simple regression or Spearman's correlation as appropriate. To test for associations between fish size classes/species, the fish data were converted to absence/presence and subjected to Fisher Exact tests of observed and expected frequencies – the null hypothesis being that these do not differ at the 95% significance level. For a comprehensive view of fish-fish and fish-variable associations, the $\log_{10}$-transformed fish data and the environmental data ($\log_{10}$+1 transformed to reduce skewness) were subjected to canonical correspondence analysis (CCA; ter Braak 1986) and graphical treatment using software by Chessel & Thioulouse (1998). CCA was used to evaluate habitat breadth for each age class of fish, combining variables into the best synthetic gradients that maximise habitat separation; the calculation used weighted averages as estimates of the species optimum given that the response curve for that species is normal. The maximum habitat separation is given by the eigen value of the ordination axis

(M e r c i e r et al. 1992, ter B r a a k & V e r d o n s c h o t 1995). From the CCA, a triplot was produced, combining the ordinations for samples, species and environmental vectors (ter B r a a k 1986).

Results

Twenty species of fish and lamprey were encountered at the fourteen sites (Table 1). Among sites, pumpkinseed length, weight and condition were greatest at sites (4 and 9) where pumpkinseed densities were lowest (Fig. 2). Indeed, condition increased with decreasing pumpkinseed density (Fig. 3), though significant at 90% only. No relationship was found between pumpkinseed condition and distance from stream source, but *K* increased significantly (Table 1) with the increasing proportion of coarse alluvia as well as water depth and bank

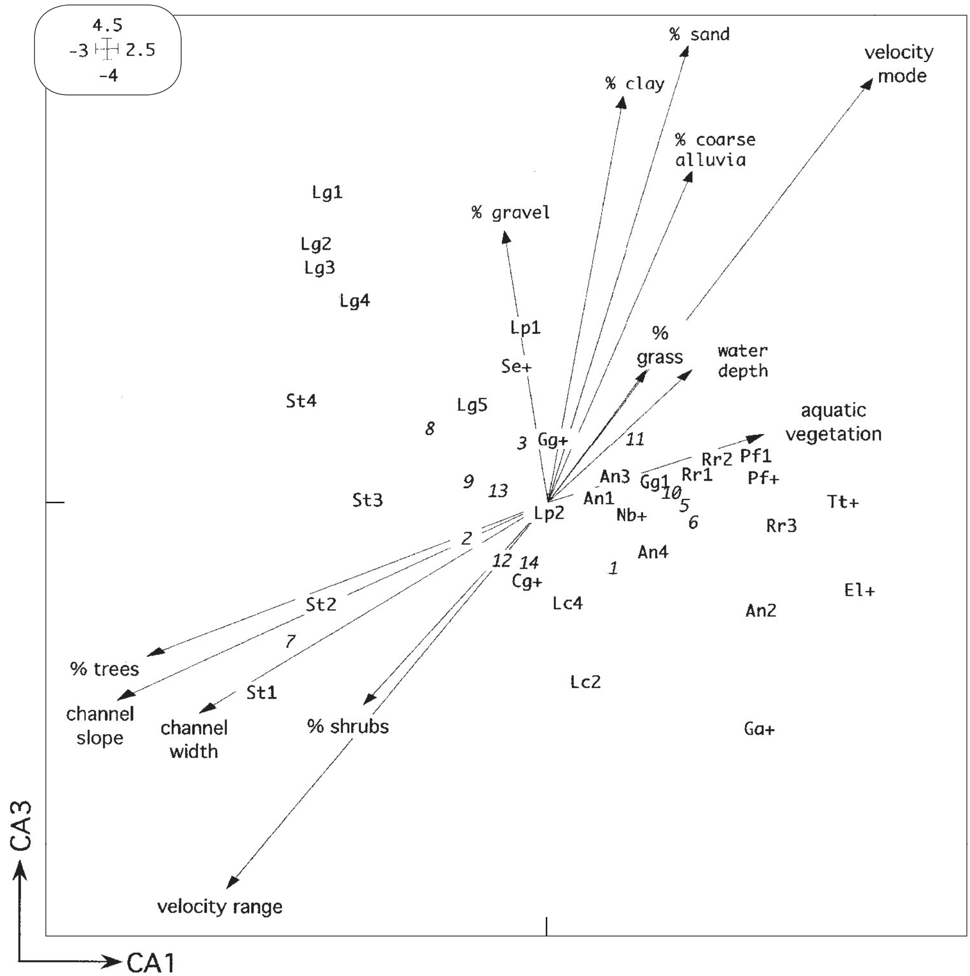

Fig. 4. Canonical correspondence analysis triplot for fish and environmental variables associations (factors 1 and 3) in the Sussex Ouse catchment, August 2001. The length of the vectors indicates their relative influence on the ordinations. Species/size class and variables codes given in Tables 1 and 2, respectively.

Table 3. Relationships between fish species/size classes (see Table 1 for codes) and environmental variables (see Table 2 for units) at 14 sites in the Sussex Ouse catchment, southern England, in July and August 2002. Positive (+) and negative (-) Spearman's correlations (*, $P = 0.10$; **, $P \leq 0.05$) and Fisher Exact higher than expected (h, $P = 0.10$; **H**, $P \leq 0.05$) frequencies for indicated categories by number (given in Table 2).

species	channel	water	channel	comp.	silty		coarse	water velocity		vegetation			
class	width	depth	slope	clay	sand	gravel	alluvia	modal	range	aquatic	trees	shrubs	grass
Gg1	*+	**+			**+				h, 1		*-		
Gg+													
Lg1				**-									**+
Lg2													
Lg3													
Lg4											**-		
Lg5		*-											
St1	**-	**-			**-	*+					**+		
St2	**-	*-			**-	*+				**-	*+		*+
St3				**-		*+				**-	*+	*-	
St4				**-									
Cg+					*-	**+			h, 2				
Lp1													
Lp2													
An1									H, 1			*-	
An2													
An3	**+		**-										
An4			*-										
Rr1	*+	*+			**+		*+		H, 3		**-		
Rr2	**+	*+			**+	*+			H, 3		*-		*-
Rr3	**+								h, 1&3				**-
Pf1	**+	*+											*-
Pf+				*-					h, 2	**+			
Lc2								H, 1&2		**+			
Lc4								H, 3&4	h, 1	**+			
El+	*+	*+								**+	*-	*+	
Nb+													
Ga+			**+		**+	**-	**-						
Tt+		**+			**+	*+				**+	*-		
Se+													

steepness. Pumpkinseed density ($\log_{10}$ transformed) was not correlated with distance from stream source, but that of brown trout (all size classes combined) decreased significantly ($F = 11.428$, df = 12, $r^2 = 0.488$, $P < 0.006$) with increasing distance from source. Pumpkinseed density did, however, increase with increasing water depth, bank steepness and proportion of coarse alluvia (Table 1). Mean FL and mean body weight (both in $\log_{10}$) both decreased with increasing pumpkinseed density at the same significance level.

The main environmental variables characterising habitat use were (in decreasing order by vector length, ter Braak & Verdonschot 1995): water velocity mode and range, various substratum types (% silty sand, clay, coarse alluvia, gravel), channel slope, channel width, and % riparian trees (Fig. 4). Note that canonical factors 1 and 3 are plotted here rather than 1 vs. 2, the latter being dominated by the high density of threespine stickleback *Gasterosteus aculeatus* at site 1. Site 7 also plays a somewhat distinctive role in the triplot due to a high density of the two smallest size classes of brown trout (St1, St2) and the absence of other fish species. The fish species/size classes are ordinated along a general trend in velocity mode and range, with limnophiles to the right and rheophiles to the left (Fig. 4). Size classes of limnophilous and ubiquitous species were characteristically

Table 4. Association analysis (Fisher Exact test) of observed and expected frequencies of occurrence between fish species/size classes (see Table 1 for codes) at 14 sites in the Sussex Ouse catchment, southern England, in July and August 2002. Higher than expected frequencies (preference) are indicated as: h ($P = 0.10$) or **H** ($P \leq 0.05$). Lower than expected frequencies (avoidance) are indicated as: l ($P = 0.10$) or **L** ($P \leq 0.05$).

	Gg+	Lg1	Lg2	Lg3	Lg4	Lg5	St1	St2	St3	St4	Cg+	Lp1	Lp2	An1	An2	An3	An4	Rr1	Rr2	Rr3	Pf1	Pf+	Lc2	Lc4	El+	Nb+	Ga+	Tt+	Se+
Gg1														l															
Gg+	—																		**H**			h					h	h	h
Lg1		—	h	h	h																								
Lg2			—	**H**	**H**	**H**				**H**		h																	
Lg3				—	**H**	**H**				**H**		h																	
Lg4					—	**H**				**H**																			
Lg5						—				h			h																
St1							—	**H**	**H**																**L**				
St2								—	h																			l	
St3									—																**L**			l	
St4										—					l														
Cg+											—																		
Lp1												—																	
Lp2													—																
An1														—										h					
An2															—		**H**				h		h		h	h			
An3																—	**H**												
An4																	—												
Rr1																		—											
Rr2																			—										
Rr3																				—									
Pf1																					—								
Pf+																						—						h	h
Lc2																							—	**H**					
Lc4																								—					
El+																									—				
Nb+																										—		**H**	
Ga+																											—	h	h
Tt+																												—	

associated with deeper, wider channels, fine sediments and/or aquatic vegetation (Table 3). However, few associations were observed with water velocity mode (chub), but roach (ubiquitous) occurred more often than expected in a wide range of velocities, whereas gudgeon, bullhead *Cottus gobio*, eel *Anguilla anguilla* and chub occurred more often than expected in areas of low or moderate velocity variance. Of these, only gudgeon (Gg1) and bullhead were correlated with a substratum type, silty sand and gravel, respectively. The rudd *Scardinius erythrophthalmus* and tench *Tinca tinca* (both limnophilous) were most probably escapees from on-line fisheries; rudd was not associated with any habitat variable, whereas tench densities correlated positively with water depth and silty sand, gravel and both in-stream vegetation and riparian trees (Table 3). Threespine stickleback correlated positively with channel slope and silty sand, but negatively with gravel and coarse alluvia.

Of particular note were the higher-than-expected co-occurrences of brown trout (St) and some pumpkinseed (Lg) size classes, in particular Lg2, Lg3 and Lg4 with St4 (Table 4). The ordination of pumpkinseed amongst the rheophilous species, in particular brown trout, does not appear to result from strong correlations with any particular habitat variables (Table 3). Rather, it may be due to the limited associations of pumpkinseed and St4 with any habitat variables as well as the higher-than-expected pumpkinseed co-occurrences with St4 (Table 4). Small trout (St1, St2), which were associated with larger trout (St3, St4) and occurred less-often-than-expected with pike, decreased significantly with increasing water depth and channel width. All three smaller size classes of trout increased significantly with increasing proportion of gravel and riparian trees (Table 3). By contrast, roach were positively correlated with water depth and channel width over a wide range of water velocities but negatively correlated with some types of riparian vegetation. Eel and chub also demonstrated intra-specific associations (Table 4).

Of additional note was the apparently suitable habitat for brook lamprey *Lampetra planeri* at Site 11 (Lower Cavewood) where a high catch-per-unit-effort coincided with substratum dominated by very fine sand and silt. However, despite occurring at a relatively high number of sites, neither size class of lamprey was correlated with any habitat feature (Table 3), and was only weakly associated ($P = 0.10$) with pumpkinseed (Table 4).

Discussion

Pumpkinseed populations in Europe are established mainly in still waters, whether they be lakes, reservoirs, floodplain lakes or ponds, marshes (e.g. Balon 1959, Crivelli & Mestre 1988, Copp et al. 2002). Of the few populations reported to have established in European water courses outside the UK, reproduction appears possible due to stable hydrological conditions that offer suitable lentic habitat (e.g. Copp & Cellot 1988, Godinho & Ferreira 1998). For example, pumpkinseed in a Spanish stream, the Guadiato (e.g. Gutiérrez-Estrada et al. 2000), occupy isolated stream pools created during aestival low discharge, June to September, which corresponds with the species' reproductive phase; these pools are shared with, among other species, introduced rainbow trout *Oncorhynchus mykiss*. Although reproduction in pumpkinseed may require lentic habitat, the species appears to be otherwise indifferent to water velocity (Fig. 4, Table 3; Copp 1993b, Černý et al. 2003), except as young-of-the-year in some situations (e.g. Gozlan et al. 1998). Unlike the Guadiato, tributaries of the Sussex Ouse are not normally subjected to such low discharge rates that pools are isolated, and movements of fish between pools are not impeded except in stretches where weirs are present.

Although correlation of our fish and habitat data is limited to the river stretch level of perception, the higher-than-expected co-occurrence of pumpkinseed and large brown trout (Table 4) could suggest co-utilisation of habitat features or other interactions (e.g. predation on smaller pumpkinseed). The sites where these species co-occurred (e.g. 3, 8, 13) were relatively long stretches, located downstream of on-line still waters in which pumpkinseed have reproducing populations. So, the apparent association between the species could be co-incidental, but the strong correlation between trout density and distance from stream source and the lack of such a correlation in pumpkinseed could suggest otherwise. Large trout are well known to prefer deeper refuges (e.g. Boussu 1954, Roussel & Bardonnet 1997), which in small streams are usually pools associated with concave bends and undercut banks. These areas also tend to be lentic under low discharge conditions, which would be attractive to pumpkinseed (Nicolas & Pont 1995). During follow-up electrofishing surveys at Old Forge Lane (Sheffield Stream) and Batts Bridge in September 2003 during low-discharge conditions, captures of pumpkinseed almost always coincided with captures of brown trout (unpublished data). Nonetheless, this potential association should receive more detailed study.

The higher-than-expected co-occurrences of various pumpkinseed size classes are not unusual given the substantial dietary overlap observed in this species (e.g. Copp et al. 2002) and that the fish derive from the same on-line lakes. In the Sussex Ouse, these strong associations appear to have important ramifications for pumpkinseed body plumpness, with condition factor *K* declining with increasing pumpkinseed density. Indeed, in the only other English pumpkinseed population (Cottesmore Pond, West Sussex) for which published data exist, the mean *K* for August was 0.96 (recalculated using the length-weight regression model derived with data from Copp et al. 2002 combined with the present data). This relatively low *K* value reflects the high density of the Cottesmore pumpkinseed population in which substantial dietary overlap and limited food resources coincided with the slowest growth yet reported world-wide and the latest maturing females (3.9 years) of any introduced European population (Copp et al. 2002). Preliminary results from a wider comparative study of growth and reproduction in pumpkinseed populations of West Sussex suggest a similar pattern of decreasing *K* with increasing pumpkinseed density (G.H. Copp, M.G. Fox & R. Horsfield, unpublished data).

Of the various biological invasion processes, dispersal rate is amongst the most likely to be density dependent, particularly in limnophilous species such as pumpkinseed. Indeed, the movement of pumpkinseed through the outflow of the upstream reservoirs (Tanyard, Boringwheel) probably results from both passive (accidental drift) and active (density-dependent) downstream movement. Active movement out of the upstream reservoirs, which contain substantial populations of pumpkinseed (unpublished data), into downstream parts of the Sussex Ouse system appear to be driven by limited food resources due to high pumpkinseed population densities. If upstream reservoirs continue to 'drip-feed' tributaries of the Sussex Ouse with pumpkinseed, then the species could eventually establish (successfully reproduce) within the stream system under favourable conditions. However, pumpkinseed have been in the UK for the last 100 years and evidence for reproduction in streams is lacking, including for the Sussex Ouse catchment (Fig. 2). Nonetheless, biological invasion theory predicts that establishment success is enhanced by increased incidence of introduction (i.e. propagule pressure). In other countries, such as France, where establishment of the pumpkinseed required sustained and repeated introductions

(K ü n s t l e r 1908), the species does reproduce in lentic parts of main river courses (e.g. C o p p & C e l l o t 1988). Once the barrier of stream establishment is overcome, the pumpkinseed could become highly invasive such it as it is in Iberia (G o d i n h o et al. 1997, G u t i é r r e z - E s t r a d a et al. 2000).

Long lag phases prior to the onset of invasiveness are common in introduced species (C r o o k s & S o u l e 1999), and within a UK context, the Chinese mitten crab *Eriocheir sinensis* is a good example. Despite being introduced to Britain about 1935, and subsequently to the rivers Thames (I n g l e 1986) and Humber (Yorkshire), dramatic increases in the mitten crab population of the Thames were not observed until the drought conditions of 1989–1992, which facilitated greater settlement of young crabs (A t t r i l l & T h o m a s 1996). The pumpkinseed could experience a similar shift from non-invasive to highly invasive in the UK should climate change result in conditions favourable to pumpkinseed reproduction, such as observed in Iberia (G u t i é r r e z - E s t r a d a et al. 2000). The record-breaking high temperatures, and invariable, low river discharges (R. H o r s f i e l d , unpublished data), in the summer of 2003 provided one such potential scenario. However, no young-of-the-year pumpkinseed were found in Sheffield and Batts Bridge streams in late August 2003 despite the presence of ripe pumpkinseed in these water courses during early June and late August 2003 (unpublished data). Nonetheless, continued study of these populations is warranted to assess the risk of establishment and dispersal of pumpkinseed within English river systems.

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