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Environmental biology of an invasive population of signal crayfish in the River Stort catchment (southeastern England)

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ABSTRACT

Assessment of population biology at early establishment stages is a fundamental component of conservation monitoring programmes, such as for invasive signal crayfish *Pacifastacus leniusculus*. Population structure, body condition (including its relation to density-dependence), spatial patterns and habitat relationships were examined between September and October 1997 along the lower River Stort catchment (Thames River catchment, UK). A higher proportion of females was observed at intermediate sizes, whereas the largest individuals were males. Body condition was positively associated with total crayfish abundance in females but not males. Principal components analysis of the population data (by gender and size) across sampling sites revealed three distinct groups (large males, large females, small crayfish of mixed gender), with large males having significantly (analysis of covariance) lower body condition. Multiple regression of crayfish population and habitat data revealed: increasing abundance was associated with high total suspended solids (e.g. burrowing behaviour) in all size/gender groups except medium and large males; decreasing abundances of large males and females with increasing hydrodynamic efficiency (i.e. Froude number); and increasing abundance of large males and females with increasing substratum roughness. Signal crayfish population structure in the River Stort suggests an elevated potential for dispersal and reinforcement throughout the River Lee catchment. The observed spatial and habitat segregation of crayfish by gender and size appears to reflect a female reproductive strategy that avoids contact between progeny and big aggressive/cannibalistic males. Furthermore, intra-male competition is the likely reason for the lower body condition of big males, given the lack of a negative relationship between male body condition and crayfish abundance. The comparison with established populations elsewhere shows that a sex-ratio biased towards females could be a good descriptor to detect invading populations. Potential threats posed by signal crayfish for the conservation of River Stort catchment are predation, competition and habitat alteration.

Introduction

Crayfish are commonly introduced in many parts of the world to enhance aquaculture as well as recreational and commercial fisheries (Holdich 2002). Introductions of non-native crayfish to European fresh waters are of particular concern because of the species' capacity to host diseases (the crayfish plague *Aphanomyces astaci* Schikora, 1906), which threaten native European white-clawed crayfish *Austropotamobius pallipes* (Lereboullet, 1858) (Lowery and Hogger 1986; Alderman et al. 1990). This is the only crayfish species native to the British Isles, and prior to the 1970s the species had strong populations throughout water courses of southern Britain (Souty-Grosset et al. 2006). Introduced crayfish also compete with native crayfish (e.g. Souty-Grosset et al. 2006) and some species are effectively bio-engineers (Holdich 1993; Robert et al. 2004; Zhang et al. 2004), with consequences for ecosystem function and foodweb structure (e.g. Stenroth and Nyström 2003; Geiger et al. 2005).

The North American signal crayfish *Pacifastacus leniusculus* (Dana, 1852) is a fast growing very fecund species, which was introduced to the U.K. from Sweden in 1976 for the purpose of expanding aquaculture (Holdich 1993; Ackefors 2000). But this species is also a successful invader (Tricarico et al. 2010) and quickly escaped captivity and established breeding populations (Guan and Wiles 1996). Its expansion during the 1990s is a cause for concern (Ackefors 2000), especially as the signal crayfish acts as a vector for the crayfish plague to which native white-clawed crayfish is

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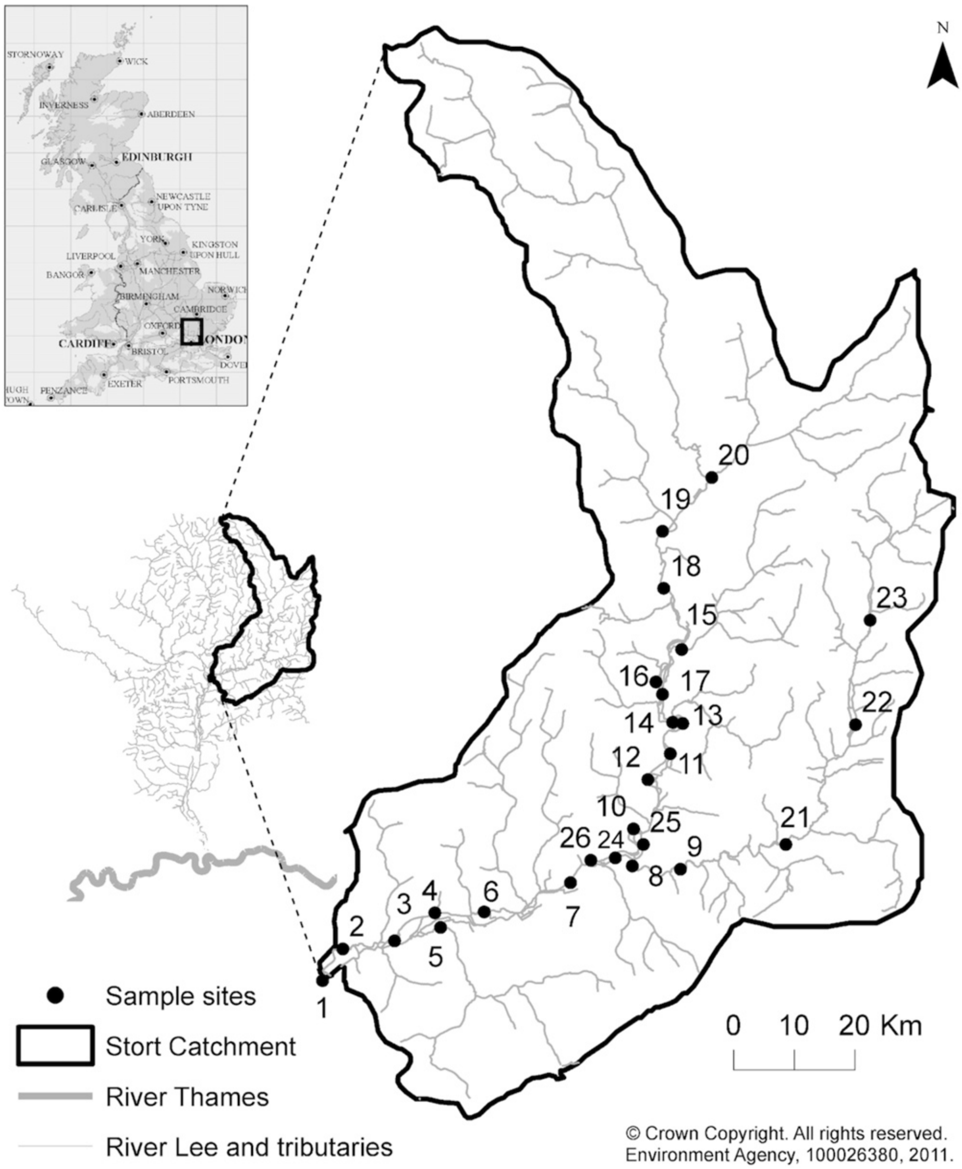

Fig. 1. Map of the River Stort catchment (River Lee basin, Hertfordshire and Essex, England) showing the 26 sampling sites (Pincey Brook sites are: 8, 9, and 21–24).

highly susceptible. As a result of this disease and the aggressive nature of signal crayfish, the numbers and distribution of native crayfish declined rapidly (Alderman 1993), and by the early 1980s the species was already listed as 'rare' in the IUCN invertebrate red data book (Wells et al. 1983) and updated to 'endangered' in 2010 (Füreder et al. 2010).

Assessment of population biology is crucial for the management of crayfish communities, both for the conservation of native species (Scalici et al. 2008) and for the control of the introduced species (Harper et al. 2002; Dana et al. 2010). In fact, population analysis has become a fundamental aspect of monitoring activities in freshwater ecosystems, contributing to the design of action plans for the preservation of these environments and their associated resources throughout Europe, as it is stated by the Water Framework Directive 2000/60 ECC. Most of population data of signal crayfish come from well-established populations in the final stages of invasion (e.g. see references in Table 5), and papers that describe signal crayfish habitat in natural environments are scarce (Guan 2000; Wutz and Geist in press). Of particular importance are data on the biology of invading populations during the establishment process, as these provide a basis for developing management programmes (e.g. Bartell and Nair 2004; Shea et al. 2010). A good example of this is the signal crayfish invasion of the River Stort, a principal tributary of the River Lee (southeastern England, Thames River catchment). Crayfish surveys in the Lee catchment had been undertaken intermittently since the 1970s, but an explosion in signal crayfish numbers in the River Stort during the mid-1990s led to the systematic collection of data on signal crayfish abundances, distribution and population features (Argent 1998). The mid-1990s represents the establishment stage for signal crayfish in the study area, as species has subsequently invaded most of the River Thames region (Ellis 2009; Ellis and England 2009; D. Almeida et al. unpublished data).

The specific objectives of the present study were to: (1) review existing information on changes in crayfish occurrence (i.e. from native to non-native) in the River Lee catchment; (2) assess the environmental biology (i.e. size structure, sex-ratio, body condition and habitat-related abundance) of signal crayfish population during the establishment stage (i.e. 1997) in the River Stort catchment; (3) compare the structural features (i.e. size range, mean size and sex-ratio) with data from established populations elsewhere; and (4) highlight potential conservation threats for the River Stort

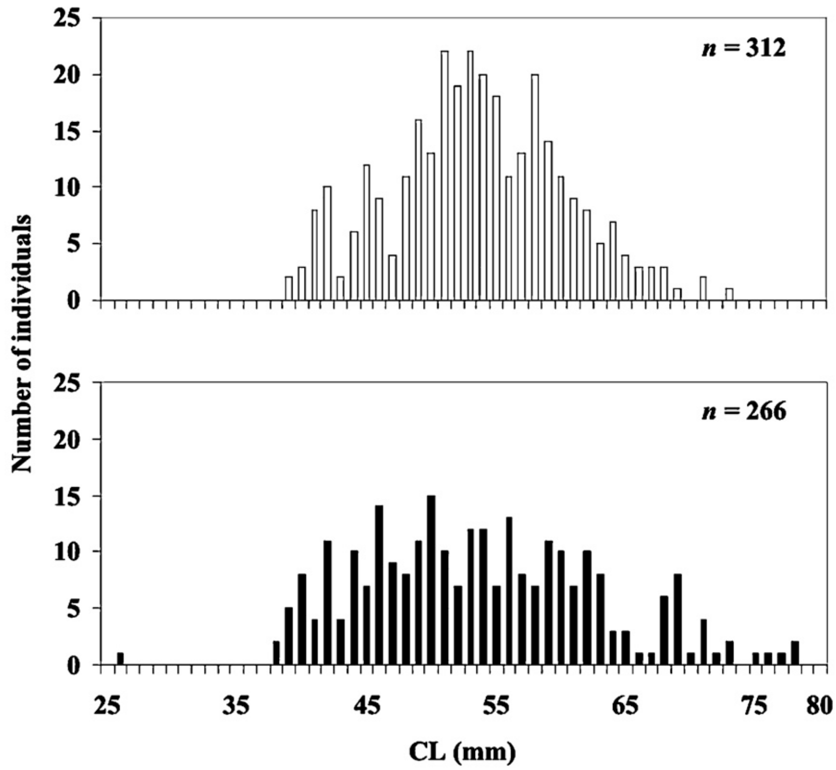

Fig. 2. Length frequency distributions of female (above) and male (below) signal crayfish in the River Stort catchment (England).

catchment. We hypothesise that the frequency of occurrence for native crayfish has decreased in the last 40–50 years as a consequence of the crayfish invasion, particularly signal crayfish (Ellis 2009; Ellis and England 2009; D. Almeida et al. unpublished data). We also hypothesise that the lower density and the subsequent lower competition and food depletion at that early invasion stage in the study area promoted a wider size range, larger sized individuals, a higher proportion of females to enhance the reproduction rate, a gender and size segregated use of different habitats, and body condition values that are not density-dependent (e.g. Sakai et al. 2001; Bohn et al. 2004; Gutowsky and Fox 2011).

Materials and methods

The River Lee catchment (area = 1420 km^2; human population = 2×10^6) is a major tributary of the River Thames and flows in a south-easterly direction from Luton (Bedfordshire) through the city of Hertford, joining the River Thames in East London (Fig. 1). The main tributary of the Lee is the River Stort (area = 278 km^2; human population = 130×10^3), which rises at Langley in Essex and flows south via Bishops Stortford to Harlow to join the River Lee at Fields Weir, Rye Meads (near Hoddesdon, Hertfordshire). The upper catchment consists of chalk overlain by alluvial deposits, where flow is maintained largely by groundwater exfiltration. Further down the catchment, the River Stort derives mainly from surface-water run-off, flowing over Boulder and London clays. Modified for navigation in the 18th century, the River Stort downstream of Bishops Stortford is mostly channelised, with 15 navigable locks that intermittently connect with remnants of the old river course, forming distinct, generally low-gradient loops. River discharge is often controlled via fixed crest weirs at the divergence point. Downstream of Bishops Stortford, the River Stort runs parallel to its main tributary, Pincey Brook, which joins the Stort just upstream of Harlow Town. Along Pincey Brook, landuse is largely arable farming, interspersed with several remnants of grazing marshes (protected local nature reserves that act as widlife corridors). Below Bishops Stortford and Harlow, the River Stort flows through several smaller conurbations before joining the River Lee at Fields Weir, Rye Meads (near Hoddesdon, Hertfordshire).

Crayfish were sampled at 26 sites along the River Stort and Pincey Brook (Fig. 1) using ten baited crayfish traps per site (Trappy^{TM} crayfish traps, Virserum, Sweden: 40 cm length, 29 cm diameter, 10 cm hole size, 2 cm mesh size), placed randomly and equi-distant (every 5 m) along a 50 m stretch of river bank. To avoid unnecessary bias, sampling was undertaken between September and October 1997, which is outside the moulting period, when crayfish are vulnerable to predation and tend to stay in refuges, therefore are not likely to be trapped. Traps were left overnight and emptied early the following morning. In the laboratory, crayfish were identified to species, gender determined, and then measured to the nearest mm using digital callipers for: carapace length (CL), from the tip of the rostrum to the base of the carapace (Peay 2003); total body length, thorax width; and body wet weight (g). Also, any missing antennae, chelae and signs of disease were recorded.

At each site, eight habitat variables were measured in the 50 cm that surrounded each trap: evening and morning water temperature (°C), total suspended solids (TSS, mg mL^{-1}) (both using a Eutech, CyberScan PC 300), trap depth (cm) in the water, distance (cm) of the trap from the nearest bank, water velocity (cm s^{-1}; Global Water, Flow Probe 101), proportion (%) of submerged vegetation cover, proportion (%) of trap shade coverage and proportion (%) of substratum composition by visual assessment according to the particle size classification as described by Platts et al. (1983).

Data analyses

Changes of the crayfish assemblage in the study area were assessed in five water courses from the River Lee catchment by means of frequency of occurrence per decade from surveys carried out since 1960–1970s (UK Environment Agency) using similar sampling methods (i.e. crayfish traps) and seasons (i.e. post-moulting period).

Gender-related size structure was examined by carapace length frequency distributions using 1 mm CL intervals (Scalici et al. 2008). Then, sex-ratio deviations from parity were tested using the chi-square (χ^2) test. Three size intervals were selected according to size structure (Fig. 2): <50 mm (small = S); 50–60 mm (medium = M); >60 mm (large = L). Crayfish catch per unit effort (CPUE) were calculated by gender and for the three size intervals from the total number of crayfish captured at each sampling site as a function of the time the ten traps were exposed.

CPUEs were depicted at each sampling site against the distance to the confluence with the River Lee to assess the distributional patterns of abundance along the fluvial gradient in the study water courses. To examine spatial patterns in the population structure of signal crayfish, detrended correspondence analysis (DCA) was performed, but this technique showed a gradient length < 2 standard deviations for the extent of variation in the abundance data. Therefore, data were submitted to principal component analysis (PCA) as per ter Braak and Smilauer (1998), who recommended linear models for subsequent analysis. Orthogonal varimax rotation was used to improve graphical illustrations. Factors with eigenvalues > 1 were extracted. The sampling site groups from this PCA biplot were compared using ANCOVA (covariate: PC1 structural size, see details below) to test for spatial variations in crayfish body condition (Moorhouse and Macdonald 2011a), with post hoc Tukey-Kramer honestly significant difference (HSD) tests employed to compare the adjusted means from more than two groups.

To control the effect of size (Freeman and Jackson 1990), structural size index (which comprises CL, total body length and carapace width measurements; Somers 1989) was calculated for every individual as the first component of PCA with varimax rotation, yielding a multivariate index of overall body size, i.e. 'structural size'. To avoid the biases of residual body condition indices, which are based on body weight regressed against body length (García-Berthou 2001; Freckleton 2002), body weight was regressed against PC1 (i.e. structural size) for each gender to achieve relationships of normalised body condition. The resulting regression slopes were compared using analysis of covariance (ANCOVA, covariate: PC1 structural size) to test for among-gender differences in body condition – a similar analytical approach has been used by Moorhouse and Macdonald (2011a). Damage score (e.g. missing chelae) was not taken into account for data analyses, since no significant statistical effect was found, probably because of the low rate of damaged individuals (less than 5%). The effect of the total crayfish abundance on body condition was assessed for each gender by partial correlations (r_P, covariate: PC1 structural size).

To assess the influence of habitat features on population structure, the eight environmental variables were combined with indices of near-bed hydraulic conditions (hydrodynamic efficiency = Froude number, shear velocity and roughness; Biron et al. 2004; Merigoux and Dolédec 2004; Brooks et al. 2005), which were calculated for each trap location, with mean values calculated for each sampling site. The environmental data and crayfish abundances (by gender and size intervals) were subjected to step-wise multiple regression analyses to assess population group–habitat relationships (e.g. MacNally 2002; Brooks et al. 2005; Almeida 2008).

For statistical analysis, which were performed with SPSS v17 (SYSTAT Software Inc., Chicago, USA), data were arcsine (proportions) or log transformed (rest of variables). The elementary units used for the statistical analyses were the sampling sites (i.e. the 10 traps) to avoid pseudoreplication. Assumptions of normality of distributions and homogeneity of variance were verified using Shapiro–Wilk and Levene tests, respectively. The significance level was set at $\alpha = 0.05$.

Table 1
Frequency of occurrence for different crayfish and crab species from surveys carried out in five water courses of the River Lee catchment (England) during the 1960–1970s to the 2000s.

Water course	Species	1960–1970s	1980s	1990s	2000s
River Ash	*A. pallipes*	100	100	100	4.8
	P. leniusculus	0	0	0	28.6
River Lee	*A. pallipes*	100	100	0	0
	A. leptodactylus	0	0	100	0.9
	P. leniusculus	0	0	0	45.1
	O. virilis	0	0	0	17.7
	E. sinensis	0	0	0	1.8
River Mimram	*A. pallipes*	–	100	100	0
	P. leniusculus	–	0	0	100
Pincey Brook	*A. pallipes*	100	100	60	0
	P. leniusculus	0	0	40	100
River Stort	*A. pallipes*	100	75	0	0
	P. leniusculus	0	25	56	100

Results

White-clawed crayfish were abundant in the River Lee catchment during the 1960s and 1970s but declined after the 1980s (Table 1). Indeed, crayfish samples from the Stort's main tributary, Pincey Brook, contained only native crayfish in surveys undertaken in 1978, 1980 and 1981. However, in 1978, signal crayfish were stocked into a lake adjacent to the Lee/Stort confluence, with a secondary (presumably later) introduction to Pincey Brook believed to have occurred (Bywater 1997). Although the first report of signal crayfish in the the River Stort was not until 1989, the species probably entered sometime in the early 1980s, given that the first report of the crayfish plague outbreak in the River Lee catchment (Hertford/Ware area) was in 1981 and at least one local person was known to have been keeping signal crayfish during that period (Lowery pers. comm.). By the 1990s, only two populations of white-clawed crayfish where known to exist, and these were situated in upper reaches of the River Lee catchment (rivers Ash and Mimram, Table 1). Signal crayfish was found during surveys of Pincey Brook in 1993 and 1994 (Bywater 1997), and subsequent surveys (Ellis and England 2009) suggest a high probability of white-clawed crayfish becoming locally extinct. By 2010, the downstream edge of signal crayfish distribution in the River Lee was estimated to be ≈12 km downstream of the Lee-Stort confluence (Environment Agency, unpublished data). In 2004, the virile crayfish *Orconectes virilis* (Hagen, 1870) was first detected (Ahern et al. 2008) and it was subsequently joined by two other invasive crustacean species: Turkish crayfish *Astacus leptodactylus* Eschscholtz, 1823, and Chinese mitten crab *Eriocheir sinensis* H. Milne-Edwards, 1853 (Table 1).

Female signal crayfish were more abundant than males, although sex-ratio did not differ significantly ($\chi^2 = 1.68$, $P > 0.05$ with Yates' correction) from parity (male:female ratio = 1:1.17). However, significant between-gender differences in size structure ($\chi^2 = 59.39$, $P < 0.05$) were observed in the study area (Fig. 2). Thus, females were more abundant (1:1.63) between 50 and 60 mm CL ($\chi^2 = 8.20$, $P < 0.01$ with Yates' correction). The size range was wider in males (26–78 mm CL), and the proportion of larger individuals was also higher (Fig. 2). No clear pattern of variation was found along the study water courses (Fig. 3A). The highest crayfish abundance was observed in the lower Stort and the upper Pincey Brook (Fig. 3A). Spatial patterns in the population structure of signal crayfish indicate segregation by gender and size (Fig. 3B), with PC1 and PC2 accounting for 67.44% and 27.02% of the variance, respectively (Table 2). All population groups were positively correlated with PC1, except for the CPUE of large males. CPUE values for both small females and males were negatively associated with PC2. However,

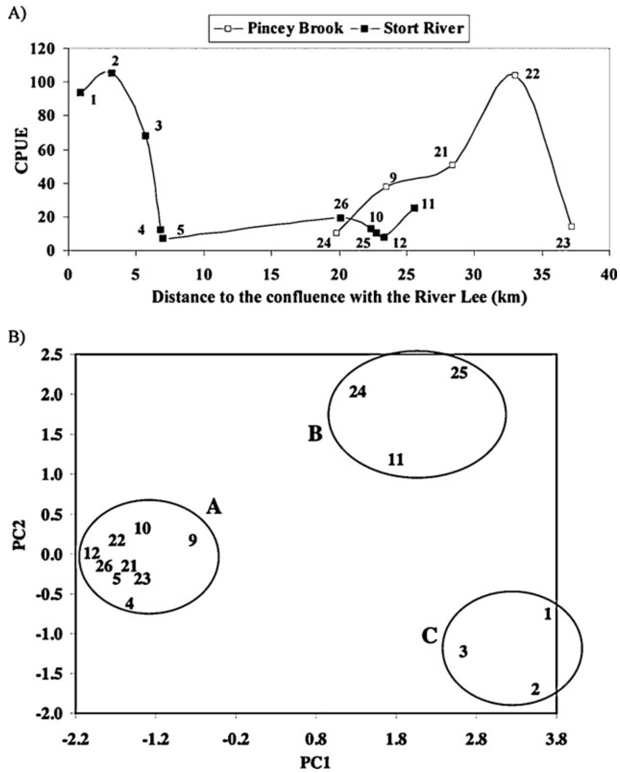

Fig. 3. (A) CPUE distribution for signal cryafish along the Pincey Brook and the River Stort (see Fig. 1); (B) principal components analysis biplot (PC1 and PC2) of ordination scores for signal crayfish population groups (see Table 2) by sampling site.

Table 2
Factor loadings of the principal components analysis for population groups (gender by size interval) of signal crayfish.

Population group	PC1	PC2
Female, S	0.89^{***}	-0.54^{*}
Female, M	0.82^{***}	0.29
Female, L	0.68^{**}	0.74^{**}
Male, S	0.83^{***}	-0.59^{*}
Male, M	0.92^{***}	0.15
Male, L	-0.53^{*}	−0.41
Eigenvalue	4.05	1.62
% variation	67.44	27.02

S, small; M, medium; L, large.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

a positive correlation was significant ($P < 0.01$) for large females. The PC1 × PC2 ordinations of the 15 sampling sites containing signal crayfish revealed three distinct groups of sites (Fig. 3B), which were characterized by a predominance of: Group A – large males; Group B – large females; and Group C – small individuals.

Signal crayfish relationships with habitat characteristics also varied according to size and gender (Table 3), with the strongest relationships being for large females and no relationships between medium-sized males and any habitat variable. Signal crayfish abundances increased with increasing TSS in all cases except medium and large males, whereas, the abundances of large males and large females decreased with increasing hydrodynamic efficiency (Froude number) but increased with increasing substratum roughness.

Crayfish body lengths were significantly correlated with PC1 (structural size), which explained 96.1% of variance (Table 4). Normalised body condition, i.e. the regression slopes of PC1 vs. body weight, was significantly higher (ANCOVA: $F_{1,574} = 8.40$, $P < 0.01$) in males (mean = 0.110, SE = 0.0019) than in females (mean = 0.103, SE = 0.0014). The results for the linear regressions were: in females, $r^2 = 0.94$, $F_{1,310} = 5457.25$, $P < 0.001$; in males, $r^2 = 0.93$, $F_{1,264} = 3369.49$, $P < 0.001$. After controlling for the effect of structural size (PC1), female body weight was positively correlated with total crayfish abundance ($r_P = 0.71$, $P < 0.01$), but this was not the case for males ($r_P = -0.14$, $P > 0.05$). Significant differences (ANCOVA) in body condition were found between the three groups from the PCA on population structure ($F_{2,574} = 14.36$, $P < 0.001$), with Group A (log-transformed mean = 1.62, SE = 0.003) having a significantly lower (HSD test, $P < 0.05$) adjusted body weight than groups B (log-transformed mean = 1.66, SE = 0.004) and C (adjusted body weight mean = 1.67, SE = 0.010).

Size ranges and means of CL were highly variable across populations (Table 5), with the widest range (60 mm CL) for population in Spain. The River Stort population had the second widest range for males (52 mm CL) and the narrowest range for females (34 mm CL). Populations in Japan showed the largest mean CL, with those for the River Stort and recently established populations (i.e. Poland, Croatia and Italy) being intermediate. Sex-ratio showed the proportions of females with respect to males were > 1 for the River Stort, Poland, Croatia and Italy, with the River Stort population acheiving the highest value (Table 5).

Table 3
Step-wise multiple regression models for population groups (gender by size interval) of signal crayfish as the dependent variables and habitat characteristics as predictive variables.

Population group	r^2	F	P	Model	Coefficient
Female, S	0.27	4.76	<0.050	TSS	4.57
				Intercept	−0.92
Female, M	0.52	13.87	<0.010	TSS	8.27
				Intercept	−2.19
Female, L	0.63	47.87	<0.001	TSS	5.44
				Roughness	2.73
				Froude number	−3.45
				Intercept	−1.97
Male, S	0.33	6.50	<0.050	TSS	5.17
				Intercept	−1.13
Male, M	–	–	NS	–	–
Male, L	0.48	5.50	<0.050	Roughness	4.28
				Froude number	−6.38
				Intercept	−0.16

S, small; M, medium; L, large; NS, not significant. $P > 0.05$.

Table 4
Factor loadings of the principal components analysis for body measurements of signal crayfish.

Body measurements	PC1
Carapace length	0.98***
Total length	0.98***
Carapace width	0.97***
Eigenvalue	2.88
% variance	96.09

*** $P < 0.001$.

Discussion

The replacement of native white-clawed crayfish by non-native crayfishes in the River Lee catchment between 1960–1970s and 2000s (Table 1) mirrors a similar pattern observed on the River Thames catchment overall (Ellis 2009; Ellis and England 2009; D. Almeida et al. unpublished data), as well as elsewhere in the UK. (Holdich et al. 2004). Low density populations of signal crayfish often go unnoticed, and the available information from the Environment Agency (unpublished data) suggests that there was more than one introduction site in the River Lee basin, though all of the initial introductions appear to have occurred within the River Stort catchment, since signal crayfish were not reported in other nearby water courses until the 2000s (Table 1). In the River Stort catchment, the signal crayfish population displayed partitioned habitat use, which may have reduced competition between sexes and cohorts. Size structure and body condition suggest good recruitment, indicating that the population had potential for further dispersal and reinforcement within the River Lee basin, and this was observed in the 1990s–2000s (Table 1). A similar pattern of downstream dispersal has been observed with the virile crayfish, which appeared in the Lee catchment in the same decade as Turkish crayfish and Chinese mitten crab (Table 1).

Signal crayfish population structure in 1997 was segregated by gender at particular sizes, with a predominance of females in size class 50–60 mm CL. This may be due to the effect of the sampling period, since females demonstrate greater activity whilst foraging in the early autumn to recover the body condition after spawning or prior to winter (Guan 1995). However, it should be noted that the traps used appear to be biased towards medium to larger individuals (>40 mm CL), both elsewhere (Peay 2004; Moorhouse and Macdonald 2011b) and in the present study (Fig. 2). The modal size from Trappy traps is typically ≈45–50 mm (Peay 2004), but one unknown factor is the possible influence that illegal trapping of signal crayfish could have on the size distribution results. Because large males (>65 mm CL) enter traps readily and represent a small proportion of the entire population, it is possible that the true size distributions at some sites were masked by the illegal trapping of large crayfish.

The spatial patterns appear to reflect a female reproductive strategy that involves spawning displacements within the river catchment (Fig. 3B), such as suggested by Guan (2000). This migratory behaviour is widely used by aquatic animals (e.g. Mumby et al. 2004; Pillans et al. 2005; Martinho et al. 2007) as a means of providing offspring with high quality habitat that is free from large (aggressive/cannibalistic) males. After spawning in areas suitable for young individuals (i.e. Group C sites), which contained a high proportion of juveniles (Fig. 3B), large females appear to have shifted to post-spawning recovery sites (Group B) during which large males occupied other suitable habitats (Group A). Only Group C seemed to form a geographic cluster at the downstream end of the study area (Fig. 1). The higher CPUE of the small size interval (< 50 mm CL) downstream in the River Stort (sites 1, 2 and 3; i.e. group C; see Fig. 3A and B) may indicate the presence of a younger population influenced by the confluence with the River Lee, e.g. immigration of juveniles from the mainstream (Fig. 1). This spatial segretation, according to the reproductive strategy, has been also suggested for other invasive aquatic species in novel environments (Bohn et al. 2004; Gutowsky and Fox 2011). However, small individuals may have not been sampled adequately by the method of trapping as it has been mentioned above.

Table 5
Minimum and maximum (min–max in mm), as well as mean carapace length (CL) and sex ratio (M:F) of introduced signal crayfish populatiosns in the U.K. and elsewhere. Where available, values are given separately for males and females.

Location	CL min–max	Mean CL	Sex-ratio	Source
River Stort (UK)	26–78 (M) 39–73 (F)	53.7 (M) 53.5 (F)	1:1.17	Present study
River Great Ouse (UK)	35–75 (M) 35–70 (F)	49.1 (M) 43.0 (F)	1:0.88	Guan (2000)
Rivers Evenlode and Thame (UK)	30–80	53.7	–	Moorhouse and Macdonald (2011a)
River Windrush (UK)	41–no data	58.5	–	Moorhouse and Macdonald (2011b)
Lake Karisjärvi (Finland)	27–78 (M) 30–79 (F)	52.8 (M) 55.7 (F)	1:0.97	Kirjavainen and Westman (1999)
Lake Iso-Majajärvi (Finland)	26–69	47.0	1:0.96	Westman et al. (1999)
Lake Slickolampi (Finland)	29–71	51.3	1:0.99	Westman et al. (2002)
River Moosach (Germany)	23–73	48.0	1:0.85	Wutz and Geist (in press)
River Riofrio (Spain)	10–70	31.2	–	Dana et al. (2010)
Mazurian lakes (Poland)*	23–66 (M) 23–62 (F)	48.2 (M) 46.7 (F)	1:1.01	Krzywosz and Krzywosz (2001)
River Mura (Croatia)*	34–78 (M) 28–72 (F)	56.6 (M) 54.1 (F)	1:1.16	Hudina et al. (2011)
Lake Brugneto (Italy)*	22–72 (M) 22–66 (F)	52.0 (M) 51.6 (F)	1:1.03	Capurro et al. (2007)
Castle Lake (California)	30–75 (M) 35–70 (F)	54.3 (M) 49.5 (F)	1:0.92	Elser et al. (1994)
Lake Onogawa (Japan)	–	56.5	–	Tomonori et al. (2006)
Lake Hibara (Japan)	–	62.6 (M) 63.5 (F)	–	Tomonori et al. (2006)

* Data from a population established within the three previous years.

Regardless, there does appear to be a size-related aspect to signal crayfish habitat. In the River Moosach (River Danube basin), large signal crayfish were associated with lentic condions, which contrasted the lotic habitat of smaller conspecifics (Wutz and Geist in press). A similar pattern was reported for the River Great Ouse basin, which is contiguous to the River Stort catchment, with large signal crayfish found more frequently in lentic, off-channel locations, and smaller specimens more frequently in riffles of the upprer stretches of the main river (Guan 2000). Data from the present study were consistent with this (Table 3) – larger individuals (both male and female adults) were more common in sites charaterized by low hydraulic stress (Froude number), and large substratum particle sizes (i.e. large interstices). This suggests a mechanism to avoid the greater energy expenditure associated with both burrow digging in mud (e.g. by using large substrata to find refuge) and holding station in elevated water velocities (Allan 1995). Also, large crayfish may outcompete small individuals for the best refuges in large substrata. In relation to suspended solids (TSS), signal crayfish is a known bioengineer species (Holdich 1993) with corresponding increases in TSS (Table 3) due to burrowing activity (Guan 1994; R. Argent pers. observ.). Thus, TSS was clearly associated to all signal crayfish population groups in the present study except medium and large males. However, it is unclear whether females and small individuals can take advantage of these conditions to be favourable (e.g. lower predatory detection) or they are forced into those locations by the larger (more aggressive, competitive, cannibalistic) males.

The higher body condition values in males than females in the study area resemble patterns observed elsewhere in British fresh waters (Guan and Wiles 1999): males achieve good condition fast in order to out-compete other males, whereas females invest in egg production (Guan 1995). Moreover, body condition should decrease greatly in large males (e.g. Group A, Fig. 3B) over the course of the breeding season (e.g. intra-male competition for territory and females). Besides this, a reduction in signal crayfish abundance in upper Thames catchment, particularly of large individuals, was found to result in an increased growth rate in the remaining population (Moorhouse and Macdonald 2011a). However, results of the present study reveal that variations in body condition were not density-dependent in males; and females had a higher index of body condition at sites with high total abundance of crayfish. This suggests that resources were not limited in the Stort catchment – a reasonable assumption if the population is still establishing itself.

Regarding this early stage of invasion, comparisons with established populations (Table 5) partly support our hypotheses on structural features of signal crayfish populations. Although the size range was very wide for males in the River Stort, females showed the opposite trend. Moreover, the rest of size ranges (together with mean CL) greatly varied across populations, which suggests that local conditions deeply influence on the growth and development of this crayfish species (e.g. Guan and Wiles 1999; Westman and Savolainen 2002), irrespective the stage of invasion. However, results on sex-ratios were clearer, with the highest value for female proportion at the present study and similar high values for other recently established populations (Table 5). This demonstrates the importance of the gender investing more resources in the reproduction. Thus and as an example, males of round goby *Neogobius melanostomus* (Pallas, 1814), which display paternal brood care, were proportionally more abundant in newly invaded areas of a Canadian river (Gutowsky and Fox, 2011). Therefore, this structural feature in signal crayfish, i.e. the sex-ratio biased towards females (above all at medium sizes) could be a good descriptor to assess whether an introduced population is at early or final stages of the invasion, and this is generally supported by the sex-ratio data for introduced populations (Table 5).

Signal crayfish have exerted multiple impacts on environments where the species has been introduced by displaying high foraging plasticity, including omnivory, fish predation and cannibalism (Guan and Wiles 1998), which complements the species' great capacity to adapt to (and bio-engineer) novel environments (Guan 1994). Thus, a major and likely adverse consequence for nature conservation in the River Stort catchment is predation on native benthic species, in particular invertebrates (Stenroth and Nyström 2003) and the young of small-bodied fishes (Guan and Wiles 1997). Amongst the latter is the European bullhead *Cottus gobio* L., 1758, which is listed in Annex II of the European Commission's COUNCIL DIRECTIVE 92/43/EEC (1) of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (Habitats and Species Directive: EC HSD) as being "of community interest whose consideration requires the designation of special areas of conservation". Note, however, that in contrast to Continental European locations, the European bullhead is wide-spread and abundant in many UK river basins (e.g. Copp 1992; Carter et al. 2004). Other species likely to be subject to predation are the eggs and young of salmonid species (Edmonds et al. 2011) and of stone loach *Barbatula barbatula* (L., 1758), in particular where big aggressive male crayfish congregate (Guan and Wiles 1997). Furthermore, competition between signal crayfish and native benthivorous fishes (i.e. endemic Iberian loaches *Cobitis* spp.) for habitat/refuge has already been observed (via snorkelling) in the River Jarama (central Spain), involving interference competition for cobbles and crevices (D. Almeida unpublished data). This strong competition would apply equally to native white-clawed crayfish (Guan and Wiles 1996; Guan 2000), which despite their demonstrated ability to partition habitat (e.g. Legalle et al. 2008; Clavero et al. 2009) do not appear able to coexist with successful, strongly competitive, non-native species such as signal crayfish (e.g. Souty-Grosset et al. 2006) and the other invasive crustaceans (Stucki and Romer 2001; Ahern et al. 2008; Gilbey et al. 2008) already present in the River Lee catchment (Table 1). Indeed, native white-clawed crayfish were not found in the 1997 surveys, which implies a clear decline due to the signal crayfish introduction and accompanying outbreak of crayfish plague in the early 1980s.

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