

Aliens versus the Natives: Interactions between Introduced Pumpkinseed and Indigenous Brown Trout in Small Streams of Southern England

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Abstract.—The pumpkinseed *Lepomis gibbosus* was introduced to Europe, including England, more than 100 years ago, but relatively little is known of its potential ecological impacts on native species and ecosystems. In England, the pumpkinseed is currently established in ponds of the River Ouse (Sussex) and its flood plain. Escapee pumpkinseeds are found in some small tributaries that contain native species of conservation interest (brown trout *Salmo trutta*, brook lamprey *Lampetra planeri*, European eel *Anguilla anguilla*, European bullhead *Cottus gobio*). We used electrofishing surveys and telemetry methods to examine the interactions between pumpkinseeds and native stream fishes (mainly brown trout), including predator–prey relationships, home range size, microhabitat preferences, home range fidelity, and habitat overlap/repartition. To assess impacts of pumpkinseed on stream food webs, a preliminary study quantified trout growth and food-web structure of a stream ecosystem (abundance of primary and secondary producers, fish, and riparian spiders) in reaches with and without pumpkinseed. Where pumpkinseeds were in high density, differences were observed in stream food-web structure, in proportional representation of fish species traits and in riparian spider community composition, but these differences cannot be attributed solely to pumpkinseed presence. From the available evidence, there appears to be little direct or indirect adverse impact of pumpkinseed on native species and the stream ecosystem when in low densities, including as a host of nonnative infectious agents. However, this could change under conditions of climate warming, which are likely to favor pumpkinseed reproduction,

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potentially to the detriment of native species. In a context in which freshwater ecosystems are impacted by several human and climate-induced factors acting synergistically, our results underline the need to study nonnative species impacts through a series of experimental and long-term studies of stream ecosystems.

Introduction

A nonnative species' ability to adapt to novel stream environments is a key factor in invasion success (Fausch et al. 2001). Biological theory predicts that species introduced to new environments should exhibit fast juvenile growth and high reproductive investment at an early age (Stearns 1976; Cadotte et al. 2006). These same attributes can be observed among species introduced from North America to Europe. One such species is the pumpkinseed *Lepomis gibbosus* in which populations recently introduced to new waters in Europe have been observed to make greater investment in reproduction than populations established prior to 1950 (Copp and Fox 2007). Pumpkinseed also fits virtually all of the criteria identified for successful invaders by Marchetti et al. (2004). For example, parental care and physiological tolerance have facilitated pumpkinseed establishment, though in France the species was said to require repeated introductions (i.e., greater propagule pressure [cf. Marchetti et al. 2004]) before it established successfully (Künstler 1908). Pumpkinseed also has a large native North American range (Scott and Crossman 1973) as well as great plasticity in life span, maximum size, and age at maturation (Copp and Fox 2007). Pumpkinseed also scores highly as regards prior invasion success (data from Copp et al. 2009) and has been successfully established in at least 28 European countries (Figure 1).

Although some biological invasions may be benign (Moyle and Light 1996), successful invaders can have implications for freshwater food webs (structure and function), with po-

tential adverse effects on native species through competition for food and habitat (Lockwood et al. 2007) that can lead to species extinctions (e.g., Clavero and García-Berthou 2005), especially species that are already endangered or threatened (Fausch et al. 1997). For some freshwater species, such as common carp *Cyprinus carpio*, there is ample evidence to support claims of adverse impacts (e.g., Struthers 1932; Fletcher et al. 1985; Coates and Ulaiwi 1995), but for others, the evidence is equivocal (e.g., Gozlan 2008). This is due to the difficulties in identifying clear, causal mechanisms to demonstrate detrimental effects on introduced species. This is very much the case of pumpkinseed, which only began to attract intensive scientific interest since the 1990s (Copp and Fox 2007). Most of the published information focuses on pond-dwelling populations, with relatively few studies that include information on the environmental biology of stream-dwelling populations (Godinho et al. 1997; Gutiérrez-Estrada et al. 2000; Villeneuve et al. 2005; Cucherousset et al. 2009).

In the UK, most pumpkinseed introductions from foreign sources occurred during the early 20th century, including sites in Scotland and England (Lever 1977), and more specifically in the English county of East Sussex at Groombridge (Wheeler and Maitland 1973). However, the species' current distribution is restricted to ponds (including small in-stream "mill" reservoirs of <2 ha) and a few streams in southern England (Villeneuve et al. 2005). Some of these ponds receive water from and discharge into tributary streams of the River Ouse (henceforth the "Sussex Ouse"), which drains parts of the two counties East Sussex



Figure 1. Map of current pumpkinseed distribution (dark gray) in European countries (updated from Copp and Fox 2007).

and West Sussex. Pumpkinseeds that escape from the ponds into receiving streams occur more often than expected in stream reaches occupied by native brown trout *Salmo trutta* (Klaar et al. 2004). These streams are also occupied by three other species of conservation interest: brook lamprey *Lampetra planeri*, European eel *Anguilla anguilla*, and European bullhead *Cottus gobio*.

Stream-dwelling pumpkinseed in Europe are associated with stream pools (e.g., Gutiérrez-Estrada et al. 2000; Klaar et al. 2004), which are preferred habitats of brown trout (e.g., Boussu 1954; Heggenes 1989; Roussel and Bardonnnet 1997; Heggenes et al. 2002). In light of this potential habitat overlap between introduced pumpkinseed and native brown trout (Klaar et al. 2004), the aims of the present paper are to (1) review the past

8 years of investigations on pumpkinseeds in two streams (Sheffield, Batts Bridge) of the Sussex Ouse catchment within the context of available information on stream-dwelling pumpkinseeds elsewhere in Europe, and (2) assess how introduced pumpkinseeds might interact with native, stream-dwelling species, principally brown trout. Following the initial investigations of Klaar et al. (2004) on pumpkinseed distribution in the Sussex Ouse catchment, recent research has focused on the life history and dispersal behavior of pumpkinseeds and their interactions with native species. Of particular interest is whether or not the escapee pumpkinseeds are having an adverse impact on native species and/or the stream ecosystem with regard to predation, habitat interactions/displacement, and food-web structure.

Study Area—The Sussex Ouse

The Sussex Ouse catchment drains an area of about 664 km², has an approximate length of 62 km (the lower 21 km being tidal), and discharges into the English Channel east of Brighton (Latitude 50:46:56N, Longitude 0:03:26E). Investigations of pumpkinseed have focused on two small tributaries that receive escapee fish from connected ponds: Sheffield Stream and Batts Bridge stream (Figure 2). Sheffield Stream rises from springs to the west of Nutley (Lat. 51:01:41N, Long. 0:03:23E) and flows southward for about 7.5 km, passing through or adjacent to a number of connected ponds (1–2 ha in area). Batts Bridge Stream rises from springs just east of Nutley (Figure 2) and flows southward (for about 10.5 km) through rural countryside, passing through a number of connected fishing lakes, and is joined by a number of smaller, spring-fed tributaries before entering the Sussex Ouse at Sharpsbridge (Lat. 50:58:00N, Long. 0:03:13E), which is situated just off the map in a location that lies directly south of Nutley (Figure 2).

Established pumpkinseed populations occur in the upper parts of the two catchments, acting as literal “drip feeds” of pumpkinseeds, which escape from connected ponds into the receiving streams. In the Sheffield Stream catchment, there is a commercial angling amenity consisting of eight connected ponds that receive water upstream from Sheffield Stream and discharges back into the stream downstream via a system of “vertical pipes” and horizontal drain pipes. On the upper Batts Bridge Stream, a commercial rainbow trout *Oncorhynchus mykiss* fishery is situated in an in-stream reservoir, which receives water from the in-flowing Batts Stream and discharges downstream via a gated weir where the stream course continues. These water courses are second-order streams that vary in width from 1.0 to 4.3 m and in depth from 0.05 to 1.5 m. The

different types of outflow used at these locations results in different rates of pumpkinseed escape, being about 30× higher via the gated weir than from the standing pipe outflow system (S. Stakėnas, unpublished data). The two streams drain predominantly rural areas with numerous villages and small towns, with the headwaters cutting deeply into the agricultural landscape, which sustains of mainly livestock (horses, cattle) and related feed cultivation, with some fruit production.

Predatory–Prey Interactions between Pumpkinseed and Native Fishes

Despite the presence of pumpkinseed in Europe for more than a century, information on its predator–prey interactions remains relatively limited (see reference list in Copp and Fox 2007), with only one paper (of about 14 containing information on pumpkinseed diet) on stream-dwelling pumpkinseed, and this study was in Portugal (Godinho et al. 1997). The European literature on pumpkinseed diet in ponds reflects the known opportunistic foraging of the pumpkinseed (Copp et al. 2002), which can result in dietary overlaps with native species (e.g., Declerck et al. 2002; Rezsű and Specziár 2006). Piscivory in European pumpkinseed is relatively rare and the species can be entirely cannibalistic (Copp et al. 2002). Elsewhere in Europe, reports of pumpkinseed piscivory include eggs (García de Jalón et al. 1993; García-Berthou and Moreno-Amich 2000) and larger specimens (Godinho and Ferreira 1998a, 1998b; Rezsű and Specziár 2006) of native fish species. However, these reports of piscivory and predation on other taxa, such as endemic mollusks (García-Berthou and Moreno-Amich 2000), are from lakes or reservoirs (i.e., >20 ha) or the data were collected in summer when Iberian streams are generally com-

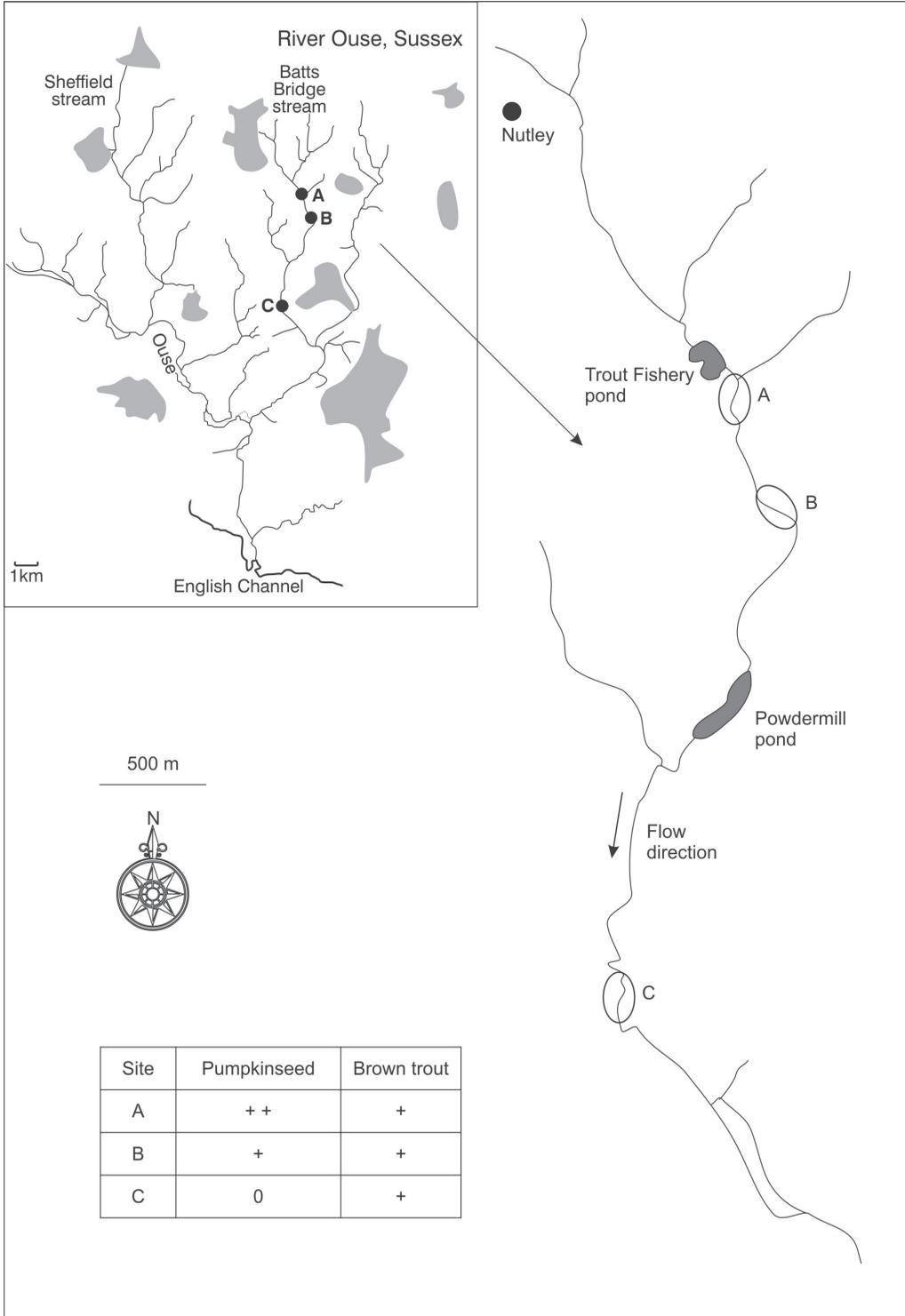


Figure 2. Map of Sussex Ouse River catchment (southern England), with study reaches along Batts Bridge Stream where pumpkinseeds were observed in high density (A), low density (B), and absent (C) during 2001–2007.

posed of isolated, lentic pools (Godinho and Ferreira 1998a). In Portuguese streams, Godinho et al. (1997) reported that fish remains occurred in less than 3% of pumpkinseeds, the dominant prey items being the larvae of *Diptera*, *Ephemeroptera*, and *Trichoptera*, with zooplankton prominent only in fish less than 50 mm total length. In Sheffield and Batts Bridge streams, the diet of more than 1,000 pumpkinseeds, collected during all seasons except winter, was examined for piscivory (the invertebrate prey are still being processed; Stakėnas and G. H. Copp, unpublished); few of the pumpkinseed gut samples contained fish remains (i.e., scales), and the scales found were from pumpkinseed. This indicates either cannibalism, as observed in pond-dwelling pumpkinseeds in England (scales found in the stomach: Copp et al. 2002; whole specimens of small pumpkinseed found in the stomach: G. Zięba and Copp, unpublished data) or alternatively contamination (residual scales on forceps) during the dissection process (Stakėnas and Copp, unpublished).

In their role as prey, pumpkinseeds were taken by all four native fish species in Sussex Ouse streams that are either obligate or facultative piscivores (Table 1). Pumpkinseeds represented at least a third of the fish prey taken, and the size range of pumpkinseeds increased with the size of the predator. Thus, in European

streams, pumpkinseeds principally act as prey for native (brown trout, eel, Eurasian perch *Perca fluviatilis*, northern pike *Esox lucius*) and nonnative (brown bullhead *Ameiurus nebulosus*, largemouth bass *Micropterus salmoides*) fish species (e.g., Guti et al. 1991; Godinho et al. 1997). Pumpkinseeds are also preyed upon by native birds (Crivelli and Mestre 1988) as well as native Eurasian otter *Lutra lutra* (e.g., Gourvelou et al. 2000; Georgiev 2006; Laski and Széles 2006; Prenda et al. 2006).

Microhabitat Overlap between Pumpkinseed and Native Fishes

Early French literature (Roule 1928, 1935) suggested that pumpkinseeds were responsible for the displacement of native Eurasian perch: "Quelle différence avec nos Perches véritables d'autrefois, qui ont presque disparu, chassées par ces fausses Perches nouvelles" (Roule 1928:235). However, this hypothesis has yet to be tested adequately, and the available evidence from subsequent research is insufficient either to support or refute this assertion. In floodplain ecosystems of the upper River Rhône, France, where Eurasian perch was observed, pumpkinseeds were rarely present or in relatively low abundance (Copp 1989), and no microhabitat association (positive or negative) was observed

Table 1. Pumpkinseed as a prey of native fish species collected from Sheffield Stream and Batts Bridge Stream (the Sussex Ouse catchment, England) during 2004 and 2005, including the proportion (%) of stomachs containing fish remains, the proportion of prey fish that were pumpkinseed, and the standard length minimum and maximum of pumpkinseed as prey (adapted from S. Stakėnas, G. H. Copp, and R. Horsfield, EAJ-Southern, Worthing, West Sussex, UK, unpublished).

	Brown trout ^a	Eurasian perch ^b	European eel ^b	Northern pike ^b
Number of fish examined	126	27	7	3
% of stomachs with fish remains	4	56	57	100
% of prey fish that were pumpkinseed	60	33	40	33
Pumpkinseed standard length (mm)	35–60	20–30	40–95	45

^a Via stomach flushing (Georges and Gaudin 1984).

^b Via dissection.

in the floodplain ecosystems where the two species coexisted (Copp 1993). Evidence for displacement of native Iberian stream fishes is evocative (e.g., Prenda et al. 2006; Ferreira et al. 2007). However, pumpkinseed invasions of Iberian inland waters appear to have been facilitated by past and current human alterations of the aquatic environments. Pumpkinseed populations flourish in reservoirs (Ferreira et al. 2007; Hermoso et al. 2008), but in natural streams, pumpkinseeds are less successful, occurring in low abundance relative to native fish species (Clavero et al. 2004; Mesquita et al. 2006; Almeida et al. 2009).

In streams of the Sussex Ouse catchment, initial investigations of the distribution of pumpkinseeds revealed a possible habitat association between pumpkinseeds and brown trout (Klaar et al. 2004), though this was at the mesohabitat scale (i.e., 75–200-m stream reaches, referred to as “segment system” by Frissell et al. 1986). Subsequent detailed studies using radio tracking methods (Stakėnas et al. 2008) revealed a

consistent (irrespective of season) preferential use of pool habitat by both pumpkinseeds and brown trout. This was revealed by constrained ordination analysis (Yee 2006) in which three microhabitat variables for depth, substratum, and velocity, along with three additional variables (submerged macrophytes; submerged refuge = shelters; and debris = drift) would represent a latent variable for “microhabitat” (Figure 3). The two species exploited different parts of the pools. Brown trout preferred higher velocities and coarser substrata, and some individuals also preferred deeper waters than pumpkinseeds. The repartition of microhabitat was greatest in spring (April–May 2005; Figure 3), with overlap being most notable during autumn (November 2004) and midsummer (June–July 2005), in particular with respect to water depth and shelter (e.g., macrophyte cover, debris).

Microhabitat segregation of pumpkinseeds and brown trout within pools is unlikely to be due to predator avoidance. Although smaller pumpkinseeds are preyed on by brown

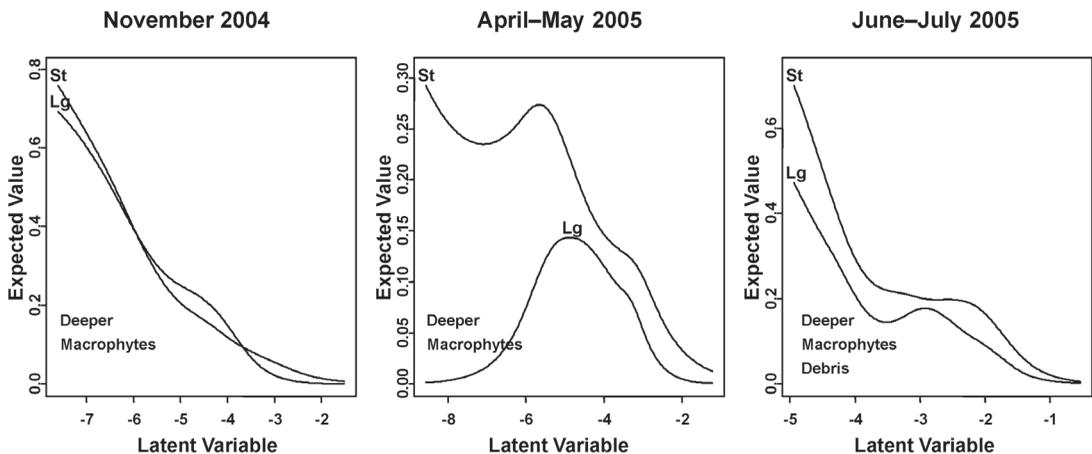


Figure 3. Constrained additive ordination (Yee 2006) profiles for pumpkinseed (Lg) and brown trout (St) over three monitoring periods (November 2004; April–May 2005 and June–July 2005; presence–absence data) in Batts Bridge Stream. Depth, velocity, substratum, submersed macrophytes, shelters, and debris are the indicators for the latent variable “microhabitat,” which is plotted against the expected values for the constrained/canonical coefficients for each indicator (these are relative to the right-hand side of the latent variable axis). Figure adapted from Stakėnas, L. Vilizzi (Murray-Darling Freshwater Research Centre), and Copp (unpublished data).

trout (Table 1), tagged pumpkinseed were unavailable to gape-limited predators. Similarly, adult sunfishes *Lepomis* spp. in their native range do not alter their depth distribution in stream pools in response to the presence of adult largemouth bass *Micropterus salmoides* and piscivorous sunfishes (Harvey 1991). Both pumpkinseeds and brown trout favor habitats with increased complexity (deeper places, macrophytes, debris), though pumpkinseeds prefer more complex structures (branches, roots) than brown trout (Stakénas, Vilizzi, and Copp, unpublished). These complex structures provide increased numbers of feeding locations (Bachman 1984; Fausch 1984), isolation from predators and competitors (Bustard and Narver 1975; Coulston and Maughan 1983) and they allow for spatial segregation to occur in pool habitats (Dare and Hubert 2003).

Such spatial segregation was observed for radio-tagged pumpkinseeds and brown trout in Batts Bridge Stream (reaches A and B, Figure 2). Telemetry data on the movements of tagged fish were analyzed using the "linear systems" version of the Ranges7 software package (www.anatrack.com), which provided seven indices of habitat use: (1) home ranges were calculated using convex cluster polygons (Kenward 1987; Kenward et al. 2001), by excluding outlying location records through truncation of the upper 5% of the nearest neighbor distance distribution (Hodder et al. 1998; Kenward et al. 2001); (2) objective cores were calculated from the distribution of the locations, using nearest-neighbor distances and exclusion of outlying locations (Kenward et al. 2001); (3) percentage overlap in home range was calculated for pumpkinseeds versus brown trout, with overlaps greater than 50% (of pumpkinseed home range overlapping those of brown trout) considered as substantial; (4) the Simpsons reciprocal index for diversity of locations across clusters also were calculated giving an index of the distribution of locations within the

cores, which increases from 1 (i.e., representing only one location) to the number of home range objective cores (Kenward et al. 2001); (5) actual range center distributions (i.e., spatial analysis) were determined using conventional nearest neighbor analysis (Clarke and Evans 1954) to determine, when comparing with 1,000 random locations, whether centers are more regularly spaced than would be expected in a normal distribution; (6) dynamic interactions analysis (Macdonald et al. 1980) was undertaken using the pumpkinseed and brown trout home range overlap data to examine the tendency of the two species to be close together at the same time by comparing the observed and possible distances between fishes. The geometric mean distances were estimated between the n observed pairs of same-time locations for fish i and j . Then the equivalent values were estimated for the $n \times n$ possible distances if fish j could be at any of its n used positions when fish i was at each of its used positions; and (7) observed and possible distances were compared using Jacobs' version of the Ivlev electivity index (Jacobs 1974), which gives a value of 0 if the observed and possible distances were the same, increasing to +1 as the observed distances are increasingly small relative to the possible distances (i.e., the specimens "prefer" each other) or decreasing to -1 as the observed distances are increasingly large relative to the possible distances (i.e., the specimens "avoid" each other). This gives a single Jacobs index for each pair of animals, which tends to be most consistent if based on the geometric mean distances (Walls and Kenward 2001).

Home range analysis revealed that both species have tightly cored home ranges (Figure 4), with up to 14 cores for both species (mean = 6.9 and 6.3 for brown trout and pumpkinseed respectively). Range center distribution showed both species were distributed nonrandomly within the stream (e.g., significantly different to the expected random locations). Home range

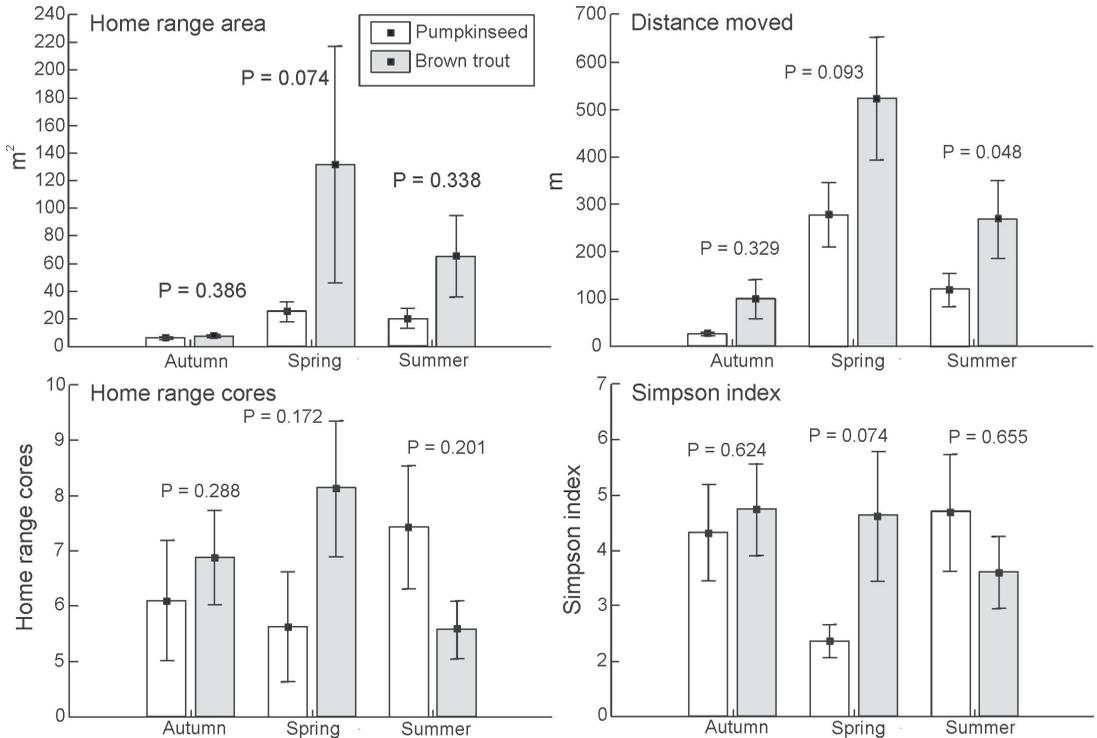


Figure 4. Mean home range area in square meters (upper left), mean distance moved in meters (upper right), number of home range cores (lower left), and the Simpson index (lower right) for diversity of locations across clusters of radio-tagged pumpkinseeds and brown trout with SE bars and Mann-Whitney U-test between species in Batts Bridge Stream (southeastern England) during all tracking seasons (November 2004; April–May 2005; June–July 2005). Graphs adapted from Stakėnas, Copp, and Horsfield (unpublished).

area of both species were relatively small (for brown trout: maximum = 728 m², mean = 65.5 m²; for pumpkinseed: maximum = 64.7 m², mean = 16.2 m²) and did not differ between species either overall (seasons combined) or by season (Figure 4), though brown trout home range in spring was almost 4× that of pumpkinseed, 3× in summer. However, within species, home range areas in spring and in summer were significantly larger than in autumn (Mann-Whitney U-test).

Tagged pumpkinseeds and brown trout showed similar seasonal trends of movement, with distances moved being significantly greater in spring and summer than in autumn (Figure 4). Brown trout moved further distances than

pumpkinseeds, regardless of season, though the differences were significant during the summer tracking period only. However, brown trout always moved furthest downstream, regardless of season. Upstream movements were also greater for brown trout than pumpkinseeds during summer and autumn, but pumpkinseeds moved further upstream in spring and demonstrated the ability to negotiate shallow rapids with current velocity up to 0.7 m/s.

There was substantial home range overlap between the two species, though this varied from 50% of pumpkinseed specimens in autumn to 75% in spring and up to all tagged in summer (Stakėnas, Copp, and R. Horsfield, EA-Southern, Worthing, West Sussex, UK, unpublished).

The overlap in home range reflects, in part, the microhabitat use of the two species (Figure 3), with clear overlap in microhabitat profiles evident in two of the three seasons and partial overlap the third. However, direct comparisons of microhabitat and home range remain inappropriate due to the very different spatial scales used. The home range centers of pumpkinseeds and brown trout were distributed nonrandomly in the stream, which suggests that the fish are selecting their home range based on preferences for specific habitat features or based on a social structure (e.g., size-related dominance) between the species. However, social associations appear to be of little importance because analysis of the dynamic interactions between pumpkinseeds and brown trout specimens with overlapping ranges (Jacobs indices) revealed a very low level of interaction. As such, there was neither attraction nor avoidance between and within species, which indicates that overall (all seasons combined), there was neither cohesion (in preferred habitats) nor strong territorial fidelity (Jacobs indices on a scale of -1.0 to $+1.0$; i.e., avoidance to preference, respectively: autumn: mean = -0.0024 ; SE = 0.0053 , min = -0.074 , max = 0.035 ; spring mean = 0.0684 ; SE = 0.0212 , min = -0.313 , max = 0.708 ; summer mean = -0.0001 ; SE = 0.0142 , min = -0.304 , max = 0.279). There was, however, slight variation in dynamic interactions during spring only with two pumpkinseeds demonstrating moderate cohesion with one trout (Jacobs indices 0.66 and 0.71).

The home range area, distance moved, overlap, distribution, or interaction of radio-tagged pumpkinseeds and brown trout did not correlate with fish age or size (Stakėnas, Copp, and Horsfield, unpublished data). This may be due to the fact that all but three of the radio-tagged pumpkinseeds were ages 4–8. However, a related study in the same stream, using pumpkinseeds over a wider range of sizes and ages tagged with

passive integrated transponder tags ($n = 347$), revealed that longer-term movements vary significantly with fish age and season, with the furthest movements observed in spring and for age-3 and age-4 pumpkinseeds (Stakėnas and Copp, unpublished data). This age range corresponds with the mean age at maturity (3.3) reported for pumpkinseed in Batts Bridge Stream during the same study period (Villeneuve et al. 2005). These upstream movements were interpreted as spawning migrations, though it should be noted that pumpkinseed reproduction in England is restricted to ponds and, so far there is no evidence of successful reproduction (i.e., hatching of progeny) in streams or rivers (Klaar et al. 2004; Copp and Fox 2007).

In summary, results from Sheffield and Batts Bridge streams suggest brown trout and pumpkinseed repartition of pool habitat without preference or avoidance of each other.

Stream Food-Web Impacts

Another possible impact of introduced pumpkinseed is on food-web structure and function. For example, in the River Guadiana flood plain (Spain), introduced pumpkinseeds were linked to a reduction in the size and number of zooplankton, leading to increased turbidity, chlorophyll *a*, total phosphorous, and nitrogen relative to sites without pumpkinseed (Angeler et al. 2002). Another example of food-web impacts is where an increase in grazing on a prey type has consequences for the riparian ecosystem (e.g., Nakano et al. 1999; Fausch et al. 2002). Research on stream food webs in northern Japan revealed that the introduction of nonnative rainbow trout resulted in reduced growth of a native salmonid, which was associated with a shift in feeding on benthic invertebrates (Fausch et al. 1997). This shift led to a reduction in emergent insects and to reduced diversity and abundance of riparian spiders (Baxter et al. 2004). In the

Sussex Ouse catchment, pumpkinseed densities are highest immediately downstream of source populations (reach A, Figure 5), and impacts of pumpkinseed on the stream food web are likely to be observed in those reaches with high densities of pumpkinseeds.

In terms of species traits (Frimpong and Angermeier 2009), differences in the reproductive and trophic guild structure of the three reaches was evident but not consistent (Table 2). Despite some variation between sampling years, the mean proportions of reproductive

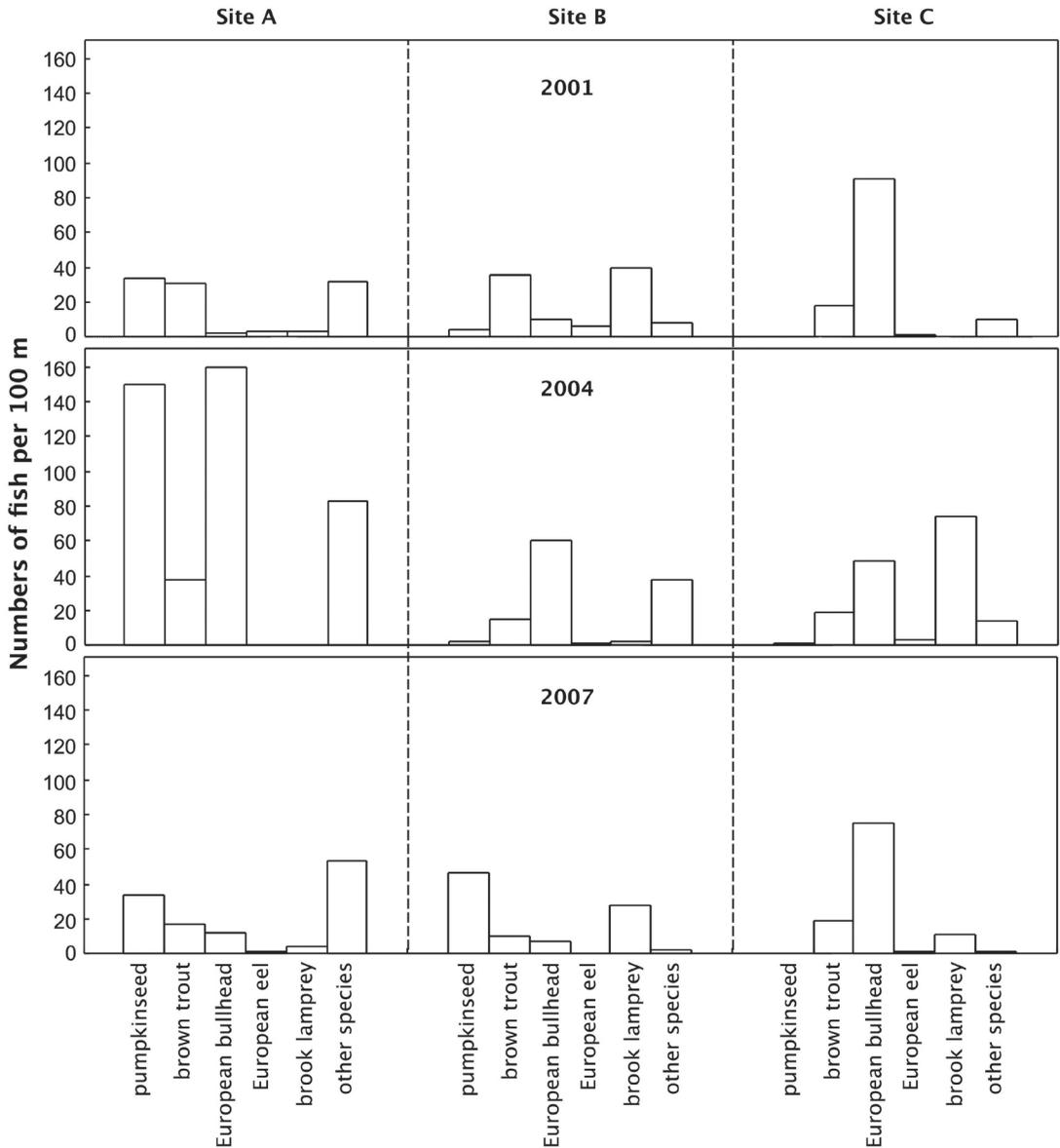


Figure 5. Number of fish captured per 100 m of stream reaches (Figure 2A–C) using single-run continuous electrofishing in August 2001 (Klaar et al. 2004), August 2004 (Stakėnas and Copp, unpublished data) and July 2007 (Copp and Cucherousset, unpublished data). See also Table 2.

Table 2. Proportional (%) representation of species traits of stream fishes (as per Frimpong and Angermeier 2009) in three reaches (pumpkinseed densities: high, low, absent) of Batts Bridge Stream (River Ouse, East Sussex, England) sampled by electrofishing in 2001, 2004, and 2007 (see Figure 5). Reproductive guilds (excluding pumpkinseed and eel) were represented by nest guarders (Nest = bullhead), egg hiders (Hider = brown trout), open substratum spawners (Open = common bream *Abramis brama*, chub *Leuciscus cephalus*, goldfish *Carassius auratus*, gudgeon, lamprey, roach *Rutilus rutilus*, stone loach *Barbatula barbatula*), and egg-clustering species (Cluster = Eurasian perch). Trophic guilds were represented by zoobenthivore (Zooben. = gudgeon, stone loach, bream), carnivores (Carn. = European bullhead, chub, eel, brown trout, pumpkinseed), benthophagous species (Benth. = goldfish, roach), and phytivorous species (Phyt. = brook lamprey). Deviant values are given in bold (see text).

	Reproductive guilds (%)				Trophic guilds (%)			
	Nest	Hider	Open	Cluster	Zooben.	Carn.	Benth.	Phyt.
High – Reach A								
2001	3.5	45.2	51.3	–	29.4	66.7	1.1	2.8
2004	56.9	13.5	18.9	10.7	10.0	87.7	2.3	0.0
2007	13.8	19.5	66.7	–	44.3	52.5	0.0	3.3
Low – Reach B								
2001	10.7	38.6	50.7	–	1.3	54.5	6.4	37.8
2004	52.2	13.0	20.9	13.9	16.9	79.7	1.7	1.7
2007	14.9	21.3	61.7	2.1	1.1	69.1	0.0	29.8
Absent – Reach C								
2001	75.6	15.5	8.4	0.4	4.2	92.1	3.3	0.4
2004	31.4	12.2	51.3	5.1	3.1	50.0	0.6	46.3
2007	70.8	17.9	10.4	0.9	0.0	89.7	0.0	10.3
Means:								
High (A):	24.7	26.1	45.6	10.7	27.9	68.9	1.2	2.0
Low (B):	25.9	24.3	44.4	8.0	6.4	67.8	2.7	23.1
Absent (C):	59.3	15.2	23.4	2.2	2.4	77.3	1.3	19.0

guilds (exclusive of pumpkinseeds and eels, which either do not or cannot spawn in the stream) were similar in the stretches with high and low densities of pumpkinseed, whereas in the reach absent of pumpkinseed, nest guarders (i.e., European bullheads) were proportionately more important and other reproductive guilds were in lower proportions. As nest guarders, pumpkinseeds could be viewed as more adept than other species at raiding the nests of European bullheads, though there is currently no evidence available of predation by pumpkinseeds on eggs of European bullheads. In contrast, where pumpkinseed were in high abundance, the mean proportion of zoobenthivores (mainly gudgeon *Gobio gobio*) was greater and the proportion of phytivorous species (i.e., brook lam-

prey) was lower than where pumpkinseeds were in low abundance or absent (Table 2).

To examine potential pumpkinseed impacts on stream food-web structure and on the stream–riparian linkage in Sussex Ouse streams, three reaches were selected along Batts Bridge Stream where patterns in pumpkinseed distribution have been remained relatively consistent between 2001 and 2007 (Figure 5): high densities at reach A, just downstream of an established, pond-dwelling population of pumpkinseed; low densities at reach B, which is about 1 km further downstream; and absent or incidental at reach C, a bit further downstream. During 16–18 July 2007, samples of fish and macrobenthic invertebrates were collected along these three reaches to examine brown trout growth,

density, and species richness of macrobenthic invertebrates. Riparian spider densities were estimated by sweep netting and hand sampling of riparian vegetation. Potential impacts of pumpkinseed on food-web structure, trophic interactions, and stream-riparian zone linkages were examined using stable isotope analyses of fish (pumpkinseeds and brown trout) and four functional groups of macrobenthic invertebrates (filters, grazers, shredders, and detritivores) (J. Cucherousset, J. R. Britton, Bournemouth University, UK, V. R. Edmonds-Brown, University of Hertfordshire, UK, J. E. Milner, Acacia Productions, UK, Stakénas, J.-M. Roussel, INRA, Rennes, France, M. J. Godard, Cefas-Lowestoft, UK, R. E. Gozlan, Bournemouth University, and Copp, unpublished). Stable isotope analysis is appropriate for this assessment because it is based on the predictable relationship between the isotopic composition of consumers and their diet (Vander Zanden et al. 1999; Fry 2006), it provides an account of long-term patterns in diet, and thus it is better at discriminating trophic groups of stream fishes than conventional (gut analysis) methods (Vander Zanden et al. 1997; Rycbczynski et al. 2008).

Pumpkinseeds are omnivorous, including benthivory, and their foraging could potentially reduce the numbers of macrobenthos (includ-

ing emergent species) available to native fishes such as brown trout, which feed upon benthic species as well as drift and allochthonous terrestrial organisms (Cucherousset et al. 2007). Macroinvertebrate communities in 2007 were found to differ between reaches with and without pumpkinseeds, with the highest diversities and densities generally occurring where pumpkinseeds were in low abundance or absent, in particular with regard to emergent insects (Table 3). Long-term data (1976, 1984, 1989, 1990, and 2007) on macrobenthic invertebrates for autumn along these reaches (Edmonds-Brown 1995) revealed a decrease in Shannon-Wiener diversity in both reaches with pumpkinseeds after the arrival of pumpkinseeds in the system (Figure 6), whereas the index remained relatively constant in the reach devoid of pumpkinseeds until 2007. Similarly, when species richness is adjusted to account for variations in macrobenthos density, a progressive increase in adjusted richness was observed in the reaches devoid of pumpkinseeds or with low densities, whereas adjusted richness decreased in the reach with high pumpkinseed densities after the suspected arrival of pumpkinseeds (Figure 6). By contrast, total macrobenthos densities varied quite considerably. Possible effects of a dietary shift on the growth of native fish, due to resource

Table 3. Community composition indices of aquatic macroinvertebrates in three reaches of Batts Bridge Stream (River Ouse, East Sussex, England) sampled on 15 July 2007 just prior to electrofishing (adapted from Cucherousset, Britton, Edmonds-Brown, Milner, Stakénas, Roussel, Godard, Gozlan, and Copp, unpublished) using a Surber (1970) sampler (area 0.0625 m², 330 µm mesh size) at five locations within each reach as per Townsend et al. (1983, 1987).

Index	Reach A	Reach B	Reach C
Shannon-Wiener diversity	0.813	1.060	0.854
Evenness (H max.)	0.625	0.757	0.710
Number of species	20	26	16
Total number of individuals	619	318	559
Number of emergent species	12	18	13
Number of emergent individuals	210	239	328
% emergent species	33.9	75.2	58.6
Emergent:predator:terrestrial ratios	01:01:04	02:01:04	02:00:02

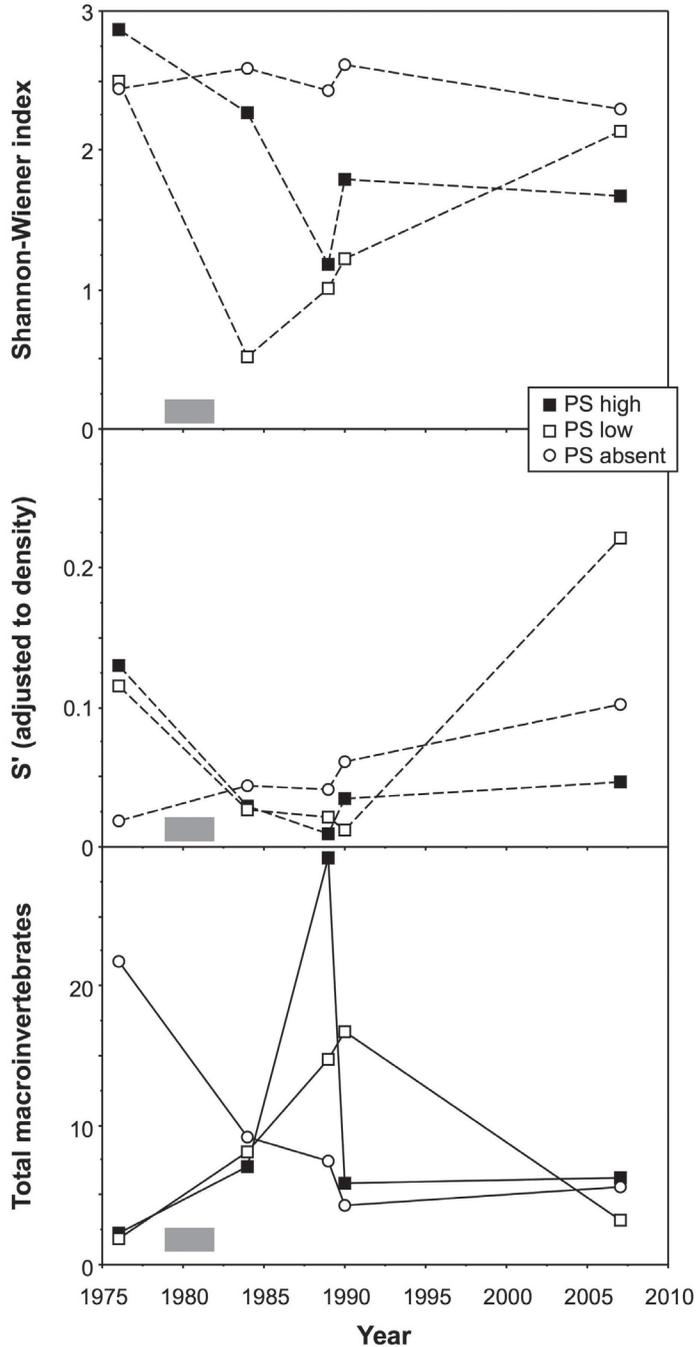


Figure 6. Shannon-Wiener index and species richness ($S' = S \div \text{total numbers of invertebrates}$) of macroinvertebrate communities, sampled during autumn using quantitative replicate Surber samples between 1976 and 2007 in reaches along on Batts Bridge Stream (see Figure 2), where pumpkinseeds were normally in high (reach A), low (reach B), and zero density (reach C) during 2001–2007 (see Figure 5). The interval when pumpkinseeds are believed to have appeared in the stream system is indicated with a gray line. Figure adapted from Cucherousset, Britton, Edmonds-Brown, Milner, Stakenas, Roussel, Godard, Gozlan, and Copp (unpublished).

repartition with an introduced nonnative species (e.g., Baxter et al. 2004), was examined in brown trout from the three reaches of Batts Bridge Stream with differing pumpkinseed densities. Where pumpkinseeds were in high

density, 0+ brown trout had significantly longer back-calculated body length (analysis of variance; $P = 0.0012$; Figure 7). There were no statistically significant differences in body lengths at age of larger/older fish, possibly

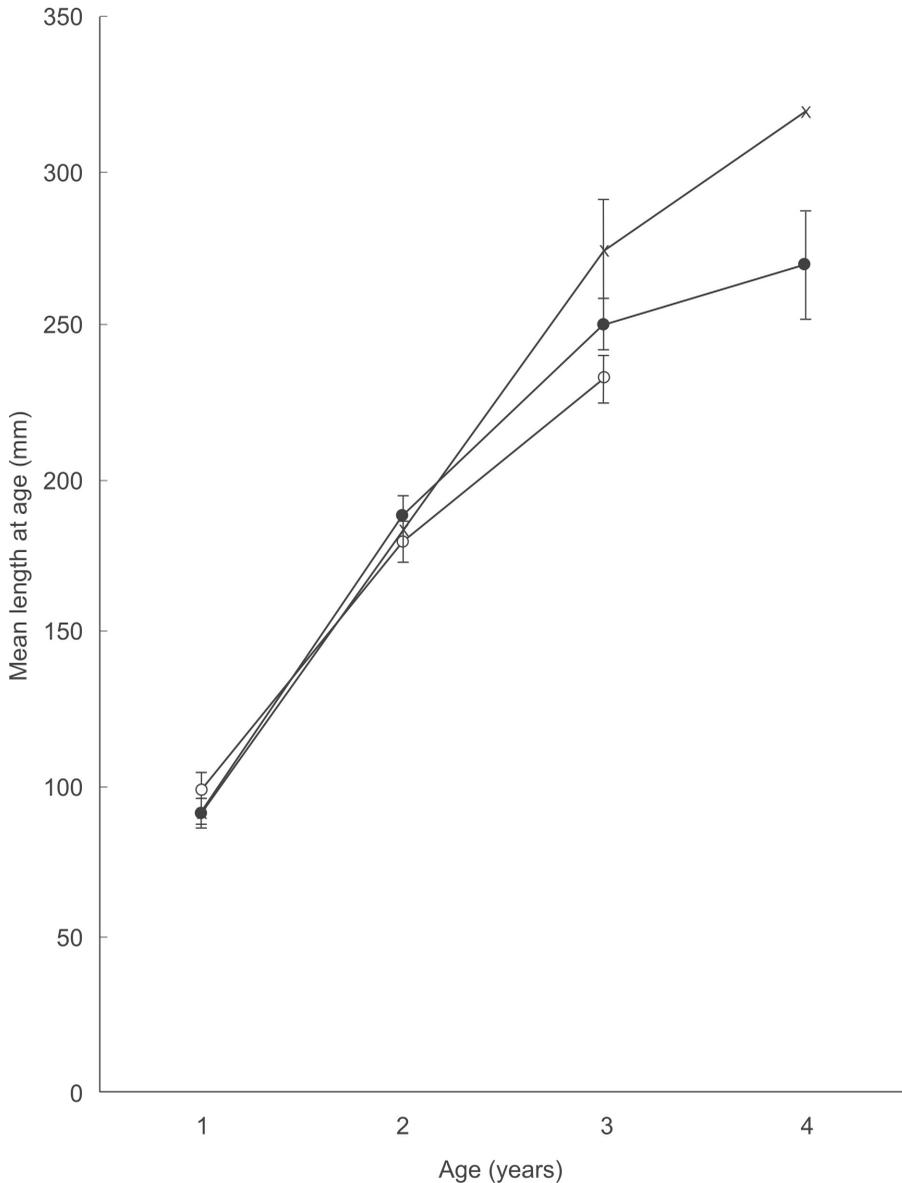


Figure 7. Mean fork length at age (with $\pm 95\%$ confidence limits) of brown trout *Salmo trutta* from reaches of Batts Bridge Stream (see Figure 2) where pumpkinseeds were normally in high density (reach A: open circles, $n = 42$), low density (reach B: filled circles, $n = 51$) and absent (reach C: \times , $n = 39$) during 2001–2007 (see Figure 5). Figure adapted from Cucherousset, Britton, Edmonds-Brown, Milner, Stakénas, Roussel, Godard, Gozlan, and Copp (unpublished).

due to high variances (Cucherousset, Britton, Edmonds-Brown, Milner, Stakénas, Rousset, Godard, Gozlan, and Copp, unpublished).

The potential effects of pumpkinseed on the density and species richness of riparian spiders was examined along riparian strips (2 m from the bank, along 50 m reaches, both banks) of the Batts Bridge Stream study reaches (Figure 2), where spiders were sampled on 15 July 2007 (i.e., just prior to the fish and invertebrate sampling), when all pumpkinseed were removed, and again on 8 October 2007. Where pumpkinseeds were present (reaches A and B; Figure 2), the densities and species richness of riparian spiders were lowest (Table 4). Some differences in riparian vegetation were noted among reaches, which would influence spider density and richness: reach A was fairly heavily shaded throughout, mainly by holly *Ilex aquifolium* with some hazel *Corylus avellana*, clumps of Buckler fern *Dryopteris dilatata*, some wild rose *Rosa complex*, rushes *Juncus* sp., and grasses in areas with less shade; reach B was heavily shaded and had less low-level riparian vegetation, consisting mainly of holly and some alder *Alnus* sp., a few hazel trees, some buckler fern, grass tussocks, and the occasional clump of rushes; reach

C was boarded mostly by hazel (lower leafy branches) with a few holly trees and some alders (virtually none whose lower branches were within reach). Some unidentified grass tussocks and some wild rose, a few tussocks of Buckler fern, and some mosses. However, of particular note was the distribution of three species typical of riparian streams (*Oedothorax fuscus*, *O. retusus*, and *Erigone dentipalpis*); they were absent along the two stream reaches (A and B) where pumpkinseeds were present, but present in the reach devoid of pumpkinseeds (C). In October 2007, riparian spider numbers increased in all reaches (Cucherousset, Britton, Edmonds-Brown, Milner, Stakénas, Rousset, Godard, Gozlan, and Copp, unpublished). However, species richness increased in both reaches where pumpkinseeds had been present but decreased where pumpkinseeds were absent (Table 4). The most notable changes in spider density and richness were in reaches where pumpkinseeds had been in high densities; however a series of long-term or controlled experiments, such as conducted by Baxter et al. (2004), will be necessary to verify the importance of pumpkinseeds in regulating spider densities.

Table 4. Riparian spider density (numbers of spiders per unit area of riparian vegetation: two banks per reach \times 50 m long of each bank \times 3 m height) and diversity (number of species as per Merrett and Murphy 2000, Harvey et al. 2002) collected along the riparian strips of three stream reaches of Batts Bridge Stream (River Ouse, East Sussex, England) on 15 July and 8 October 2007 (i.e. the week prior to and two months after the fish and invertebrate sampling) using of a terrestrial insect sweep net (0.75 m diameter net, <0.5 mm mesh, 1 m long pole). (adapted from Cucherousset, Britton, Edmonds-Brown, Milner, Stakénas, Gozlan, and Copp, unpublished).

Spider	Month in 2007	Pumpkinseed abundance		
		High ^a (reach A)	Low ^a (reach B)	Absent (reach C)
Density	July	8	22	31
	October	64	23	39
Number of species	July	7	6	16 ^a
	October	18	12	9

^a Typical riparian species (*Oedothorax fuscus*, *O. retusus*, *Erigone dentipalpis*) absent.

To assess resource overlap between pumpkinseeds and brown trout, stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of brown trout, pumpkinseeds, and macrobenthic invertebrates from stream reaches A–C (Figure 2) were performed. We tested the hypothesis that stable isotope signatures of brown trout show gradual change with increasing pumpkinseed density due to increased competition for food resources with the nonnative species (Cucherousset et al. unpublished). Analysis of the stable isotope values revealed similar signatures of pumpkinseeds between reaches A and B (Table 5), although slightly ^{13}C -depleted ($\approx 1.4\text{‰}$) at reach A relative to reach B (Figure 8). Differences in brown trout stable isotope signatures between reaches and between total length (TL) size-classes (<100 mm, 100–200 mm and >200 mm) were measured. Trout of the 100–200 mm and >200-mm-TL classes had similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures at the three reaches (Table 5), but within reaches, small trout (<100 mm TL) were ^{13}C -depleted relative to larger brown trout (>200 mm TL). The depletion in ^{13}C increased when increasing pumpkinseed density, averaging -6.31‰ , -4.27‰ , and -3.73‰ in reaches A,

B, and C (Figure 8), respectively. Consequently, the presence of pumpkinseeds may be influencing the stable isotope signature of smaller brown trout, and there are two mechanisms that could induce these changes: (1) competition for food (i.e., brown trout diet shifts to ^{13}C -depleted prey), or (2) modification of the food-web structures (i.e., trout diet remained similar but $\delta^{13}\text{C}$ signatures of prey changed). Indeed, the interpretation of fish stable isotope values can be biased by changes in the food-web baselines (e.g., Fry 2006; Hoetinghaus and Zeug 2008).

In Batts Stream, stable isotope values of the four functional groups of macrobenthic invertebrates (i.e., baselines) differed between reaches, notably with a general ^{13}C -depletion (i.e., mean $\delta^{13}\text{C}$) with increasing pumpkinseed density (Figure 8): reach A (mean = $-32.89\text{‰} \pm 0.98\text{ SE}$), reach C (mean = $-33.01\text{‰} \pm 1.44$) and reach B (mean = $-29.29\text{‰} \pm 0.69$). This corresponds to changes in $\delta^{13}\text{C}$ amplitude (of macrobenthos invertebrates) of -3.72‰ for reaches C to B and 0.12‰ for reaches B to A (Figure 8). Although the general amplitudes of ^{13}C -depletion of small brown trout and macrobenthos invertebrates between reaches A and C

Table 5. Mean and standard error (SE) stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, in ‰) of pumpkinseed and brown trout (three total length [TL] classes: <100 mm, 100–200 mm and >200 mm; “–” indicates size-class absent) in the three study reaches where pumpkinseed (PS) were normally in high density (reach A, PS high), low density (reach B, PS low) and absent (reach C, PS absent) (adapted from Cucherousset, Britton, Edmonds-Brown, Milner, Stakénas, Gozlan, and Copp, unpublished).

Species	Reach	<i>n</i>	$\delta^{13}\text{C}$	SE	$\delta^{15}\text{N}$	SE	
Pumpkinseed	A–PS high	44	30.97	(0.16)	10.90	(0.08)	
	B–PS low	51	29.60	(0.17)	11.25	(0.11)	
Brown trout	(< 100 mm TL)	A–PS high	16	–32.95	(0.32)	10.23	(0.09)
		B–PS low	15	–29.71	(0.16)	10.57	(0.11)
		C–PS absent	10	–29.36	(0.15)	11.76	(0.11)
	(100–200 mm TL)	A–PS high	–	–	–	–	–
		B–PS low	15	–26.12	(0.16)	9.41	(0.26)
		C–PS absent	9	–25.95	(0.15)	10.16	(0.25)
	(> 200 mm TL)	A–PS high	16	–26.64	(0.23)	10.47	(0.15)
		B–PS low	25	–25.44	(0.16)	9.71	(0.14)
		C–PS absent	26	–25.63	(0.08)	10.14	(0.14)

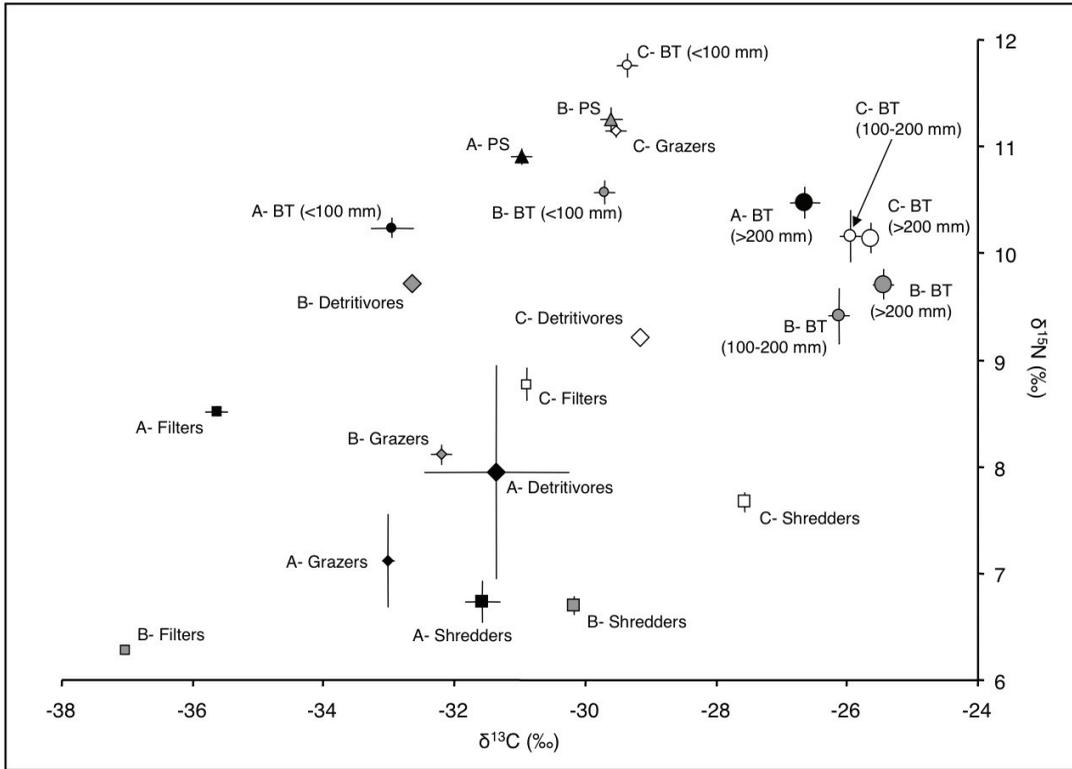


Figure 8. Mean and standard error (SE) stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, in ‰) of macrobenthic invertebrates (filters, grazers, shredders, and detritivores), pumpkinseeds (PS), and brown trout (BT; <100 mm, 100–200 mm and >200 mm total length) in July 2007. Black symbols are for reach A (PS high), gray symbol are for reach B (PS low), and white symbols are for reach C (PS absent) (adapted from Cucherousset, J. R. Britton, V. R. Edmonds-Brown, J. E. Milner, Stakénas, R. E. Gozlan, and Copp, unpublished).

were somewhat similar, changes between all reaches demonstrated different patterns. Small brown trout demonstrated the strongest depletion from reaches B to A (-3.24‰), whereas invertebrates demonstrate the strongest depletion from reaches C to B (-3.72‰). However, the low number of species (fish and invertebrates) involved in the stable isotope analysis prevents further statistical analysis (e.g., circular statistics as per Schmidt et al. 2007) to examine changes between reaches. Consequently, further investigations are needed to disentangle (1) the relative contribution of competition for food and modification of the food-web structures to brown trout stable isotope shift, and (2) how and to which extend pumpkinseed modify the

food-web structures that might affect, indirectly, the trophic ecology of the native fish species.

Discussion

The association between introduced pumpkinseeds and native brown trout hypothesized by Klaar et al. (2004) was confirmed in subsequent telemetry studies; however, this relationship is one primarily of resource repartition (Figures 3, 4, and 8; Table 5). The two species occupy stream pools and certain microhabitat features therein without apparent preference or avoidance of the other species, except if the pumpkinseed is small enough to be preyed upon (Table 1). Habitat repartition is apparent in

the brown trout's preference for faster-flowing (deeper) parts of the pools with less complex debris than the pumpkinseed. There appears to be no evidence from the Sussex Ouse streams that pumpkinseeds prey on native fish species, but pumpkinseeds are taken as prey by at least four native species (Table 1). It should be noted that two of these native species (Eurasian perch and northern pike) are present in these "trout streams" primarily due to their escape from the same connected ponds from which the pumpkinseeds emanate.

The evidence for adverse impacts by pumpkinseeds on the stream ecosystem is equivocal. Decreased growth of older brown trout in the reach where pumpkinseeds occurred in high density (Figure 6) may be due to a lower diversity of benthic invertebrate species diversity (Figure 7), and in particular the reduced proportion of emergent insects (Table 3). However, other taxonomic groups compensated numerically for emergent insects, so total invertebrate densities in reaches with (A) and without (C) pumpkinseed were similar. It is also unclear whether stream food-web structure is affected by high densities of pumpkinseeds. In terms of species traits, the reach without pumpkinseeds has the highest proportion of European bullheads (Table 2), the only nest-guarding species known to spawn in the stream, but without evidence of predation by pumpkinseeds on bullhead eggs, any cause-effect relationship is hypothetical. In contrast, decreased proportions of phytophagous fishes (i.e., brook lampreys) coincided with high pumpkinseed densities, which contrast the weak, mesohabitat scale, association observed between pumpkinseeds and brook lampreys by Klaar et al. (2004). The differences in brown trout and invertebrate stable isotope signatures in reaches with and without pumpkinseeds may be confounded by a range of factors, including distance from the upstream source pumpkinseed population as well as differences in riparian

and in-stream invertebrate communities due to variations in some environmental variables. There also may be an effect of pumpkinseed introductions on adjacent riparian ecosystems through a reduction in emergent insects, with a corresponding reduction in the densities and species richness of riparian spiders (Table 4). Of particular note is the absence of three spider species typical of the riparian zone along reaches where pumpkinseeds were present (Table 3).

In conclusion, there appears to be relatively little direct adverse impact by pumpkinseeds when in low densities, even as a host of non-native diseases. Pumpkinseed is a species for which relatively few parasites or pathogens are reported in Europe (Kritscher 1980; Piasecki and Falandysz 1994; Sterud and Jørgensen 2006). However, pumpkinseeds from the Sussex Ouse catchment (England) appear to carry a previously unreported monogenean, *Onchocleidus similis* (E. Sterud, Standards Norway, Lysaker, Norway, personal communication), and the implications of this require clarification and further study. As such, the state of investigations on the ecological impacts of stream-dwelling, introduced pumpkinseed (cf. previous sections of this chapter) is symptomatic of other nonnative freshwater fish introductions in European streams and elsewhere—there is a plethora of studies that attribute impacts to freshwater fish introductions, but there have been relatively few studies (e.g., Angeler et al. 2002; Cucherousset et al. 2007) that have tested directly for quantifiable impacts. Similarly rare are studies that examine the biological response of introduced nonnative fishes to climate-warming scenarios (e.g., Dembski et al. 2006) and the consequences for native species. Buisson et al. (2009) predict that coolwater species such as brown trout and European bullhead will decline under conditions of climate change while warmwater species will benefit. The input variables upon which the predictions were made do not in-

clude groundwater inputs and stream shading, which are important variables in determining stream fish assemblage structure through shading (temperature control) and flow stabilization (e.g., Jones et al. 1999; Pusey and Athington 2003; Baxter et al. 2004). These appear to be important factors in the string-fed streams of the Sussex Ouse and are likely to compensate for the projected 2–3°C increase in stream temperatures by 2080 (Hulme et al. 2002). If this indeed occurs, then pumpkinseeds would be expected to begin spawning in lentic areas of English water courses where reproduction has yet to be observed. Correspondingly, juvenile growth would be expected to increase and age at maturity decrease (Copp and Fox 2007). Within the European context of pumpkinseed population life history characteristics, this is likely to enhance the species' ability to invade a wider variety of inland waters of the British Isles than has been observed to date (Villeneuve et al. 2005; Cucherousset et al. 2009).

In Batts Bridge Stream, the observed differences in the structure of the stream food web and the riparian spider community may or may not be the result of the additional predation pressure exerted by pumpkinseeds on emergent insects, but more detailed study along a greater number of stretches, long-term monitoring of stream and riparian communities, and/or controlled experiments would be required to assess this. However, there are only a few streams in England that are subjected to high densities of escapee pumpkinseeds, and logistical problems in the Sussex Ouse catchment (relatively easy access to ramblers, lack of landowner agreement to restrict livestock access to the streams) make it impossible to replicate the field experiments of Baxter et al. (2004). Therefore, alternative methods of investigation may be required to determine whether or not pumpkinseeds are having an impact on these complex stream ecosystems.

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