

RESEARCH ARTICLE

The 'Pritchard Trap': A novel quantitative survey method for crayfish

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Abstract

1. As crayfish invasions continue to threaten native freshwater biota, a detailed understanding of crayfish distribution and population structure becomes imperative. Nonetheless, most current survey methods provide inadequate demographic data. The quantitative 'Triple Drawdown' (TDD) dewatering method has highlighted the importance of such data, yet practical constraints prevent its large-scale application.
2. Here, we introduce the 'Pritchard Trap', a novel passive sampling method that reliably generates quantitative crayfish population data while requiring substantially lower sampling effort than TDDs. This quadrat-style sampler was extensively tested in headwater streams of North Yorkshire, England, along an invasion gradient for signal crayfish (*Pacifastacus leniusculus*) from well-established sites to mixed populations of signal crayfish and native white-clawed crayfish (*Austropotamobius pallipes*).
3. The Pritchard Trap was trialled over several time intervals to determine the minimum required trap deployment time. TDDs at the same sites allowed for a robust evaluation of Pritchard Trap sampling accuracy in representing crayfish densities and population structure.
4. The Pritchard Trap successfully sampled both invasive and native crayfish (8–42 mm carapace length). A minimum passive deployment time of 4 days was required. At low crayfish densities (0.5 individuals m⁻²), increased trapping effort was necessary to achieve accurate population density and size class distribution estimates. The Pritchard Trap required substantially less sampling effort (working hours) and resources than the TDD, whilst also posing less risk to non-target species.
5. The Pritchard Trap, for the first time, affords logistically simple, truly quantitative investigations of crayfish population demographics for headwater systems. It could be integrated into crayfish research and management, for example to explore density-dependent ecological impacts of invasive crayfish and their management

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responses or to monitor populations and recruitment in native crayfish conservation initiatives.

KEYWORDS

crayfish density, crayfish sampling, population demographics, signal crayfish, triple drawdown, white-clawed crayfish

1 | INTRODUCTION

Crayfish (Astacidea) represent one of the most widely introduced freshwater taxa (Twardochleb et al., 2013). Impacts of resulting non-native crayfish invasions range from ecological and geomorphological to economic and cultural (Lodge et al., 2012). Most notably, non-native invasive crayfish commonly displace native crayfish species through direct competition and transmission of disease (Richman et al., 2015), primarily 'crayfish plague' *Aphanomyces astaci* (Holdich et al., 2009; Lodge et al., 2000). Further impacts include a reduced abundance and diversity of macrophyte (Nyström & Strand, 1996), macroinvertebrate (Mathers et al., 2016) and fish communities (Galib et al., 2020; Peay et al., 2009; Reynolds, 2011), and habitat degradation through burrowing and bioturbation (Harvey et al., 2011). Non-native crayfish invasions generally have strong and complex consequences for freshwater biodiversity and ecosystem services (Kouba et al., 2014). Nature and strength of invasion impacts are furthermore closely linked to the population density of invasive crayfish (Bubb et al. 2009; Parker et al., 1999). Good knowledge of the distribution and demographics of both native and non-native freshwater crayfish populations is therefore critical for understanding their impact on the structure and functioning of aquatic ecosystems.

Crayfish surveys have employed a variety of methods and approaches (see Parkyn, 2015), including baited traps (e.g. De Palma-Dow et al., 2020), passive traps (e.g. artificial refuge traps (ARTs); Green et al., 2018), manual handsearches (Bradley et al. 2015; Hilber et al., 2020), electrofishing (e.g. Alonso, 2001) and environmental DNA (Chucholl et al., 2021). However, these methods each have inherent limitations and biases, such as low spatial resolution (eDNA; Harper et al., 2018), or selecting for specific crayfish life stages, sexes or species (Price & Welch, 2009; Rabeni et al., 1997). Baited traps are the most widely used crayfish survey method (Parkyn, 2015). Their low cost, ease of use and suitability across a wide range of habitats make traps generally a convenient tool for basic survey and management. However, standard trap samples are biased towards large (≥ 35 mm carapace length CL), active males (Chadwick et al., 2021; García-De-Lomas et al., 2020; Gherardi et al., 2011), generating semi-quantitative catch-per-unit-effort abundance estimates limited to large size classes.

A range of modified equipment and new methods have been suggested to survey small crayfish size classes in various aquatic systems. These include finer mesh sizes for baited traps (Stebbing et al., 2016), and trials of quadrat samplers (Distefano et al., 2003) and enclosure

traps (Byrne et al., 1999; Fjälling, 2011). For example, Stebbing et al. (2016) observed smaller signal crayfish to sometimes be retained when using a decreased mesh size in baited funnel traps. Nonetheless, larger crayfish present in the traps deterred juvenile and female crayfish, and a strong sample bias remained. A modified quadrat design somewhat resembling a large Surber sampler has been tested (Distefano et al., 2003; Larson et al., 2008; Rabeni et al., 1997). Here, the survey area is enclosed with a mesh-sided frame, and the substrate is methodically disturbed to collect the crayfish within the frame. This method revealed spatial and temporal differences in crayfish population densities in large (20–25 m width) streams (Distefano et al., 2003), but was prone to both under- and over-estimations of the overall population size (Larson et al., 2008), as well as bias towards small size classes (Rabeni et al., 1997).

An enclosure trap was designed by Fjälling (2011) and further tested by Engdahl et al. (2013) with the explicit aim of sampling juvenile signal crayfish in Swedish lentic systems. Small circular traps (0.09 m²) were filled with suitable juvenile refugia (small gravels, then naturally occurring bed materials). Traps were left in situ at depths of 1–3 m along the littoral margin of a lake for several weeks to passively colonize. This method proved highly effective at sampling small crayfish, with the juvenile size class (<37.5 mm total length) comprising 97.8–98.6% of the total catch. The reported juvenile densities were strongly influenced by the substrate type, and very few adult crayfish were captured – likely in response to the substrate composition (Engdahl et al., 2013). Therefore, whilst effectively capturing juvenile crayfish, this enclosure trap remains unsuitable for generating whole population density or structure estimates.

Chadwick et al. (2021) assessed in situ crayfish demographics using a triple drawdown (TDD) approach in headwater streams in Northern England. The TDD involved isolating small sections of stream and sequentially dewatering them to form depletion 'sweeps'. Crayfish refugia, including cobbles, boulders and woody debris, were removed from the channel and exposed crayfish were captured by hand or net. The TDD enabled robust estimates of the total crayfish population and its structure, sampling on average 92% of the estimated crayfish population. The TDD revealed extremely high crayfish densities (21–110 individuals m⁻²), with juveniles and sub-adults comprising the majority of the population (90% of individuals < 25 mm CL). Nonetheless, this approach is extremely resource intensive and widely impractical for use in frequent or remote surveys.

The biases associated with conventional crayfish sampling methods and the technical limitations of the TDD highlight a crucial need for an

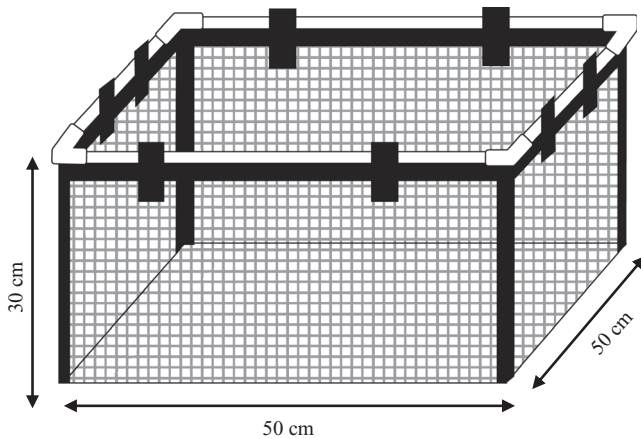


FIGURE 1 Technical drawing of the PT illustrating the square mesh bag, webbing hems and loops and plastic quadrat

intermediate method that combines the simplicity and cost efficiency of conventional trapping techniques with the data quality of the TDD. In response to this need, we designed and tested a novel sampling technique, the 'Pritchard Trap' (PT), for the passive sampling and subsequent characterization of crayfish population density and structure in rocky streams.

We assessed the performance and practicalities of the PT in rocky headwaters in Northern England, where both native white-clawed crayfish and invasive signal crayfish were present. We tested the hypothesis that these new traps successfully sample crayfish across a range of size classes. Additionally, we hypothesized that crayfish numbers in PTs would reach a stable equilibrium once a 'minimum deployment time' was exceeded. The efficacy of PTs was evaluated through comparison with 'true' population demographics generated using the TDD technique at the same study site. Overall, we aimed to determine whether PTs can provide robust quantitative data on crayfish populations.

2 | MATERIALS AND METHODS

2.1 | Pritchard trap design

The PT consists of a five-panel mesh bag and rigid plastic quadrat frame. The quadrat comprises four detachable plastic pipes with corner piece sections (50 cm in length), attached to the mesh bag through webbing loops (Figure 1). The base of the mesh bag measures 50 cm × 50 cm, creating a base trap area of 0.25 m². Mesh bag panels measure 30 cm in height and are reinforced with strong webbing – this height could be adjusted in response to water depth requirements. While the mesh is strong and rigid, it can be compressed flat during deployment. The mesh bag is green in colour (Figure 2a) with a 1.9 mm × 1.9 mm mesh size to allow passage of water and small invertebrates, whilst retaining all crayfish. This quadrat can be dismantled, and the mesh bag folded down for convenient travel and storage. Details of materials and the manufacturing process are provided in Supporting Information (SI 1 and 2).

2.2 | Practical operation of PTs in this study

To set a trap, substrate (boulders, cobbles, gravel, woody debris) was first removed from the 0.25 m² trap footprint and collected into a bucket to expose the riverbed (typically 10–20 cm substrate depth; Figure 2b). The PT was pressed flat into the created depression so that the mesh panels were fully collapsed, being folded over themselves underneath the plastic quadrat frame, to maintain a consistent base area. Quadrat corners were weighted down with large cobbles, and the collected substrate was then replaced on top of the flattened PT to reform the original channel profile (Figure 2c). Placement of PTs within the channel was not observed to encourage or impede the mobilization of bed materials. Crayfish were able to freely enter and exit the trap area, accessing the substrate for refuge and foraging. Upon retrieval, the quadrat was sharply pulled upwards, so that the mesh panels were fully extended, thus entrapping any crayfish residing within the PT (Figure 2d). The entire contents of the PT including substrate and crayfish were emptied into buckets to be processed. Substrate and PTs were redeployed to the same position between sampling events, with substrate returned following the sampling completion. Both the initial deployment and subsequent retrievals and re-deployments of a PT typically took one operative 15 minutes.

2.3 | Study area

The study was conducted at the upland headwater streams Bookill Gill Beck (BGB) and Long Preston Beck (LPB) in the Ribble catchment of North Yorkshire, England. Extensive details of the study stream are presented in Chadwick *et al* (2021). For this work, we used four sites along the study system; one site, Double Gate Bridge (DGB), is located on BGB, and three sites, Confluence, Footbridge and Farm, are situated on LPB (Figure 3). BGB is a small, steep headwater stream; approximately 1.5 m wide at the DGB sampling site. LPB is consistently approximately 4 m wide for sites Confluence, Footbridge and Farm. The average water depth across the sites was 10–25 cm during summer flows. In-channel substrate was dominated by cobbles and boulders throughout.

Fieldwork was undertaken during the summers (June–September) of 2018 and 2019. The use of the PTs was authorized by the Environment Agency (CR1 licence).

2.4 | Experimental design

Two experiments were undertaken to evaluate PT performance. A deployment time experiment established the minimum trap deployment time for crayfish densities in the PTs to stabilize. The second experiment enabled comparisons of crayfish population density and structure reflected by PT and TDD samples (Table 1). PTs were used at a higher sampling effort (7.5 m²) for population structure analyses

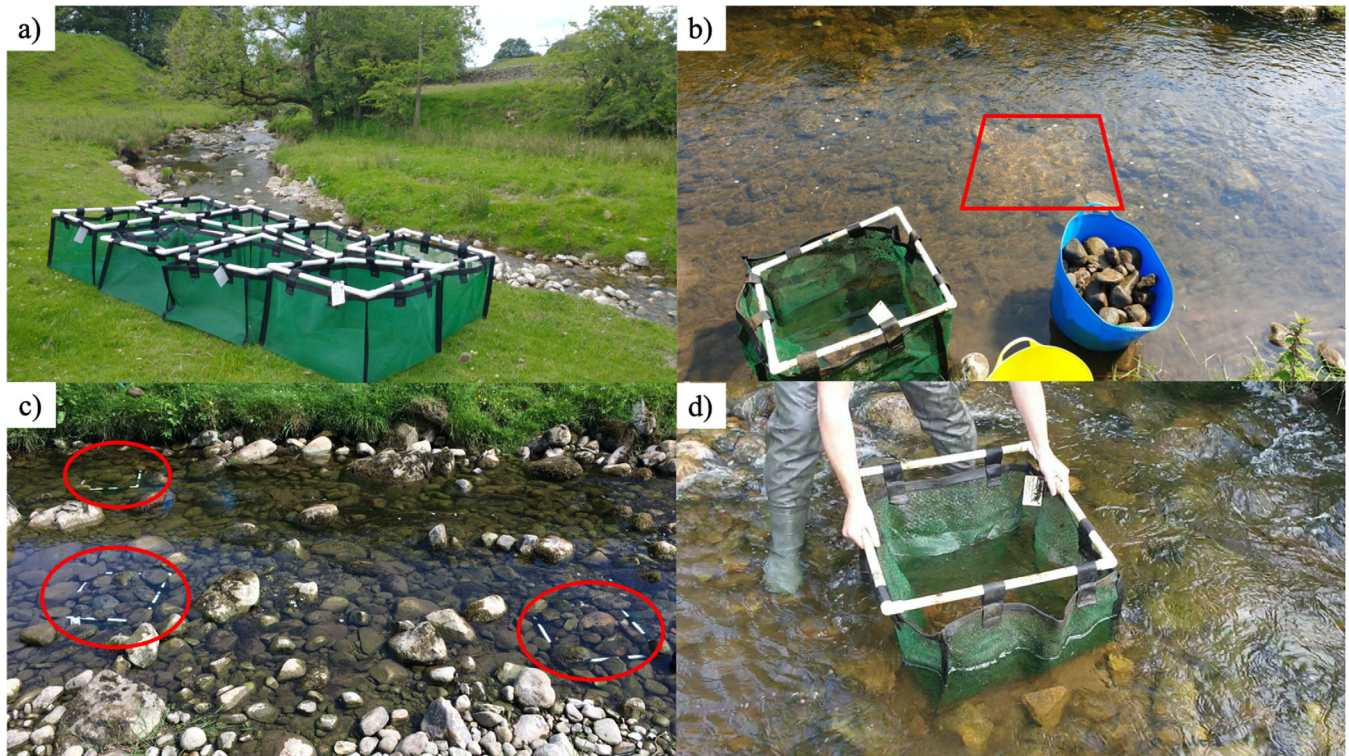


FIGURE 2 Photographs of PTs in the field: (a) PTs assembled ready to set, (b) substrate collected in a bucket from the footprint of the PT to be set (0.25 m² sample location outlined), (c) PTs set in the river (red circles) and (d) retrieval of PT from a river

TABLE 1 Summary table of field studies, including deployment time analyses, density estimates and population structure comparisons at sites along BGB and LPB

Experiment	Method	Year	Months	Site(s)	Sample size (m ²)
Deployment time	PT	2019	June–September	All	$n = 3$ (0.75 m ²)
PT vs. TDD comparison	PT (density)	2018	July–August	All LPB	$n = 4$ (1 m ²)
	PT (density)	2019	August	DGB, BGB	$n = 3$ (0.75 m ²)
	PT (structure)	2019	June–September	All	$n = 30^a$ (7.5 m ²)
	TDD	2018	August	DGB, BGB	$n = 1$ (15 m ²)
	TDD	2018	July	Confluence, LPB	$n = 1$ (45.5 m ²)
	TDD	2018	July	Footbridge, LPB	$n = 1$ (45.5 m ²)
	TDD	2018	July	Farm, LPB	$n = 1$ (50 m ²)

Abbreviations: BGB, Bookill Gill Beck; DGB, Double Gate Bridge; LPB, Long Preston Beck; PT, Pritchard Trap; TDD, triple drawdown.

^aComprised of three individual traps lifted 10 times each over the 2019 field season.

(2019, all sites) and a low sampling effort (0.75–1 m²) for all other analyses (Table 1).

All crayfish were identified to species level in the field. White-clawed crayfish were measured on the bankside and immediately released back at the site in a safe, undisturbed area. All PT-sampled signal crayfish were processed and then released back at the site to prevent skewing catch results of the next repeat (method statement approved by Environment Agency). Signal crayfish captured in TDDs were stored on ice and humanely destroyed by freezing, before pro-

cessing in the laboratory. Carapace length (CL, mm), mass (g) and che- liped damage (absent or regenerating) were recorded for all crayfish. Crayfish over 12 mm CL were processed for sex (male/female), while crayfish ≤ 12 mm CL were too small to be reliably sexed and were clas- sified as juveniles in this study.

The PT crayfish samples from the mixed population at the Farm site were split into two separate datasets, one for each species present ('Farm WCC' for white-clawed crayfish and 'Farm SC' for signal crayfish).

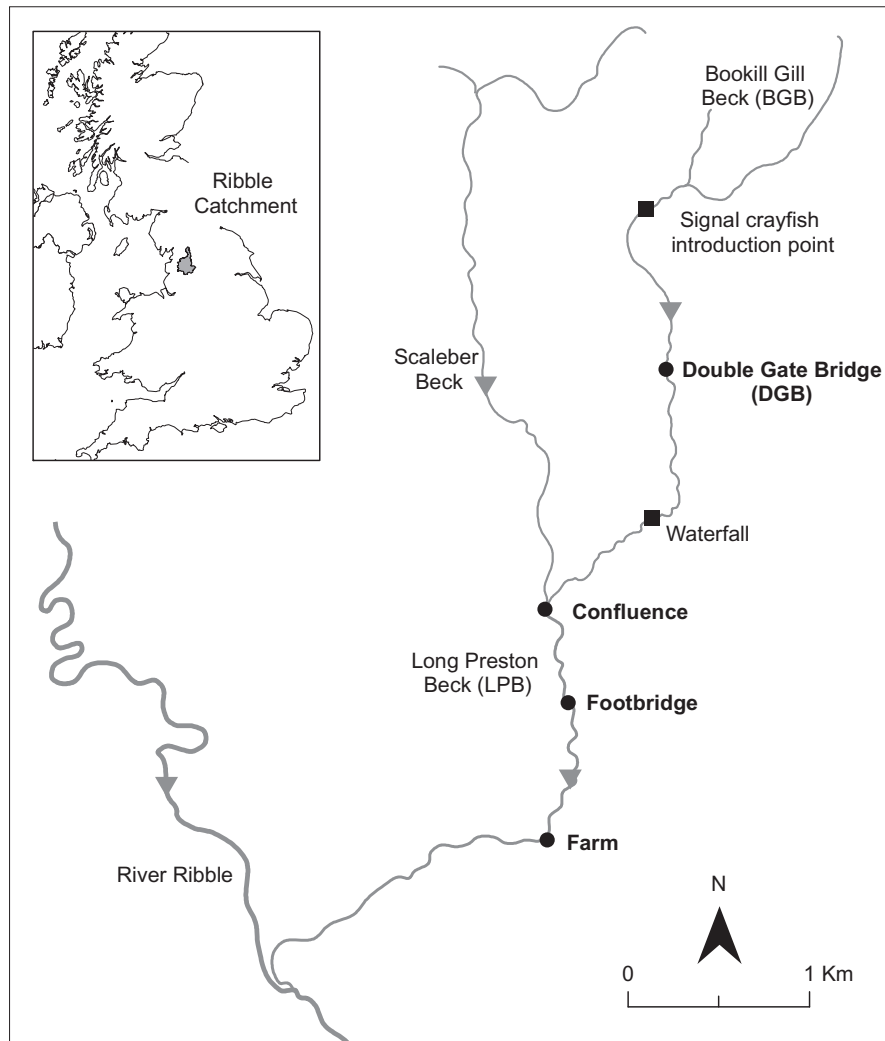


FIGURE 3 Site map of the study area, including the four study sites, DGB on BGB and Confluence, Footbridge and Farm along LPB

2.5 | Deployment time experiment

PTs were set at all four sites ($n = 3$ per site) to estimate the minimum deployment time. All traps were set by the same two personnel for consistency, across a range of habitat types including pools, riffles, central channel, margins, shaded and unshaded areas. Five different time interval treatments were used; 1, 2, 4, 7 and 10 days over which time PTs were left submerged without disruption. On experiment completion, all traps were retrieved and disinfected with Virkon™ Aquatic S.

The deployment time experiment was conducted over the summer period (2019), when young-of-year hatch, potentially leading to considerable variations in crayfish numbers at each site through hatching events and subsequent mortality. The PT catch data (density per time interval) was therefore presented as two size groups (≥ 13 mm CL and ≤ 12 mm CL), with the population structure of larger individuals expected to remain comparatively stable during the summer months. Detection rates were calculated as the percentage of PTs that caught at least one crayfish individual at each site. Two density estimates were provided for each site ((1) sub-adults and adults ≥ 13 mm CL and (2) all

sizes) at 95% of the respective TDD catch (see below for approach) to give a broad indication of expected density.

2.6 | Pritchard trap and TDD comparison

TDDs were undertaken in July–August 2018 (Table 1). The TDD at DGB was conducted following the method described in Chadwick *et al* (2021) with one pump (Honda Trash pump 3 inches), three consecutive sweeps and four operatives. However, due to the larger area of the sites along LPB (45.5–50 m²), some adjustments to the TDD method were required. Firstly, two pumps (Honda Trash pumps 2 and 3 inches) were used simultaneously at each site to overcome the greater inflow of water. Secondly, a total of four dewatering ‘sweeps’ were conducted to ensure a satisfactory depletion in crayfish numbers, with a total of 6–10 operatives required for each TDD. The presence of fish was also a key consideration at the LPB sites (fish were absent at the BGB site) and fish rescues by electrofishing were undertaken before the TDD to mitigate this. In this study, a TDD was also carried out at a

white-clawed crayfish site (Farm) under licence (licence number 2016-21910-CLS-CLS), with all work overseen by the licence holder.

TDD depletion calculations and total crayfish density estimates were made using the Carle Strub maximum weighted likelihood estimation method (Equation (1), SI 3; Carle & Strub, 1978) in the FSA package (Ogle, 2018) in R (version 3.5.1). The efficiency of the TDD method was calculated using the total number of crayfish caught in a TDD as a fraction of the Carle Strub-derived total estimated population. Basic demographic descriptors were calculated in SPSS (version 27).

2.7 | Density

To determine density estimates, PTs ($n = 4$) were deployed for 4 days at each site before the TDDs in 2018. PTs were retrieved and processed immediately before the start of the TDD. Effective trap deployment at DGB in 2018 was disrupted by low water levels due to a drought event (NHMP, 2018), and as such PT data from 2019 (0.75 m^2) at the same location was used for density comparisons. Whilst TDD and PT data were therefore collected in subsequent years, typical seasonal conditions were observed in 2019, and 2016–2017 TDD samples indicate consistently high crayfish population densities ($86\text{--}110 \text{ m}^{-2}$) at this site (Chadwick et al., 2021). The DGB 2019 traps were retrieved at a similar date to the 2018 TDD (5 August 2019 and 6 August 2018, respectively), to standardize for seasonal fluctuations in population density related to juvenile release and mortality. PTs in LPB remained fully submerged during the sampling interval, and hence the original 2018 data were used in comparisons.

2.8 | Structure

Repeat PT sampling was undertaken between June–September 2019 to assess the ability of PTs to determine crayfish population structure. PT ($n = 3$) were set at all sites and retrieved a total of 10 times throughout the summer to increase sampling effort ($n = 30$ lifts, total sampling area 7.5 m^2). Traps were set for a minimum soak time of 4 days. SPSS was used to derive statistical descriptors and undertake post hoc analyses on demographic data including sex ratios (chi-squared). Graphical representation of the population structures was achieved through ggplot 2 package (Wickham, 2016) in R (version 3.5.1).

3 | RESULTS

3.1 | Deployment time experiment

PTs successfully sampled signal crayfish at all study sites and white-clawed crayfish at Farm. The PTs detected both species at the minimum tested deployment time of one day (Figure 4). Crayfish were consistently detected by PTs ($n = 3$) across all sampling times and sites except for signal crayfish at Farm 2-day deployment time (Figure 4). At the signal crayfish-only sites, PTs consistently (44/45 PTs) detected crayfish

presence. At the mixed-population site (Farm), individual PT detection was more variable, but the detection rate for each deployment time treatment remained high.

At the high-density DGB site, only a 2-day deployment time was required to generate density values that were comparable with subsequent samples representing longer deployment times (Figure 4a). At lower density sites, crayfish numbers in PTs stabilized after 2–4 days for signal crayfish, again providing densities broadly within expected ranges (Figure 4b–d). The PTs successfully detected white-clawed crayfish at Farm, where numbers also stabilized after 2–4 days (Figure 4e).

3.2 | Pritchard trap and TDD comparison

3.2.1 | Density

Based on Carle Strub depletions, the TDDs consistently caught >90% of the total estimated population (DGB 99.0%, Confluence 90.5%, Footbridge 96.6%, Farm SC 96.3%, Farm WCC 98.9%), and thus allowed accurate total population estimates for each site (Table 2). Similar to past work on the study system (Chadwick et al., 2021), the TDDs confirmed a wide range of signal crayfish densities along the invasion gradient, including 63 m^{-2} for the well-established, high-density population (DGB), medium densities at Confluence and Footbridge (19.9 and 7.1 m^{-2} , respectively), and a very low density of 0.5 m^{-2} at the invasion front (Farm). The TDD also revealed a strong population of native white-clawed crayfish at the invasion front (9 m^{-2} at Farm). At a lower sampling effort ($n = 4$, 1 m^2 at LPB; $n = 3$, 0.75 m^2 at BGB) the PTs produced density estimates congruent with TDD estimates derived over a much larger area ($15\text{--}50 \text{ m}^2$ survey area). In addition, the PTs estimated the same changes in density along the invasion gradient as derived from TDDs (Table 2). The total estimated crayfish density calculated from TDD depletion curves was within the PT lower and upper density estimates for DGB, Confluence and Footbridge (Table 2). However, at Farm, PTs failed to detect the low-density signal crayfish population ($<1 \text{ crayfish m}^{-2}$) and slightly underestimated the density of white-clawed crayfish.

3.2.2 | Structure

Repeat PT sampling (7.5 m^2 , 2019) provided larger sample sizes (820 crayfish sampled in total) from which population demographic data could be explored (Table 3). Male to female sex ratios generated from PT surveys were consistent with those from the TDDs (χ^2 , $p > 0.05$) at all sites, apart from Footbridge, where PTs showed a female-biased sex ratio ($\chi^2 = 5.439$, $df = 1$, $p = 0.02$). The incidence of cheliped damage reported through PT sampling was lower than for the TDDs for signal crayfish, but was slightly higher for white-clawed crayfish (Table 3). The PTs sampled crayfish from a wide size range (8–42 mm CL). The median CL obtained through PTs was similar to that produced by the TDDs for both species, except for signal crayfish present at an extremely low

FIGURE 4 Cumulative density of crayfish (≥ 13 mm CL, dark grey and ≤ 12 mm CL, pale grey) derived from various deployment time intervals (days) of PTs ($n = 3$) across all sites (June–September 2019). Error bars show the deviation of minimum and maximum from average catch densities (m^{-2}). Crayfish detection rates (% PTs containing ≥ 1 crayfish) are presented above each bar. Past density estimates (95% of 2018 TDDs) are provided for reference (≥ 13 mm CL, dashed line and all crayfish, solid line)

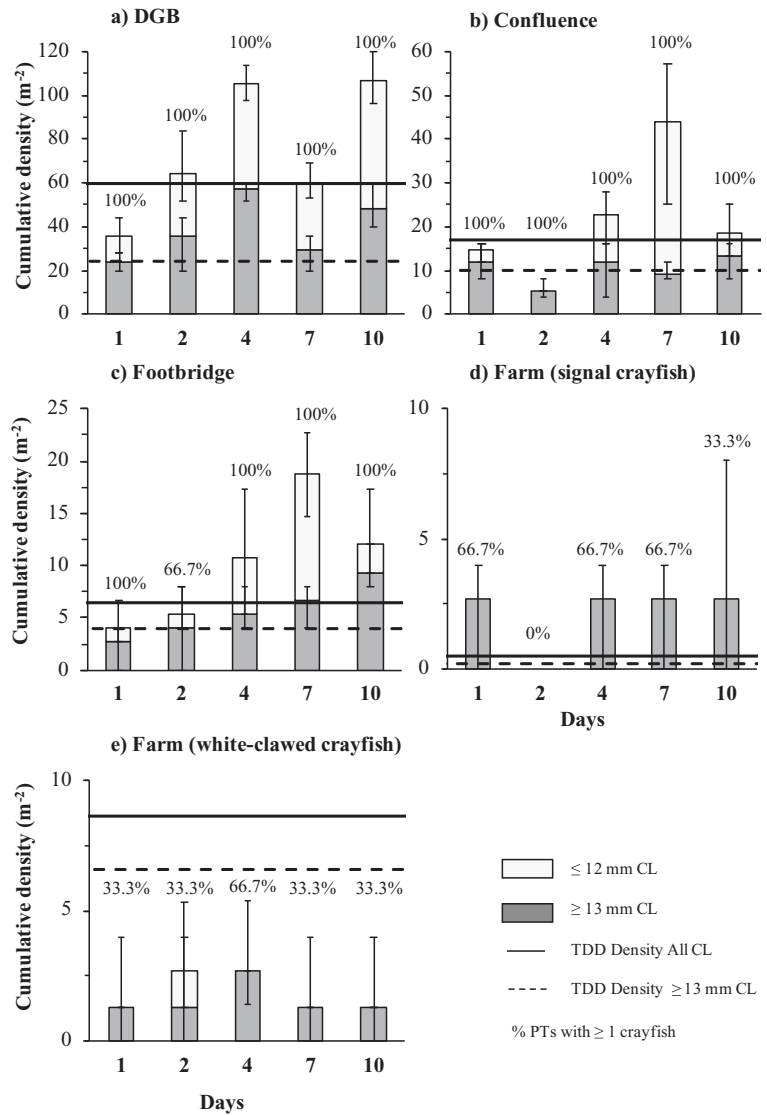


TABLE 2 Crayfish population density values generated from PTs (2018/2019) and TDDs at all sites (2018)

Site	Pritchard Trap Density estimate (m^{-2})			Triple drawdown Density estimate (m^{-2})			
	Average	Lower	Upper	Raw	Total	Lower	Upper
Double Gate Bridge ($n = 3$, 2019)	54.7	32	72	62.7	63.3	62.8	63.7
Confluence ($n = 4$, 2018)	23	12	32	18.0	19.9	19.1	20.6
Footbridge ($n = 4$, 2018)	6	4	8	6.9	7.1	6.9	7.3
Farm SC ($n = 4$, 2018)	0	0	0	0.5	0.5	0.5	0.6
Farm WCC ($n = 4$, 2018)	6	4	8	9.0	9.1	9.0	9.2

density at Farm (Table 3). Crayfish size class distribution derived from PT sampling was analogous to that from the TDDs at DGB, Confluence and Footbridge (Figure 5), showing the majority of the population to be juvenile or sub-adult (≤ 25 mm CL) with very few large adults (≥ 35 mm CL). At Farm, however, the number of white-clawed crayfish and signal crayfish sampled was too low to permit a robust evaluation of the data. The repeated PT sampling also provided density estimates con-

gruent with the TDD values for signal crayfish, despite sampling occurring throughout summer, and thus population density estimates being vulnerable to fluctuations due to recruitment and predation. The PTs were able to detect and accurately report the low-density population ($0.5 m^{-2}$) of signal crayfish at Farm. The PTs recorded a lower density of white-clawed crayfish at Farm in comparison to density estimates from the TDD in the previous year.

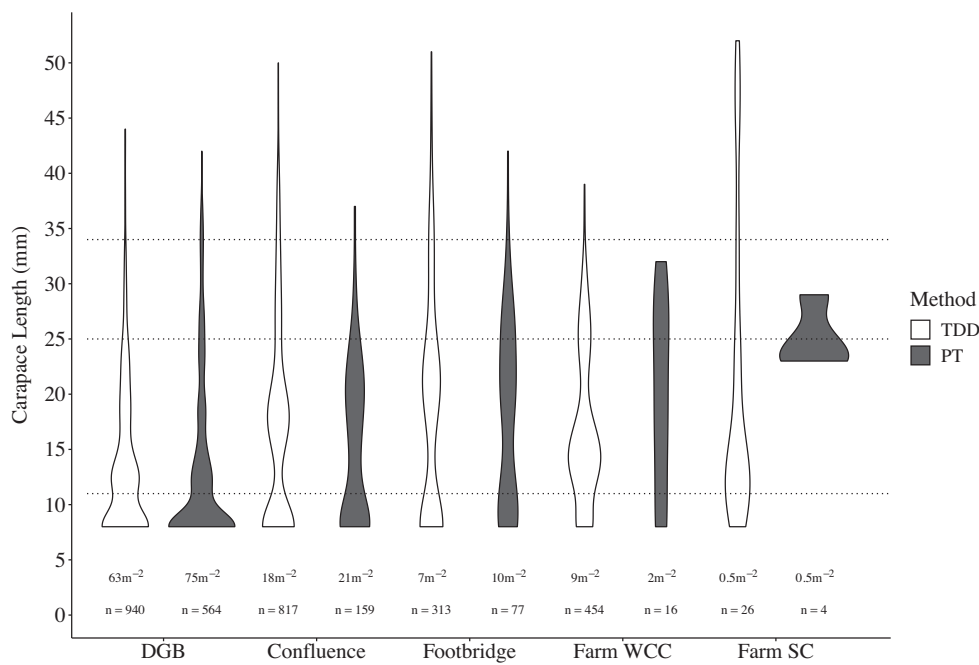


FIGURE 5 Bean plot (i.e. probability density of the catch data) of crayfish size class distribution (mm CL) captured through TDD (2018) and PT (2019) across all study sites. The density of crayfish (m⁻²) and the number captured (n) are also denoted

4 | DISCUSSION

4.1 | Performance of the method

The PT presents a novel and accurate method for surveying freshwater crayfish. Evaluation of PT use in rocky headwater streams in our study area demonstrated its ability to produce quantitative survey data. PTs detected the presence of crayfish after the minimum tested deployment time of 1 day using a relatively small (1 m²) sampling area (four PTs), across a range of densities. In medium to high density populations, a small sampling area (≤ 1 m²) sufficed to accurately report population densities. However, an increased sampling intensity was required to accurately report the density of signal crayfish at Farm (0.5 individuals m⁻²). We recommend a deployment time of 4 days when detailed demographic data are required (i.e. to evaluate links between crayfish demographics and environmental and ecological impacts; Bubb et al., 2009). Demographic estimates can be further improved with increased sampling effort, for example using more traps and repeated lifting of traps over successive 4-day periods.

Crayfish show a strong association with in-channel substrate, and habitat features that provide shelter like boulder substrates positively correlate with crayfish presence (Rosewarne et al., 2017). The success of PTs in sampling crayfish populations in the surveyed headwater streams is therefore likely also related to abundant in-channel rocky substrate. Under these conditions, retrieving PTs during daytime hours when crayfish are typically less active and hide under boulders and cobbles as refugia from predation (Barbaredi & Gherardi, 2001) was highly successful. However, there remains a need to evaluate the effectiveness of PTs in systems that widely lack suitable in-channel crayfish

refugia and where crayfish consequently tend to live in burrows in the banks. Here, night-time retrieval of PTs when crayfish are expected to emerge to forage may prove effective (Hilber et al., 2020), but needs to be tested.

One big advantage of the PTs, particularly in relation to the TDD approach, is the possibility of estimating microhabitat-use within sites. In heterogeneous environments, the clearly defined sampling area of the PTs for the first time enables the direct investigation of associations between crayfish density and microhabitat usage. Microhabitat associations can be explored by setting PTs at distinct specific habitats, or by varying the substrate used in the traps. To increase capture rates, PT deployment could also specifically target areas with refugia considered suitable for crayfish like rocky substrate, woody debris and shaded areas (Rosewarne et al., 2017). In these latter instances, density can only be considered in the context of habitat suitability and should not be extrapolated across the entire site.

The PTs consistently showed a lower density of white-clawed crayfish at Farm than TDD estimates from the previous year. This could represent a notable temporal decline in white-clawed crayfish or behavioural responses (ousted from refuges and the seeking of alternative refuges; see Bubb et al., 2006), both potentially linked to active signal crayfish invasion. Invasive signal crayfish are known to dominate over native crayfish species in interspecific competition for shelter, eventually contributing to the displacement of native species (Holdich et al., 2009). Further sampling of white-clawed crayfish and mixed-species populations will be required to specifically investigate crayfish habitat use and its implications for PT sampling efficiency of co-occurring species.

TABLE 3 Population demographics from PT repeat sampling (7.5 m² in 2019, June - September) and TDD (2018) at each site. PT estimates are compared to TDD baselines

Parameter	Double Gate Bridge			Confluence			Footbridge			Farm WCC			Farm SC		
	PTs	TDD		PTs	TDD		PTs	TDD		PTs	TDD		PTs	TDD	
Density (m ⁻²)	75.2	62.7		21.2	18.0		10.3	6.9		2.1	9.0		0.5	0.5	
Minimum CL (mm)	8	8		8	8		8	8		8	8		23	8	
Maximum CL (mm)	42	44		37	50		42	51		32	39		29	52	
Median CL (mm)	8	12		15	17		19	19		18.5	15		24	12	
Mean CL (mm)	13.17.44	13.66.72		16.79.06	18.310.15		17.88.39	16.96.92		19.68.57	25.02.83		25.02.83	20.713.58	
(mm)Standard deviation (2 d.p)			15.37.17												
M:F ratio	45.7:54.3	45.3:54.7	37.9:62	42.6:57.4	48.1:51.9	28.9:71.1	50:50	46.5:53.5	50:50	50:50	50:50	50:50	50:50	50:50	50:50
Cheliped damage of > 12 mm CL (%)	29.1	30.4	26.4	30.8	34.8	20.0	16.6	12.4	0.0	40.0					

Abbreviations: CL, carapace length; PT, Pritchard Trap; TDD, triple drawdown.

4.2 | Practicalities of the PT method

Overall, the PTs performed very well and the materials proved robust and hard-wearing through repeat sampling over several months. The traps were also easy to clean and quick-drying, aiding thorough biosecurity procedures. The small size and lightweight collapsible design of the trap (~700 g weight, 0.25 m² sampling area per trap) provided a good balance between sampling effort, data quality and suitability for remote fieldwork. The PT design trialled here is adaptable, with shape and size open for modifications to tailor the traps to specific site conditions, for example using a rectangular shape for narrow streams or shorter/taller panels for different water depths. At approximately £15 per trap to self-manufacture, PTs are accessible and competitively placed within the current trap market (NHBS, 2020) – and remain significantly cheaper than methods that require specialist equipment such as electrofishing (Evans et al., 2017) and TDDs (Chadwick et al., 2021).

Deployment of PTs requires the surveyor to enter the water-course and manually lift in-channel substrate. In this regard, setting PTs requires additional time and labour than baited funnel traps (e.g. Fjälling, 1995), but in our experience represents comparable effort to other methods also suited to shallow rocky systems such as hand-searches or quadrat sampling (e.g. Distefano et al., 2003; Bradley et al., 2015). The applicability of PTs in other aquatic systems, such as larger waterbodies with deeper water or less available refugia, remains to be tested, with modifications to trap design and deployment (e.g. scuba as in Engdahl et al., 2013) potentially required. Although PTs should be deployed for a minimum time (four days), this is still relatively short compared to other passive techniques like ARTs and enclosure traps that commonly require deployment for entire months or seasons (e.g. Engdahl et al., 2013; Green et al., 2018).

A key aspect of the PT design is that they are passive, designed to survey crayfish in their natural environment and only entrapping crayfish upon retrieval. This avoids issues of unknown bait attractiveness (Rach & Bills, 1987) and bycatch, which are recognized survey concerns, especially for baited funnel trapping (De Palma-Dow et al., 2020). Mitigating risks to non-target organisms is a key consideration for more intrusive methods such as TDDs (Chadwick et al., 2021). However, the PT poses minimal risk of harm to non-target organisms when operated following strict biosecurity protocols. During testing, several non-target species, including macroinvertebrates and benthic fish species, were recorded entirely unharmed in the PTs (SI 4).

4.3 | Implications for conservation

The biases associated with conventional crayfish sampling techniques have hindered quantitative assessments and thus meaningful comparisons of crayfish populations. With 32% of the world's crayfish species vulnerable to extinction and a further 21% considered data deficient (Richman et al., 2015), and with many other crayfish species being invasive and threatening native ecosystems (Twardochleb et al., 2013), the ability to accurately describe the structure of crayfish populations,

including their recruitment and overall size class distribution, is becoming paramount. The PT presents a promising tool to determine crayfish demographics that is applicable in a range of scenarios in research, management and conservation.

PTs can be used for long-term monitoring campaigns, mark-recapture experiments and substrate preference studies to advance our understanding of crayfish behaviour and invasion ecology, ultimately benefitting any control programmes. Equally, such information on threatened crayfish species would be beneficial to enhance conservation efforts and their effectiveness. One of the great advantages of PT deployment is the passive nature of sampling, greatly limiting any impact on sensitive species or non-target organisms. As such, the PT can be used repeatedly within protected areas with minimal wider environmental risk and is therefore well suited for long-term monitoring programmes of native crayfish, and for evaluating translocations and reintroductions (Rosewarne et al., 2017; Seddon et al., 2007).

4.4 | Implications for management

A thorough understanding of the impacts of invasive crayfish on biodiversity and ecosystem functioning is vital to inform management decisions (Galib et al., 2020; Jackson et al., 2014; Lodge et al., 2012). In this respect, the population size of the invader is likely a key determinant of the extent of impact and associated management costs (Yokomizo et al., 2009). For example, the hyper-dense signal crayfish populations established at BGB corresponded with severe declines in native biota (Chadwick et al., 2021; Peay et al., 2009). However, the degree to which this scenario plays out elsewhere and hence the true extent of the signal crayfish problem is little known in the UK. Furthermore, as the evidence of ecosystem impacts from multiple invasive crayfish species worldwide continues to grow (e.g. Lodge et al., 2012; Haubrock et al., 2021), there is an ever-growing demand for accurate data on crayfish distribution and population structure to drive effective management (Madzivanzira et al., 2020).

The PT method presents a new means of exploring crayfish density-dependent impacts in the field and hence of evaluating crayfish population dynamics and community-scale impacts, when coupled with other environmental surveys. This approach could be employed for spatial comparisons along invasion gradients (e.g. Hudina et al., 2012) and used to investigate temporal impacts of invasion. Whilst such combined studies are scarce (see Mathers et al., 2016; Galib et al., 2020), they are vital in understanding the processes by which invasive crayfish become established, dominant and impactful.

Whole population assessments are necessary to directly inform the effectiveness of invasive species control measures, with meaningful evaluations requiring before-and-after density and population structure estimates. The PT approach provides a robust foundation for such surveys, as well as for assessing and optimising invasive crayfish control techniques. Knowledge of crayfish behaviour, activity levels and seasonal trends will help identify times when management efforts can have greatest impacts (Rogowski et al., 2013). For example, targeting berried females could substantially reduce juvenile recruitment which

is a benefit of ARTs over other techniques (Green et al., 2018). Similarly, the ability of PTs to capture a wide range of size classes across different densities may facilitate their role in the physical management of crayfish populations.

5 | CONCLUSION

The PT presents a promising approach to survey crayfish, combining ease and cost-effectiveness of some traditional techniques with the generation of quantitative data on crayfish population structure and density. The passive nature of the PT method reduces impact on bycatch and eliminates bias regarding bait attractancy – two factors regarded as major limitations of conventional crayfish survey methods. The PT performed very well in the studied rocky headwater streams, and future work should evaluate the efficacy of this novel trapping technique in other aquatic systems. Use of the PT method should, for the first time, facilitate large-scale accessibility to density and demographic data for the conservation and management of freshwater crayfish.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

E.G.P designed the initial methodological approach; D.D.A.C and I.P helped to develop the trap design; E.G.P, D.D.A.C and P.B collected the data; E.G.P analysed the data while E.G.P led the writing of the manuscript. All authors contributed critically to the drafts and the overall project design, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the University College London (UCL) Research Data Repository. <https://doi.org/10.5522/04/14484084.v1> (Pritchard et al., 2021).

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