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# Predicting non-native fish dispersal under conditions of climate change: case study in England of dispersal and establishment of pumpkinseed *Lepomis gibbosus* in a floodplain pond

Emily Fobert<sup>1,2</sup>, Grzegorz Zięba<sup>2,3</sup>, Lorenzo Vilizzi<sup>4</sup>, Michael J. Godard<sup>2</sup>, Michael G. Fox<sup>5,6</sup>, Saulius Stakėnas<sup>2,7</sup>, Gordon H. Copp<sup>1,2,8</sup>

<sup>1</sup>Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON Canada

<sup>2</sup>Salmon & Freshwater Team, Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, Suffolk, UK

<sup>3</sup>Department of Ecology & Vertebrate Zoology, University of Łódź, Łódź, Poland

<sup>4</sup>Murray-Darling Freshwater Research Centre, Wodonga, Victoria, Australia

<sup>5</sup>Environmental and Resource Studies Program, Trent University, Peterborough, ON Canada

<sup>6</sup>Department of Biology, Trent University, Peterborough, ON Canada

<sup>7</sup>Department of Freshwater Ecology, Institute of Ecology of Nature Research Centre, Vilnius, Lithuania

<sup>8</sup>Centre for Conservation Ecology & Environmental Science, Bournemouth University, Poole, Dorset, UK

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**Abstract** – Predictions of future climate change include shifts in patterns of precipitation, evapotranspiration and water run-off, resulting in increased periods of drought as well as variability and intensity of rainfall events. In the United Kingdom, the non-native North American sunfish, pumpkinseed *Lepomis gibbosus* (L.), is expected to benefit from these changes. We examine how hydrological variability induced by predicted changes in climate will affect the dispersal and spread of pumpkinseed in England by: (i) determining the relationship between discharge regime and pumpkinseed propagule pressure; (ii) examining a newly-established pumpkinseed population following a flood event in 2007; and (iii) comparing the growth and life-history traits of this new population with fish collected from the source population to demonstrate how the pumpkinseed's life-history plasticity contributes to its success as a coloniser. Using Bayesian modelling, we determined that the number of pumpkinseed escapees is likely to increase with increasing discharge. The newly-established pumpkinseed population showed fast juvenile growth, early age at maturity and small size at maturity. These traits differed significantly from the source population, specifically total length (TL) means at ages 1 and 2 were significantly greater in the new population, whereas TL at age 4 was significantly greater in the source population, and a significantly higher proportion of mature females were found at smaller size classes in the newly established pumpkinseed population. This study demonstrates the potential link between hydrological variability (current and future) and the dispersal of non-native pumpkinseed, leading to the establishment of new populations.

**Key words:** alien species; Bayesian modelling; propagule pressure; global warming

## Introduction

Invasive species are becoming an increasing concern worldwide, as general principles of invasive biology

suggest that most aspects of climate change will favour non-native species (Dukes & Mooney 1999; Thuiller et al. 2007; Hellmann et al. 2008; Rahel & Olden 2008). In freshwater ecosystems, climate

*Correspondence:* G. H. Copp, Salmon & Freshwater Team, Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft NR33 0HT, UK. E-mail: gordon.copp@cefas.co.uk

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change is predicted to aid non-native invasions through warmer temperatures, altered stream discharge patterns, and increased variability and frequency of storm events (Rahel & Olden 2008), resulting in increased periods of drought for many regions and thus modifying disturbance regimes and altering the magnitude and frequency of flood events. These rising temperatures and hydrological changes are modifying current habitats and causing a shift in the range of suitable habitat for many species, and therefore, species currently unable to persist in certain locations because of climatic constraints may be increasingly able to survive and colonise new regions (e.g., Root et al. 2003; Hellmann et al. 2008; Rahel & Olden 2008; Graham & Harrod 2009). Shifting habitat suitability can also potentially weaken a native species' ability to compete with recently introduced species if environmental conditions become unfavourable to the native species (Byers 2002; Hellmann et al. 2008). These environmental changes are expected to impact the distribution and phenology of species (Parmesan 2006; Rahel & Olden 2008), facilitate invasions by some currently noninvasive species and increase the dispersal and possibly the impact of some established invasive species (Hellmann et al. 2008; Rahel & Olden 2008; Graham & Harrod 2009).

In the United Kingdom, current predictions of future climate for southern England include an increased mean temperature of 3–5 °C, reduced discharges and increased hydrological variability (Jenkins et al. 2009). These altered discharge regimes are likely to create new pathways of introduction for non-native species into novel environments, leading to an increase in the frequency and intensity of connectivity between floodplain aquaculture facilities and adjacent water courses during flood events (see Padilla & Williams 2004; Rahel & Olden 2008). This is particularly relevant to the North American sunfish, pumpkinseed *Lepomis gibbosus* (L.), which is one of six non-native fish species expected to benefit from changes induced by climate warming (Britton et al. 2010).

Introduced to Europe during the late nineteenth or early twentieth century, pumpkinseed populations have become established in at least 28 countries of Europe and Asia Minor, and the species is considered one of the most successful introduced fishes in Europe (Copp & Fox 2007). In the United Kingdom, all known populations of pumpkinseed are located in England, south of the Thames basin, with established populations currently observed in ponds but not in water courses (Villeneuve et al. 2005). The colonisation success of the pumpkinseed in its introduced range has been attributed to its flexibility in habitat and diet requirements and plasticity of life-history

traits (Copp & Fox 2007; García-Berthou 2007; Tomeček et al. 2007).

Throughout most of its southern distribution, pumpkinseed populations are characterised by fast juvenile growth and early age and size at maturity (Copp & Fox 2007). In these warmer regions of its non-indigenous distribution, the pumpkinseed is considered invasive. In contrast, the pumpkinseed is not considered invasive in most of its northerly range, including England, where it has been established for over a century, the populations being characterised by slow growth, older age at maturity and longer life-span (Copp et al. 2002; Villeneuve et al. 2005). Even in the more northerly countries, such as the Netherlands, where pumpkinseed invades ponds disturbed by rehabilitation management to favour native plants and is considered a pest species (Van Kleef et al. 2008), this pattern of slow growth and late maturity generally applies (Cucherousset et al. 2009). Recent studies, however, suggest that under climate change conditions, pumpkinseed populations in England could shift to invasive status as a result of increased recruitment and stronger competitive effects on native species (Zięba et al. 2010; Fobert et al. 2011).

Understanding how hydrological variability affects dispersal is critical for predicting the spread and management of invasive species. The aim of this study is to: (i) determine the relationship between discharge regime and propagule pressure for the North American pumpkinseed in order to understand how increased hydrological variability, such as under conditions of climate change, could affect the species' dispersal in England; (ii) examine a newly-established pumpkinseed population found in an artificial pond following a flood event in 2007, providing a rare natural opportunity to examine specific population level responses that facilitate the persistence of a species in a novel environment; and (iii) compare the growth and life-history traits of this new population with fish collected from the source population to demonstrate how the pumpkinseed's life-history plasticity contributes to its success as a coloniser.

### **Study area, material and methods**

The study was undertaken on two small tributaries (Sheffield Stream, Batts Bridge Stream; Fig. 1) of the River Ouse (Sussex) catchment, which drains an area of about 664 km<sup>2</sup>; river length is ≈62 km of which the lower 21 km is tidal and discharges into the English Channel east of Brighton (50.782222N; 0.057222E). Rising from springs to the west of Nutley (51.028056N; 0.056389E), Sheffield Stream flows southward for about 7.5 km, passing through or adjacent to seven connected ponds (1–2 ha in area) in its upper reaches that comprise the commercial angling

fishery, Tanyard Fishery (51.021368N; 0.016122E); the ponds receive water upstream from Sheffield Stream and discharge back into the stream downstream through a drainage system that receives overflow from each pond via 'vertical drain pipes' that drain off excess water directly into Sheffield Stream. A few kilometres downstream, Sheffield Stream passes through a small reservoir at Sheffield Mill before continuing southward towards its confluence with the Ouse.

Batts Bridge Stream rises from springs just east of Nutley, draining rural countryside for  $\approx 10.5$  km as it flows southward, passing first through Boringwheel Lake, a commercial rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* fishery (400-year-old, spring-fed former mill pond,  $\approx 2.6$  ha, depth min-max = 0.9–2.75 m, mixed marginal vegetation that includes non-native ornamental plants), discharging downstream via a gated weir and continuing a further several kilometres of countryside through a number of 'on-line' fishing lakes before joining the Ouse. Both tributaries, which are second-order streams of variable width (1.0–4.3 m) and depth (0.05–1.5 m), receive escapee fish from connected water bodies, in particular the above-mentioned commercial fisheries.

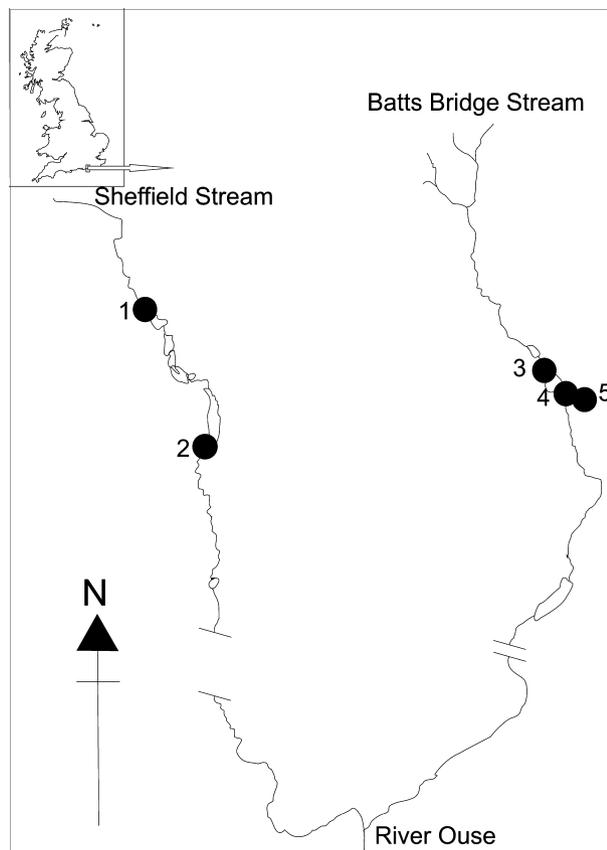


Fig. 1. Location of study sites in River Ouse (Sussex) catchment, south-east England: (1) Tanyard Fishery; (2) Sheffield Mill; (3) Boringwheel Lake; (4) Cackle Street; (5) Watersmeet Pond.

### Fish dispersal sampling

Between 12 May and 9 June 2004, 2467 pumpkinseed from Boringwheel Lake and three ponds at Tanyards (all receive water from, and discharge back into, the adjacent streams) were tagged without anaesthetic using coded wire (CW) tags ( $0.25 \times 1.10$  mm; Northwest Marine Technology Inc., Shaw Island, WA, USA), as described by Stakėnas et al. (2009). Electrofishing surveys of the receiving streams (Sheffield, Batts Bridge) downstream of the above-named fisheries were then undertaken in August 2004 (see Copp et al. 2010), with all pumpkinseed captured scanned with a CW (metal) tag detector. All pumpkinseed were killed according to UK 'Schedule 1' methods (Stakėnas et al. 2009), the CW tags recovered during dissection in the laboratory and the origin pond was determined from the tag's number sequence.

In the absence of discharge gauging stations in the Sussex Ouse tributaries, stream discharge data were collected between 9 July 2008 and 17 March 2010 at five locations in two tributaries of the River Ouse (Sussex) catchment: adjacent to three outflow pipes from Tanyard Fishery on the upper reaches of Sheffield Stream (51.021368N; 0.016122E); a fourth site located a few kilometres downstream on Sheffield Stream at Sheffield Mill (51.013403 N; 0.008648E); and the fifth in Batts Bridge Stream about 50 m downstream of Boringwheel Lake, where the stream is traversed by Cackle Street (51.018548N; 0.074459E).

Over the same period, sampling of escapee fish was undertaken using a sock-shaped pipe net ([www.efe-uk.com](http://www.efe-uk.com)), which was attached to the end of the outflow pipes to catch any fish escapees from the ponds. Sampling dates were irregular, but included periods of both normal and elevated discharge (the latter emphasised to assess fish escape rates), with the duration of sampling varying as a function of the elevated discharge period; nets were checked frequently (depending on discharge intensity, but never exceeded 12 h) to avoid mortalities in the animal bycatch. To determine the rate of escape (fish per volume) via each outflow pipe, pipe discharge ( $1 \cdot s^{-1}$ ) was determined at the beginning and end of each sampling period using a stopwatch to measure the time required to fill a 1 l container.

At Sheffield Mill, fish sampling employed a drift net (1 m long) as described by Copp et al. (2002), that is, 1-mm mesh,  $0.26 \times 0.52$  m opening, square-to-conical shape leading to a 5-cm-diameter opening fitted with a 1-l neoprene bottle (Peñáz et al. 1992). The net was fitted to a large metal frame set in the middle of the 6-m, square-shaped, concrete weir spill-over at the downstream end of Sheffield Mill reservoir. Mean stream discharge was calculated from

triplicate measurements (Valeport Open Channel flow meter; Braystoke Model 001, Totnes, Devon, UK) taken immediately after setting the drift net and then again just prior to emptying the net at the end of the sampling period. Water depth and stream width were measured with a ruler. At the Batts Bridge Stream site, fish and stream velocity sampling were similar to those at Sheffield Mill except that 6–8 measurements (including stream depth and width) were taken, depending on the water level, at the start and end of sampling intervals due to the diversified cross-stream profile. Captured fishes were identified, counted and measured for total length (TL), with all native species retained in a bucket and then released into the stream once the drift net had been emptied.

#### Stream discharge data analysis

Discharge data were acquired from the National River Flow Archive and are available for Ouse at Barcombe Mills (50.914881N; 0.037124E) only. In 1994, this discharge measurement station was described as a four-path ultrasonic gauge superseded (except for minimum discharges) complex structure (weirs and sluices) that is subject to drowning, with sluice operation further complicating the derivation of discharges. The gauge was moved upstream of abstraction intake in 1999, but high discharge measurement problems remained, with the river going out of bank during high discharges. Data for the last 10 years of values were retained for extrapolating the tributary stream discharges.

Stream discharge was estimated for Sheffield stream from the water velocity, depth and channel width measurements collected from Sheffield Mill weir using the method of Buchanan & Somers (1969), using the formula:

$$Q = A\bar{u}$$

where  $Q$  is the discharge ( $\text{m}^3 \cdot \text{s}^{-1}$ ),  $A$  is the cross-sectional area of the portion of the channel occupied by the flow ( $\text{m}^2$ ), and  $\bar{u}$  is the mean water velocity ( $\text{m} \cdot \text{s}^{-1}$ ).

The relationship between fish escapement rate (calculated as total number of fish) and stream discharge was modelled by a Bayesian approach. This was preferred over the classical (or frequentist) approach owing to the small data set available, so that the use of credible intervals (analogous to confidence intervals in ‘frequentist’ statistics) was deemed a more informative option than setting significance levels (Hilborn & Mangel 1997). A simple linear regression model was implemented in WinBUGS v1.4 (Lunn et al. 2000). Uninformative priors were used for all model parameters, including the two regression

coefficients and the precision (=inverse of the variance), for which a normal and a gamma distribution were used, respectively (McCarthy 2007). Predicted values for fish escapement rate were then computed based on back-calculated discharge values from the relationships between discharge in the River Ouse and both the Tanyard and Cackle Street sites during the July 2007 flood (4 days in total: 20–21 July 2007 and 23–24 July 2007). Parameters were estimated by sampling 100,000 times from the posterior distribution by Markov chain Monte Carlo methods, after discarding a ‘burn-in’ sample of 10,000 (McCarthy 2007).

#### Sampling of a newly established pumpkinseed population

To assess the life-history traits of a newly-established population, which resulted from stream over-topping during a spate, pumpkinseed were collected on 8 June 2010 by repeated passes with a backpack electrofishing unit (Bretschneider EFGI 650, Reichenbröder Strasse 4, D-09224 Chemnitz/Gruna, Germany) along the littoral zone of Watersmeet Pond (51.018548N; 0.074459E). This private garden pond ( $\approx 0.02$  ha; depth = 0.5–3 m; various ornamental plants), which is situated = 5 m from Batts Bridge Stream, contained no pumpkinseed prior to 2007 (S. Stakėnas, F. Villeneuve, unpublished data). A total of 91 pumpkinseed were captured and euthanised as per UK Home Office licence and retained for later examination.

In the laboratory, each specimen was measured for TL (nearest mm), weighed (wet weight; nearest 0.1 g), and a sample of scales was taken from the posterior edge of the pectoral fin for age determination. Gonads were removed, weighed and examined to determine sex and maturity. Females with ovaries containing nonyolked or indistinguishable eggs were classified as immature, and those with ovaries containing yolked eggs were classified as mature.

Age was determined as per Steinmetz & Müller (1991) using scale impressions on acetate strips, with annuli identified using criteria outlined by Regier (1962). Ages were cross-checked using independent readings by a second reader. Back-calculations of TL at age were undertaken using the linear relationship between scale radius and TL (Creaser 1926).

Mean age and TL at maturity were assessed on female pumpkinseed only, because male reproductive indices are less reliable indicators of responses to environmental variability (see Danylchuk & Fox 1994). Mean age at maturity was calculated for females using the formula from DeMaster (1978) as adapted by Fox (1994):

$$\alpha = \sum_{x=0}^w (x) [f(x) - f(x-1)]$$

where  $\alpha$  is the mean age of maturity,  $x$  is the age in years,  $f(x)$  is the proportion of fish mature at age  $x$ , and  $w$  is the maximum age in the sample. A modified version of this formula (10 mm TL intervals in place of age classes) was used to calculate mean TL at maturity as per Fox & Keast (1990). A Fisher's exact test was used to test for an association between the number of mature versus immature females in the pivotal age classes (i.e., the earliest age classes that achieved 50% maturity in a given year; Fox & Keast 1991) in the Watersmeet and Boringwheel populations. A Fisher's exact test was preferred over a chi-square ( $\chi^2$ ) test because expected frequencies in some cases were below those permitted by  $\chi^2$  assumptions (Sokal & Rohlf 1981).

The gonadosomatic index (GSI:  $100 \times$  ovary weight/total body weight) was calculated for mature females only, as GSI is not a good indicator of reproductive allocation in male pumpkinseed (see Danylchuk & Fox 1994). The gonad weights of individual fish in the two populations were compared with analysis of covariance, with ovary weight as the response variable, population as the independent variable and TL as the covariate. Mean TL at age was calculated for each age in both Watersmeet and Boringwheel populations. Student's  $t$ -tests were used to test for differences in mean TL at pivotal age classes (ages 2 and 3) between the two populations for all available cohorts. Mean TL at age 2 was used as a measure of juvenile growth rate, as age 2 is the earliest recorded age at which female pumpkinseed mature in most native and introduced temperate zone populations (Fox 1994; Villeneuve et al. 2005).

To assess the growth and life-history traits of the newly-established pumpkinseed population in Watersmeet Pond relative to its presumed source population, Boringwheel Trout Fishery (Fig. 1), pumpkinseed data from Villeneuve et al. (2005), collected 3 June 2003, were used. The same calculations and procedures were carried out on both Watersmeet and Boringwheel populations. Similarly, published data on 18 other English pumpkinseed populations from single-run depletion (Reid et al. 2008) electrofishing and minnow trapping (Villeneuve et al. 2005; Cucherousset et al. 2009) were used for the comparison of pumpkinseed life-history traits from the newly established Watersmeet population to established populations in southern England. The data were also examined within a wider European context using the invasiveness model for pumpkinseed, based on juvenile growth and age at maturity (Copp & Fox 2007).

## Results

### Stream discharge and pumpkinseed dispersal

Discharge data for the Sussex Ouse from 2001 to 2010 revealed great hydrological variability, with frequent flood/spate events over the last decade (Fig. 2). The 2007 flood responsible for pumpkinseed colonisation of Watersmeet Pond was not an unusual event within this 10-year timeframe. During 2004 and during the 2008–2010 study period, when discharge data were collected from Batts Bridge Stream at Cackle Street and from Tanyard Lakes, stream discharge variability was limited, more so for 2004 (Fig. 2a) than for 2008–2010 (Fig. 2b,c).

During the 2004 tagging study,  $\approx 30 \times$  more fish were recaptured in Batts Bridge Stream below (i.e., had escaped from) Boringwheel Lake following a localised spate/flood event than in Sheffield Stream below Tanyard ponds (Fig. 3), despite pumpkinseed population density estimates for those two commercial fisheries being similar (41.1 and 46.5 pumpkinseed per 10 min of electrofishing, respectively). This potential relationship between number of pumpkinseed (as a measure of fish escapement rate) and discharge, examined at Tanyard Fishery in 2008–2010, showed an increase in escapees with increasing discharge. Based on this relationship, the predicted number of pumpkinseed escaping from Tanyard during the July 2007 flood ranged from 0 to 7, and for each  $0.01 \text{ m}^3$  increase in discharge an additional 0–3 pumpkinseed would be expected to enter the stream through the standing pipes (Table 1). Note that equivalent outflow data were not available for Boringwheel Lake due to access restrictions to that site.

### Growth and life-history traits

In 2010, the Watersmeet population showed a very different growth trajectory than its source population in Boringwheel Lake (Fig. 4). Watersmeet pumpkinseed showed relatively fast juvenile growth that slowed with age, whereas Boringwheel pumpkinseed had much slower juvenile growth but a larger adult size. Mean TLs at ages 1 and 2 were significantly greater for pumpkinseed in the new Watersmeet population compared with those in the source Boringwheel population (age 1:  $t = 13.90$ ;  $P < 0.001$ ; d.f. = 189, age 2:  $t = 3.61$ ;  $P < 0.001$ ; d.f. = 187). At age 3, there was no significant difference in mean TL between Watersmeet and Boringwheel populations (66 and 68 mm, respectively). At age 4, pumpkinseed TL in Boringwheel Lake surpassed that of Watersmeet pond, and Boringwheel pumpkinseed reached a significantly greater TL than their newly established counterparts ( $t = -5.18$ ;  $P < 0.001$ ; d.f. = 46).

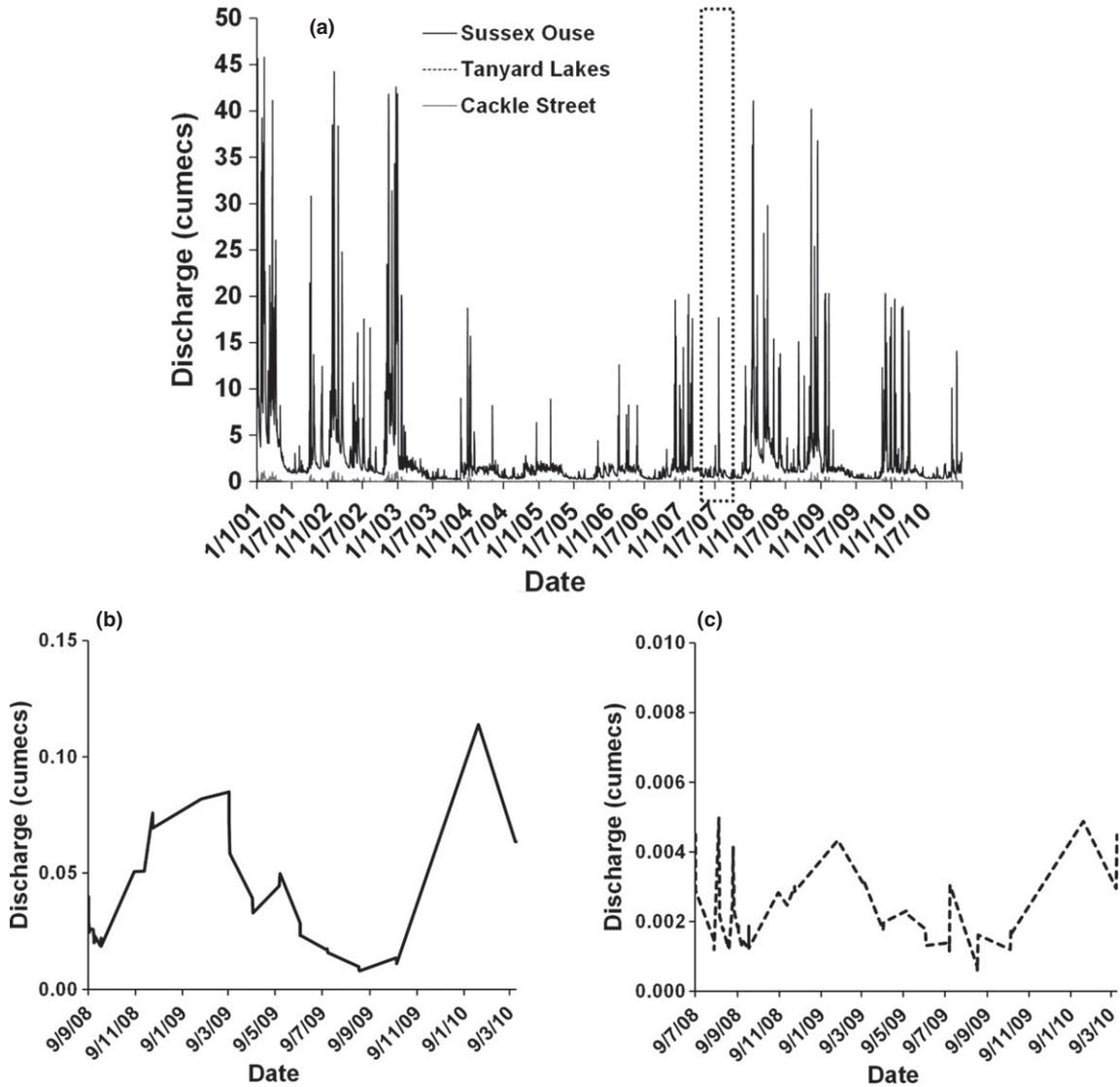


Fig. 2. Hydrological variability in the Sussex Ouse region between 2001 and 2010 (a). Dashed box indicates the flood in 2007 that resulted in pumpkinseed colonisation of Watersmeet Pond. Black box indicates the 2008–2010 drift study period when stream discharge data were collected from Batts Bridge Stream at Cackle Street (b) and from Tanyard Lakes (c).

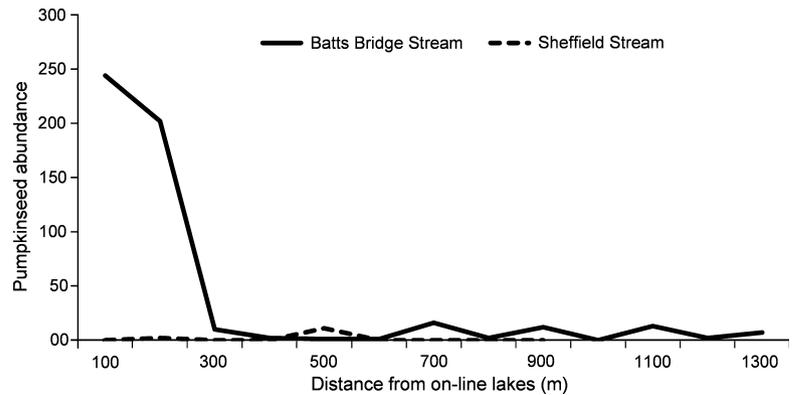


Fig. 3. Number of coded wire tagged pumpkinseed recaptured from Batts Bridge Stream and Sheffield Stream fish communities, for every 100 m of stream following a flood event in 2004.

A comparison of per cent females mature in each age and size class showed that the Watersmeet pumpkinseed population matured at an earlier age and at a

smaller size (Fig. 5). The proportion of mature females at age 2 and age 3 in the Watersmeet population was higher than the source population in

Table 1. Bayesian estimates for a simple, linear relationship between number of pumpkinseed (as a measure of fish escapement rate) and discharge at Tanyard Fishery.  $n_{1-4}$ : predicted number of pumpkinseed (rounded values in brackets) during the 4-day July 2007 flood (1 = 20/07/2007; 2 = 21/07/2007; 3 = 23/07/2007; 4 = 24/07/2007).

Parameter	Mean	SD	Credible intervals		
			2.5%	Median	97.5%
$a$	0.98	0.34	0.29	0.98	1.67
$b$	45.15	108.10	-172.00	44.91	262.00
$n_1$	2.08	2.37	-2.66 (0)	2.08 (2)	6.83 (7)
$n_2$	2.08	2.37	-2.66 (0)	2.08 (2)	6.83 (7)
$n_3$	2.08	2.37	-2.66 (0)	2.08 (2)	6.85 (7)
$n_4$	2.08	2.37	-2.68 (0)	2.08 (2)	6.81 (7)

Boringwheel; however, this difference was not statistically significant (Fisher’s exact test: age 2,  $P = 0.23$ ; age 3,  $P = 0.99$ ). The mean age at maturity (2.4 years) for female pumpkinseed in the Watersmeet population was 0.8 years earlier than that of its source population in Boringwheel pond (3.2 years; Table 2). Mean age at maturity in Watersmeet was also slightly earlier than the means (excluding Watersmeet) for all previously studied pumpkinseed populations in the Sussex Ouse catchment and in England overall (Table 2).

Relative to its source population, there were significantly greater proportions of mature females in the Watersmeet population in both the 60–69 mm (Fisher’s exact test:  $P = 0.005$ ) and 70–79 mm (Fisher’s exact test:  $P = 0.005$ ) size classes (Fig. 5). The mean TL at maturity for the Watersmeet population (67.5 mm) was smaller than that of pumpkinseed in Boringwheel (78.9 mm) as well as the means for all Sussex Ouse populations and all English populations (Table 2). Mean TL at age 2 in Watersmeet population was greater than that of the Boringwheel population (60 and 53 mm, respectively). The mean GSI for Watersmeet pumpkinseed (6.0) was also lower than that of the Boringwheel population (8.4)

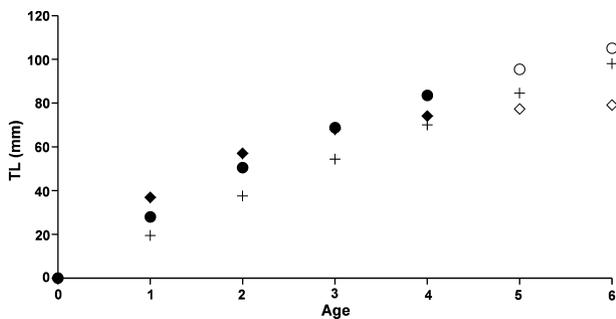


Fig. 4. Pumpkinseed total length (TL) at age trajectory generated from the von Bertalanffy growth model calculated from the observed (solid) and projected (unfilled) mean TL at age. Data points in the graph are mean values from the Boringwheel (+), Watersmeet (•) and Cackle Street (◐) pumpkinseed populations.

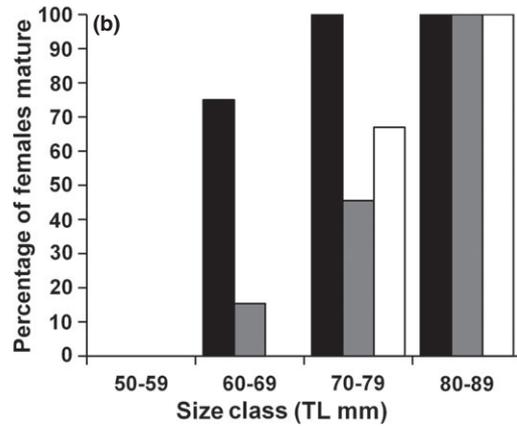
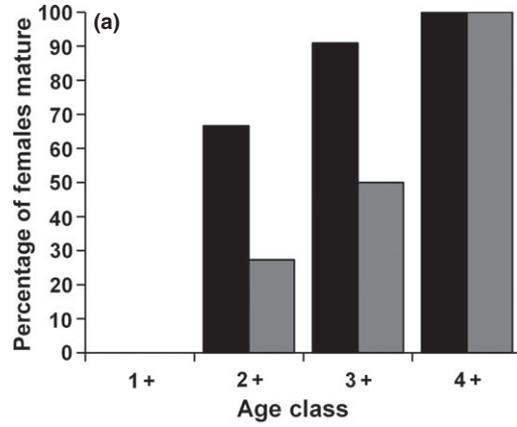


Fig. 5. Percentage of mature females by (a) age class and (b) size class in the Watersmeet Pond population (black) from 2010, the source population, Boringwheel Lake (grey), from 2003, and caught in the Cackle Street stretch of Batts Bridge Stream, which connects the two bodies of water (white) from 2006. Data for per cent mature by age class was not available for Cackle Street pumpkinseed in 2006.

and the overall means for the Sussex Ouse and for English populations (Table 2); however, the significance of this difference could not be assessed because of the significant difference between populations in the slope of the pumpkinseed ovary weight and TL relationship [ANCOVA (Population  $\times$  TL):  $F_{1,61} = 13.2$ ,  $P < 0.001$ ]. To account for differences in size between the Boringwheel (larger) and Watersmeet (smaller) populations, the analysis was re-run using females of equivalent size ( $\leq 80$  mm TL) only, which revealed Watersmeet pumpkinseed to have significantly higher gonad weight than those sampled from Boringwheel (ANCOVA:  $F_{2,27} = 13.2$ ;  $P < 0.0001$ ).

**Discussion**

The establishment success of non-native species has been predicted to be positively correlated with propagule pressure, that is the number of individuals introduced and the frequency of their introduction (Williamson 1996; Williamson & Fitter 1996;

## Spate-related non-native fish dispersal and establishment

Table 2. Growth and life-history traits of pumpkinseed populations in southern England (mainly East and West Sussex), adapted from Villeneuve et al. (2005) with data for the present study site (Watersmeet Pond) given in bold text, including back-calculated total lengths (TL) at age, mean age at maturity (AgeM) in years, mean TL at maturity (TLM) in mm, mean gonado-somatic index (GSI) in %.

Site	Mean back-calculated TL at age (mm)									Life history and condition				
	1	2	3	4	5	6	7	8	9	Age <sub>M</sub>	TL <sub>M</sub>	GSI	K	n
Batts Bridge Stream (upper)														
Cackle Street	36	57	75	87	98	108				3.3	84.6	2.3	1.01	148
Cackle Street (2006*)	36	61	83							2.5	78.3	4.1	0.97	
Boringwheel Lake	35	53	68	83	93	109				3.2	78.9	8.4	1.01	100
Watersmeet Pond (2010)	43	59	66	71						2.4	67.5	6.0	–	91
Batts Bridge Stream (lower)														
Powdermill Upper Lake	41	77	96	107	122	131	141			2.0	70.0	9.2	1.13	123
Powdermill Side Pond	41	78	97	102						2.2	81.7	9.5	1.16	70
Powdermill Lower Lake	40	72	104	118	136					2.1	83.8	8.7	1.08	35
Batts catch. mean (ex. Watersmeet)	39	65	84	95	112	116	141			2.6	79.6	7.0	1.06	
Sheffield Stream (Ouse catchment)														
Tanyards Lake 1	42	69	85							–	–	9.1	0.98	34
Tanyards Lake 2	40	70	92	103						2.1	75.5	8.9	0.99	62
Tanyards Lake 3	38	58	68	78	90	97	100			2.7	72.1	8.1	1.03	81
Tanyards Lake 4	36	58	70	82	93					3.4	78.3	6.7	0.89	100
Tanyards Lake 5	38	59	73	88	105					2.8	75.7	6.8	0.89	100
Tanyards Lake 6	40	68	84	105						2.0	65.0	9.8	1.09	81
Tanyards Lake 7	36	59	71	86	97					2.6	66.0	8.5	1.03	73
Sheffield catchment mean	39	63	78	90	96	97	100			2.6	72.1	8.3	0.99	
River Mole (Thames catchment)														
Cottesmore School Pond (1994†)	36	48	63	72	81					3.9	78.6	6.0	0.97	112
Cottesmore School Pond (2006*)	35	56	76	92						2.8	75.0	9.8	0.88	66
Cottesmore Middle Pond	37	55	66	76	91	104	107			3.1	80.8	5.2	0.92	200
Cottesmore Lower Pond	36	53	65	78	93	104	113	126		3.1	69.1	5.2	0.88	105
Island Pond	34	54	78	92	107	120				3.0	75.0	10.0	1.08	104
Douster Pond	35	49	61	72	82	90	102	110	114	2.8	66.9	4.7	0.91	106
Milton Mount Pond	40	71	89	99	109					2.1	80.0	7.1	1.23	121
Mole catchment mean	36	55	71	83	94	105	107	118	114	3.0	75.1	6.9	0.98	
Elsewhere in southern England														
Airport Pond (Isle of Wight) (2005*)	36	72	97	121						2.4	95.0	6.7	1.07	29
Dunwear Pond (Somerset)	41	67	98	107	116	129				2.5	83.3	9.9	1.09	70
England Mean (ex. Watersmeet)	38	62	80	92	101	110	113	118	114	2.7	76.8	7.5	1.01	

Data are grouped by geographical location within English hydrosystems. The source population for the Watersmeet population is Boringwheel Lake via Batts Bridge Stream at Cackle Street, which runs adjacent to Watersmeet Pond, then further downstream adjacent to the Powdermill sites before joining Sheffield Stream and the Sussex Ouse. All data were collected in June, with all data from 2003 (Villeneuve et al. 2005) except for Watersmeet (the present study, June 2010) and as indicated (from \*Cherousset et al. 2009; from †Copp et al. 2002). Latitude is 51°N in all cases except the Powdermill sites and Airport Pond (50°N). The River Mole sites are presented in upstream-to-downstream order (excluding Milton Mount Pond, which is isolated).

Colautti & MacIsaac 2004). The results of the present study demonstrate how current and predicted hydrological variability can contribute to the propagule pressure of the non-native pumpkinseed in the UK, leading to the establishment of new populations in floodplain water bodies that connect to the water courses during flood/spate events.

A spate in 2004, which was localised to Sheffield and Batts Bridge streams and therefore does not appear in the overall Sussex Ouse discharge regime (Fig. 2a), resulted in a large number of pumpkinseed escaping into Batts Bridge Stream (Fig. 3). The massive difference in the numbers escaping from Boringwheel Lake and Tanyard Fishery during 2004 can be attributed to the different outflow systems used, a simple spillover weir and a vertical pipe overflow system, respectively. This highlights how a relatively simple management mitigation measure (Britton et al.

2011), that is, modification of an outflow system, can reduce the number of escapees (i.e., propagule pressure) into river systems (e.g., Copp et al. 2006; Gozlan et al. 2010), and this is particularly important for on-line fisheries (Hickley & Chare 2004).

The flood event in 2007, which the landowner reported had inundated the Watersmeet study site, resulted in escapee pumpkinseed from an upstream water body colonising a downstream water body that is not normally connected to the adjacent water course. When examined in the context of a 10-year period, it becomes evident that the 2007 flood was not particularly unusual, as more extreme floods and variable discharge regimes were frequently recorded in the Sussex Ouse region. Under the predicted scenarios for future climatic conditions, precipitation patterns and discharge regimes are expected to be altered and the magnitude, frequency, duration and timing of

floods, droughts and intermittent flows will fundamentally impact aquatic ecosystems (Rahel & Olden 2008). The predicted changes to discharge regimes in England are expected to benefit pumpkinseed by increasing rates of dispersal and pathways of invasion.

The study period was less than ideal for examining this phenomenon due to the relatively invariable stream discharges in the study area. However, the CW tagging results and subsequent Bayesian modelling both indicate that pumpkinseed 'escapement' rate (from enclosed waterbodies into neighbouring streams during flood events) increases with increasing stream discharge.

Although we were not able to predict confidently how many fish will escape, many more fish are likely to escape under elevated discharge even where there is a mitigating mechanism (e.g., standing pipe system), and such flood pulses would increase the likelihood of new populations being established (e.g., Watersmeet) in downstream floodplain water bodies.

Evaluation of the Watersmeet pumpkinseed population reveals life-history traits characteristic of a newly-established population, as predicted by invasion theory (Copp & Fox 2007). Relative to its source population (Boringwheel Lake), pumpkinseed found in Watersmeet Pond exhibited fast juvenile growth, early age at maturity and small size at maturity. These opportunistic traits (*sensu* Winemiller & Rose 1992) are typically adopted by recently introduced fishes as a strategy to establish self-sustaining populations in novel environments, where intraspecific competition is often absent and interspecific competition is often minimal due to the absence of indigenous competitors (Stearns 1976; Copp & Fox 2007; Fox et al. 2007). Despite a time gap between the collection of samples from the Boringwheel and Watersmeet populations, mean monthly temperatures were not significantly different (UK Meteorological Office 2012) during the lifetime of fish from Boringwheel (2000–2003) and Watersmeet (2007–2010), indicating that the differences in life-history traits would not be attributable to differences in climatic conditions.

The Watersmeet pumpkinseed population had a lower mean GSI than would be predicted for an expanding population. However, restricting the analysis to equivalent (smaller) size better illustrates the difference in reproductive allocation between the Watersmeet pumpkinseed, which were generally smaller in size and matured earlier, than the Boringwheel pumpkinseed. There are, however, concerns with using GSI as a measure of reproductive investment due to the underlying assumption that the number of spawning events is equal in both populations, and this apparent difference in energy allocation to gonadal development should be tested with GSI data

throughout the spawning period before being considered definitive (see Danylchuk & Fox 1994).

The relationship between juvenile growth and age at maturity has been suggested (Copp & Fox 2007) as a useful means for assessing the potential invasiveness of pumpkinseed populations in England and Europe and that the populations with the highest potential for expansion are those with short generation times, fast juvenile growth and high fecundity at an early age. The mean TL at age 2 for Watersmeet and Boringwheel populations, when plotted against means of all available noninvasive and invasive pumpkinseed populations (Villeneuve et al. 2005; Cucherousset et al. 2009), reveals that the Watersmeet and Boringwheel populations both fall within the noninvasive region of the graph. However, relative to its source population, the new Watersmeet pumpkinseed population is much closer to the 'physiological transition phase' of invasive populations, which are characterised by faster juvenile growth and younger mean age at maturity (Fig. 6).

Previous studies have shown that phenotypic plasticity of life-history traits has contributed to the success of the pumpkinseed as an invader in Europe and that its invasion success is greatest in warmer

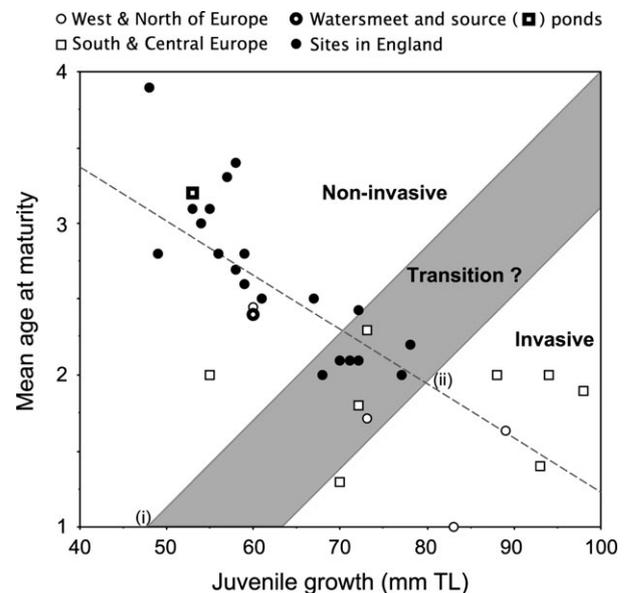


Fig. 6. Mean age at maturity (in years) as a function of mean juvenile growth [total length (TL)] at age 2 for the newly established Watersmeet populations (thick open circle), the source Boringwheel population (thick open square), and English (solid dots) and Continental European (thin open squares) pumpkinseed populations. The proposed physiological transition phase between non-invasive and invasive pumpkinseed populations is hypothesised as extending from the minimum age at maturity (the 45° line that traces from the intercept) and the end of juvenile growth (which for many pumpkinseed populations is age 2; the 45° line that traces through the age 2 intercept with the regression slope). Adapted from the original (Copp & Fox 2007) and a subsequent version (Cucherousset et al. 2009).

environments (Fox et al. 2007). This suggests that in warmer waters in England brought on by climate change, pumpkinseed ‘escapees’ will have an increased ability to survive and establish new populations. In addition, studies have shown that in warmer water conditions, pumpkinseed will spawn earlier (Zięba et al. 2010) and will have an increased competitive advantage when competing with native fish for food resources (Fobert et al. 2011); thus, climate change is predicted to have a positive impact on pumpkinseed survival, recruitment and propagule pressure in England.

In conclusion, although pumpkinseed are not currently considered invasive in the United Kingdom, the pumpkinseed’s status in the United Kingdom is likely to shift to invasive under predicted future conditions (*Op. cit.*). With increased survival and recruitment under conditions of a warmer climate, and life-history traits that enable colonisation and establishment in novel environments, the pumpkinseed will be able to exploit the increased hydrological variability and the extensive connectivity of canals and water course in southern England to expand its introduced range. Management strategies will be required to mitigate the impacts of pumpkinseed on the native species and ecosystems and should include control and containment initiatives to enhance outflow systems to control fish escapement (Britton et al. 2010).

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