RESEARCH ARTICLE

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A novel 'triple drawdown' method highlights deficiencies in invasive alien crayfish survey and control techniques

Daniel D. A. Chadwick[1,2] | Eleri G. Pritchard[1] (iD) | Paul Bradley[2] | Carl D. Sayer[1] (iD) | Michael A. Chadwick[3] (iD) | Lawrence J. B. Eagle[2] (iD) | Jan C. Axmacher[1,4] (iD)

[1]Department of Geography, Environmental Change Research Centre, University College London, London, UK

[2]PBA Applied Ecology Ltd, Settle, UK

[3]Department of Geography, King's College London, London, UK

[4]Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Reykjavík, Iceland

Correspondence
Eleri G. Pritchard
Email: eleri.pritchard.15@ucl.ac.uk

Abstract

1. Freshwater crayfish can be successful invaders that threaten native biota and aquatic ecosystems in numerous countries worldwide. Nonetheless, the inability of conventional crayfish survey techniques like trapping and handsearching to yield quantitative population data has limited the understanding of crayfish invasion biology and associated ecological impacts.

2. Here, we employed a novel 'triple drawdown' (TDD) method to sample invasive populations of signal crayfish *Pacifastacus leniusculus* in a headwater stream in Northern England. The method was compared with conventional techniques of trapping and handsearching.

3. The TDD method proved to be an effective technique with high capture efficiency, reporting signal crayfish densities from 20.5 to 110.4 animals/m^2 at our study sites. These numbers exceed any previous estimates for similar streams.

4. The TDD showed the vast majority of individuals across all sites were juvenile or sub-adult (<26 mm CL), with only 2.3% of the population large enough (≥35 mm CL) to be caught in standard traps.

5. *Synthesis and applications*. The triple drawdown (TDD) method demonstrates strong inefficiencies and biases in conventional crayfish survey and management techniques. Trapping is not recommended for representative sampling or control of juvenile dominated populations. TDDs, which can be adapted and modified to operate in multiple habitat types and freshwater systems, generate robust quantitative data on invasive crayfish population demographics in situ. This can advance our understanding of the biology of an important invader of freshwater systems around the world. Obtaining this data prior and post-intervention is fundamental to evaluate invasive crayfish management, and we recommend the TDD method to assess the effectiveness of future control measures.

KEYWORDS
aquatic invasive species, crayfish density, crayfish management, population demographics, signal crayfish, trapping, triple drawdown

1 | INTRODUCTION

Crayfish are successful invaders negatively impacting aquatic ecosystems in numerous countries worldwide (García-Berthou et al., 2005; Gherardi, 2010; Holdich, James, Jackson, & Peay, 2014). Several techniques have been developed to evaluate geographical distributions, quantify population dynamics, and to potentially control invasive crayfish populations. The most common method is baited traps (Parkyn, 2015), allowing semi-quantitative catch-per-unit-effort (CPUE) estimates of population size. This method is often used to survey invasive crayfish populations (e.g. Donato et al., 2018; Hudina, Hock, Žganec, & Lucić, 2012; Peay, Guthrie, Spees, Nilsson, & Bradley, 2009). Trapping samples are generally biased towards active males with carapace lengths ≥35 mm (Almeida, Argent, Ellis, England, & Copp, 2013; Gherardi, Aquiloni, Diéguez-Uribeondo, & Tricarico, 2011; Moorhouse & Macdonald, 2011) and there are concerns over bait attractancy (Rach & Bills, 1987), crayfish retention rates (Kozák & Policar, 2003), and the ability to sample juveniles (e.g. Distefano, Gale, Wagner, & Zweifel, 2003).

Other survey methods include handsearches and hand netting (e.g. Bradley, Hall, & Peay, 2015; Bubb, Thom, & Lucas, 2005), artificial refuge trapping (e.g. Green, Bentley, Stebbing, Andreou, & Britton, 2018), electrofishing (e.g. Alonso, 2001), torching (e.g. Reynolds, Lynn, & O'Keeffe, 2010), snorkelling/SCUBA diving (e.g. Panicz et al., 2019) and environmental DNA (eDNA; e.g. Harper, Anucha, Turnbull, Bean, & Leaver, 2018). Repeat depletion sampling, involving multiple pass electrofishing surveys, has been used extensively in fisheries studies to generate capture efficiency and total population estimates (see Beaumont, 2016). Electrofishing can be effective at determining crayfish presence but provides variable populations estimates due to low capture efficiencies ranging from ~30% to 60% (Alonso, 2001; Reid & Devlin, 2014). Furthermore, electrofishing effectiveness is influenced by factors such as conductivity and crayfish behavioural responses (see Zalewski, 1983). Current sampling methods present advantages and limitations, in terms of size biases, catch efficiencies, and logistical and environmental constraints (e.g. Bradley et al., 2015; Price & Welch, 2009). Consequently, most crayfish population estimates crucially lack the ability to accurately describe the demography of a population (Rabeni, Collier, Parkyn, & Hicks, 1997). This has been a key limitation for assessing the ecological impacts of invasive crayfish populations on native ecosystems, and for informing conservation and management.

Given the significant threats posed by invasive crayfish (Twardochleb, Olden, & Larson, 2013), several methods have been employed in attempts to locally control invasive populations (reviewed in Stebbing, Longshaw, & Scott, 2012). In particular, intensive removal through sustained trapping has been widely trialled (Hein, Roth, Ives, & Vander Zanden, 2006; Manfrin, Souty-Grosset, Anastácio, Reynolds, & Giulianini, 2019; Moorhouse & Macdonald, 2011; Stebbing, Longshaw, & Scott, 2016) for many species across their invasive ranges, including signal crayfish *Pacifastacus leniusculus* in the United Kingdom (Stebbing et al., 2016), rusty crayfish *Orconectes rusticus* in the United States (Hein et al., 2006) and red swamp crayfish *Procambarus clarkii*

in Brazil (Gonçalves Loureiro, Anastácio, Luiz de Siqueira Bueno, & Araujo, 2018). However, the perceived management success of trapping is often dependent on sustained efforts (Stebbing et al., 2016; West, 2017), with success commonly reported as leading to a reduction in CPUE over time (Hein et al., 2006).

There have been some efforts to determine limitations and successes of crayfish control strategies. For example, Peay and Dunn (2014) sought to evaluate the potential for effective biocide treatment on signal crayfish in laboratory experiments and at a small (0.54 ha) lentic site in Wales using partial dewatering. Crayfish retention in artificial burrows was reported both in the laboratory (4.4%–32.5%) and in the field (>45% remaining for at least 1 night), indicating the limited potential for successful eradication via biocide treatment. Assessments of invasive crayfish control or eradication methods, particularly in lotic in contrast to more isolated lentic habitats, have generally been hampered by the limitations of existing survey techniques (see above; Rabeni et al., 1997; Stebbing, Longshaw, & Scott, 2014).

Responding to the need to develop more accurate survey methods, we developed and tested a novel depletion sampling technique involving the temporary dewatering of isolated sections of streams called a 'triple drawdown' (TDD). We used the TDD approach to collect unbiased crayfish density and demographic data based on standard depletion curves and to compare the size-class distributions with handsearching and trapping methods for invasive signal crayfish populations in North Yorkshire, UK. Implications for invasive crayfish management strategies are discussed.

2 | MATERIALS AND METHODS

2.1 | Triple drawdown

The TDD is based on the principle that a defined area of watercourse or waterbody can be completely isolated (e.g. with dams). First, pumps are used to dewater the isolated study reach and, as far as possible, all suitable crayfish refugia are carefully removed by hand. This allows for a thorough investigation of the benthos and hand-removal of all visible crayfish within the study reach (see Figure 1 for lotic example). The isolated study reach is then re-wetted, maintaining a closed population of crayfish. Re-wetting facilitates the capture of crayfish by encouraging hidden individuals to remobilise, and detritus and sediment to disperse. The procedure of dewatering and sampling is repeated until operatives cease to encounter crayfish, with a minimum of three sweeps. After all sweeps are completed, refugia materials are returned and the dewatered area is re-wetted. Depletion curves are then used to extrapolate the 'true' population density of crayfish.

2.2 | TDD methodology in this study

In this study, drawdowns were conducted by experienced operatives utilising fuel-based pumps (Honda trash pumps, 2 and 3 inch) and pipe

FIGURE 1 Schematic diagram showing the triple drawdown site and equipment setup. Direction of flow is depicted by black arrows
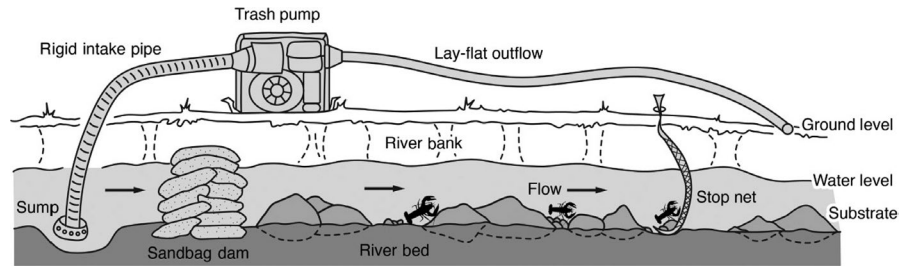

attachments to divert water around dammed, isolated river sections (Figure 1). Study sites were <20 m in length and isolated at both the upstream and downstream limits using stop nets (2 mm mesh size) to prevent crayfish movement in or out of the study reach. A sump and watertight dam were built at the upstream limit. The water was then pumped out from the sump around the study reach to re-enter the channel below the downstream limit. The intake pipe head was fitted with a 1-mm mesh net to prevent organisms from being sucked through the pump.

The pump power was adjusted to first exceed and then match the incoming flow, to dewater the sump and then the study reach. As work was undertaken, the pump was left running on a drip tray to contain any fuel spillages. As the study reach dewatered, any suitable crayfish refugia (at our study sites mainly cobbles, boulders and wood pieces) were removed and placed onto the river bank to reveal the bare channel bed. A narrow, centralised channel was dug by hand to allow remaining pools to drain, and manual searches of the exposed banks were conducted. All crayfish were removed by hand or by use of a small aquarium net (1-mm mesh size) and transferred into buckets of fresh water as they were encountered during dewatering, refugia removal and manual search.

The first 'sweep' was completed when the operatives ceased to find crayfish. The pump was switched off to allow the site to re-wet for 15–20 min. A downstream dam was installed to allow a sufficient water depth to effectively re-wet the site. Pumping was resumed and subsequent sweeps commenced in a similar fashion, for a total of three sweeps. Once the collection of crayfish had finished, the pump was switched off and all removed substrate was returned to the channel. All equipment was disinfected and dried following each drawdown, in accordance with standard biosecurity protocols (NNSS, 2018).

2.3 | Study area

The study site was Bookill Gill Beck (henceforth BGB), a rocky limestone headwater stream in the upland area of the Yorkshire Dales, England (Figure 2). BGB is a steep, fast-flowing tributary of Long Preston Beck in the Ribble catchment. It runs approximately 5.1 km from source to its confluence with Scaleber Beck, increasing in width from an average 0.7–1.9 m (Peay et al., 2009). BGB is situated in a sub-catchment of unimproved or semi-improved grazed pasture.
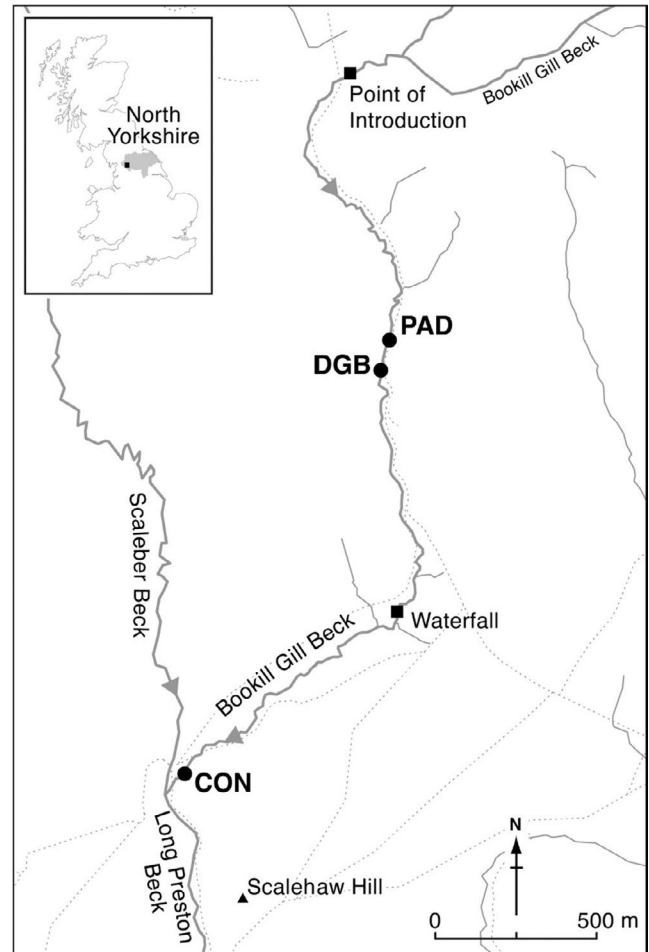
FIGURE 2 Location of Bookill Gill Beck within the Ribble catchment in Northern England showing location of the three sampling sites for the four triple drawdowns (PAD, DGB and CON)

Historically, BGB supported strong populations of native white-clawed crayfish and a diverse fish community, including Atlantic salmon *Salmo salar*, brown trout *Salmo trutta*, European bullhead *Cottus gobio* and European eel *Anguilla anguilla* (Peay et al., 2009). An illegal introduction of signal crayfish occurred in approximately 1995, and this species has since become established along the entire length of the stream (reported in Peay et al., 2009).

Three separate sites, Paddock (PAD), Double Gate Bridge (DGB) and Confluence (CON), were selected for our study to represent a continuum along the invasive population range downstream of the introduction point (Figure 2). DGB and CON were sampled in 2016,

and PAD and DGB in 2017, resulting in a total of four drawdown events (DGB2016, CON2016, DGB2017, and PAD2017). All drawdowns were undertaken in summer (June–August) under low flows, with each drawdown conducted over a 10-hr period. All drawdown sites were <2 m wide, dominated by cobble substratum and characterised by well-oxygenated, mostly shallow (<15 cm) alkaline water with some deeper pools.

2.4 | Additional sampling methodologies

For comparative purposes, handsearching and baited funnel trapping (henceforth trapping) were conducted prior to the TDD across the study sites. Both of these methods are commonly employed in crayfish studies and monitoring both in the United Kingdom and internationally (Bradley et al., 2015; De Palma-Dow, Curti, & Fergus, 2020; Gil-Sánchez & Alba-Tercedor, 2002; Moorhouse & Macdonald, 2011; Parkyn, 2015; Rabeni et al., 1997). Handsearching was conducted following common standards monitoring (CSM) guidance established for native crayfish in the United Kingdom (Bradley et al., 2015). A total of 250 suitable refuges (stones) were turned for each handsearch at each site, with the exception of DGB2017, where only 125 stones were turned. Trapping involved the deployment of Swedish-style 'Trappy' traps (see Fjälling, 1995; dimension: 51 cm × 21 cm, entrance size 5 cm, mesh size 3 cm × 2 cm). All traps were modified with an extra 5-mm mesh in place to increase their efficiency in retaining smaller individuals (e.g. Johnsen, Skurdal, Taugbøl, & Garnås, 2014). Sets of 10 traps were baited with fresh oily fish and deployed nightly over four nights, totalling 40 trap nights for each study site, with the exception of CON2016, where only 25 trap nights were possible. Trapping was undertaken in deeper water where traps could be fully submerged, with distances between individual traps ≥3 m. As such, both trapping and handsearching operated over a greater longitudinal survey reach (50–200 m bank length) than any individual drawdown to replicate the common, in-practice, use of both methods.

Handsearching and trapping were undertaken in the week preceding each respective drawdown. Following handsearching and trapping, all crayfish were temporarily returned to the river sites (method statement authorised by the Environment Agency), while all crayfish captured with the TDD were despatched on site humanely and biosecurely, to enable subsequent measurement in the laboratory. For handsearching, CPUE was recorded as the number of crayfish captured per stone turned. Trapping CPUE was given as the average number of crayfish per trap. Consent to trap crayfish was granted by the EA (CR1 authorisation).

For all captured crayfish individuals, carapace length (CL, tip of rostrum to posteriomedial edge of the cephalothorax, Vernier callipers, 1 mm), wet weight (digital scale, 0.1 g) and gender were recorded. Only invasive signal crayfish were encountered during the study. Gender for all crayfish >12 mm CL was categorised as

male or female. Crayfish ≤12 mm CL were categorised as juveniles because small individuals cannot reliably be sexed. Length and weight of juvenile crayfish were averaged from counts of 100 animals from each TDD, with these values applied to hatchlings (5 mm CL, 0.1 g wet weight) and juveniles (9–12 mm CL, 0.3 g wet weight), respectively. Any berried females had their hatched young removed using forceps, with these individuals added to the total counts; unhatched eggs were counted but not included in the analyses. All equipment was dried and disinfected (with Virkon™ Aquatic) to maintain biosecurity standards. No fish were present at PAD and DGB, with low-density populations present at CON. Fish captured at CON were relocated quickly and safely by hand, with no mortalities observed.

2.5 | Statistical analyses

Statistical analyses were performed in R (version 3.4.2) and SPSS (version 24). TDD depletion calculations were made using the 'Carle–Strub method' (Carle & Strub, 1978) function in the Fish Stock Assessment (FSA) package (Ogle, 2018) in R. Capture efficiency was determined through the Carle–Strub method, and was defined as the likelihood of catching any individual crayfish in any given sweep. The total estimated percentage of the population successfully captured through the drawdowns was calculated using total catch as a fraction of the Carle–Strub derived total estimated population. Furthermore, Carle–Strub depletion analyses of grouped size classes were run for both juvenile crayfish (CL ≤ 12 mm) and combined sub-adult and adult crayfish (CL > 12 mm) for each drawdown event (as in Alonso, 2001), to determine if crayfish size influenced 'catchability'.

The smallest berried female in this study was 26 mm CL, and for the purpose of methods comparison analyses, all crayfish above this length were hence classified as 'sexually mature'. Crayfish ≥35 mm CL were classified as 'trappable' through conventional trap sampling (see data and review in Almeida et al., 2013), although capture of smaller animals is possible (Peay & Dunn, 2014; Stebbing et al., 2016). As such, the crayfish were split into four distinct size classes; juvenile (≤12 mm CL), sub-adult (13–25 mm CL), sexually viable adult usually too small to be caught in conventional traps (26–34 mm CL) and trappable adult (≥35 mm CL). Population distributions and bean plots were generated in the GGPLOT 2 package (Wickham, 2016).

3 | RESULTS

3.1 | Estimated population demographics based on the TDD technique

Raw densities of signal crayfish ranged between 20.5 and 110.4 crayfish/m^2 across the study reaches (average 66.2/m^2; Table 1). Juvenile crayfish (CL ≤ 12 mm) were numerically dominant at all

TABLE 1 Key population demographic data from triple drawdown (TDD), handsearching and trapping catches

Parameter	DGB2016	CON2016	DGB2017	PAD2017
TDD raw density (m²)	110.4	20.5	86.0	44.0
TDD median CL (mm)	5	14	12	12
TDD biomass (g/m²)	97.1	40.1	126.0	102.8
Handsearch CPUE	1.4	0.6	0.7	1.2
Handsearch median CL (mm)	15	15	16	16
Trap CPUE	5.6	3.0	5.9	4.7
Trap median CL (mm)	31	33	33	39

FIGURE 3 Population structure with percentage juvenile (≤12 mm CL; light grey), sub-adult (13–25 mm CL; medium grey), sexually viable adult too small to be caught in conventional traps (26–34 mm CL; dark grey) and trappable adult (≥35 mm CL; black) size classes from triple drawdowns (left), handsearching (middle) and trapping (right) across the four study sites
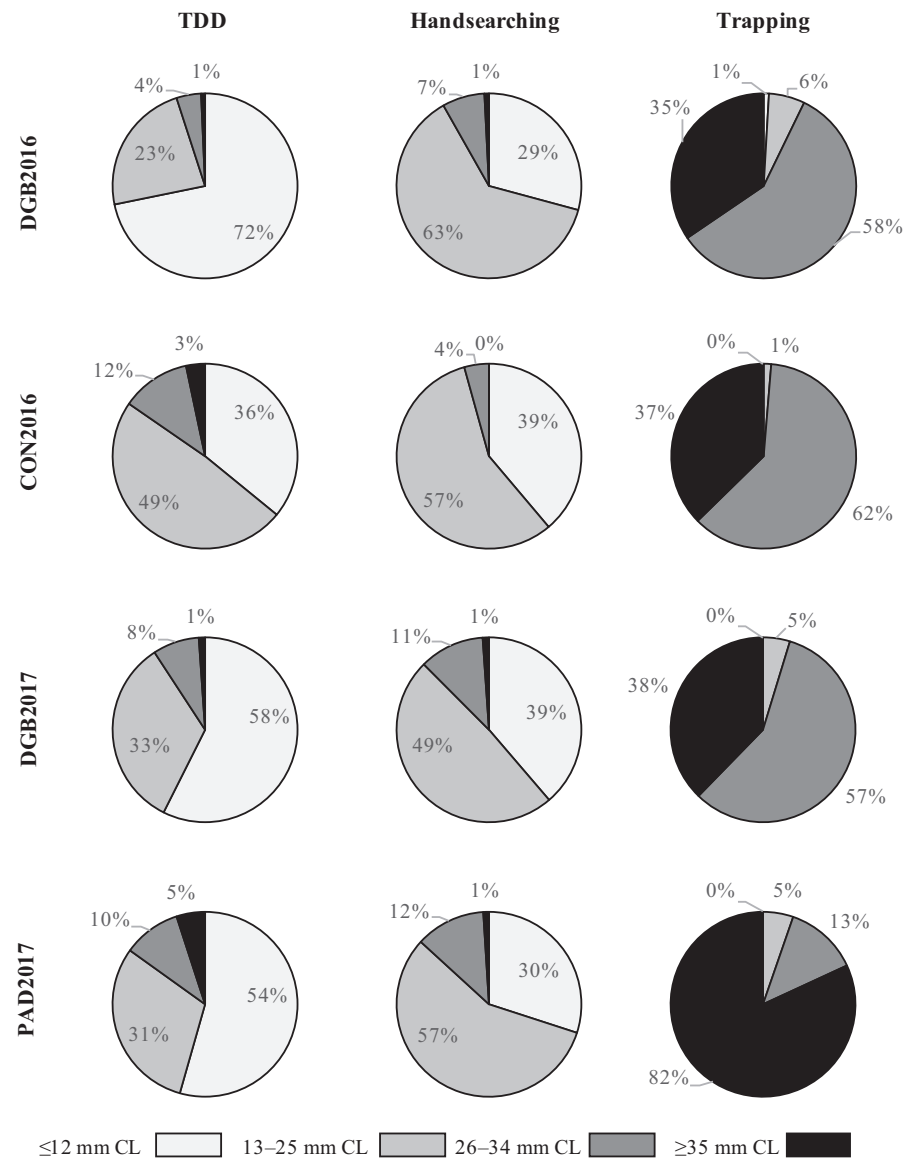
sites, on average comprising 55% of the total population (range: 36%–72%). Male:female ratios were 45:55, 46:54, 49:51 and 46:54 at DGB2016, CON2016, DGB2017 and PAD2017, respectively. Median carapace length and biomass per m² varied among the populations reported through the TDD (Table 1). CON2016, the only site to contain fish, had the lowest density of signal crayfish (Table 1).

Crayfish abundance dramatically decreased with increasing CL at all sites. Proportions of the four crayfish size classes (Figure 3) differed significantly between the different drawdowns ($\chi^2 = 307.7$, $df = 9$, $p < 0.001$). Post-hoc comparisons (adjusted $\alpha = 0.003$) showed significantly more juveniles and less animals in all other size classes at DGB2016 while significantly less juveniles and more sub-adult and sexually viable animals were found at CON2016.

DGB2017 contained more adults of trappable size, and PAD2017 contained significantly less juveniles and more sexually viable and trappable adults.

The smallest berried female (26 mm CL), found in the DGB2016 drawdown, was carrying a brood of 37 hatched young and five unviable eggs. The largest berried female found, also sampled at the DGB2016 drawdown (46 mm CL), was carrying a brood of 189 hatched young and six unviable eggs. The percentage of the sexually viable population (taken as ≥26 mm CL) from each drawdown of trappable size (≥35 mm CL) was 14.3% at DGB2016, 21.7% at CON2016, 11.8% at DGB2017 and 33.2% at PAD2017.

3.2 | Carle–Strub depletion

Catch depletions were observed across all drawdowns (Figures 4 and 5), allowing for estimations of 'true' population densities (Table 2). Based on the depletion curves, the drawdowns successfully sampled the vast majority of the estimated total signal crayfish population within each study reach (average 92%; Table 2).

Capture efficiencies ranged from 34.8% to 84.0% (average 66.4%). When considered separately, average capture efficiencies of juveniles and combined sub-adults and adults (excluding CON2016

juveniles) were 76.7% (range 63.5%–93%) and 74.8% (range 71.4%–76.7%), respectively. The number of crayfish caught in each subsequent sweep was strongly linearly associated with the sum of the previous sweeps ($R^2 = 0.99$) in all drawdowns apart from CON2016, which had a weaker linear relationship ($R^2 = 0.77$; Figure 5). CON2016 represents an exception, since the third sweep had a marginally greater catch than the second sweep. Despite CON2016 failing to achieve depletion between the second and third sweeps, Carle–Strub estimates could be calculated, as a strong depletion was observed between the first and second, and first and third sweep, respectively. However, Carle–Strub depletion estimates for juvenile crayfish for the CON2016 depletion were not possible because consecutive sweeps failed to 'deplete' with respect to sweep 1.

3.3 | Comparison of TDD with handsearching and trapping

In total, 883 signal crayfish were sampled through handsearching across all sites. CPUEs ranged from 0.6 to 1.4 crayfish per stone turned (Table 1). The highest and lowest CPUEs were found at DGB2016 and CON2016, respectively, as consistent with the drawdown results (Table 1). However, CPUE values were incongruent with changes in

FIGURE 4 Catches from the DGB2016 triple drawdown, reflecting the strong depletion between sweep 1, n = 1,339, sweep 2, n = 227 and sweep 3, n = 88. Berried females with detached young in clear bags

FIGURE 5 Three-sweep depletion per drawdown, with solid lines indicating total catch, and dotted lines the Carle–Strub estimated true population available to be caught
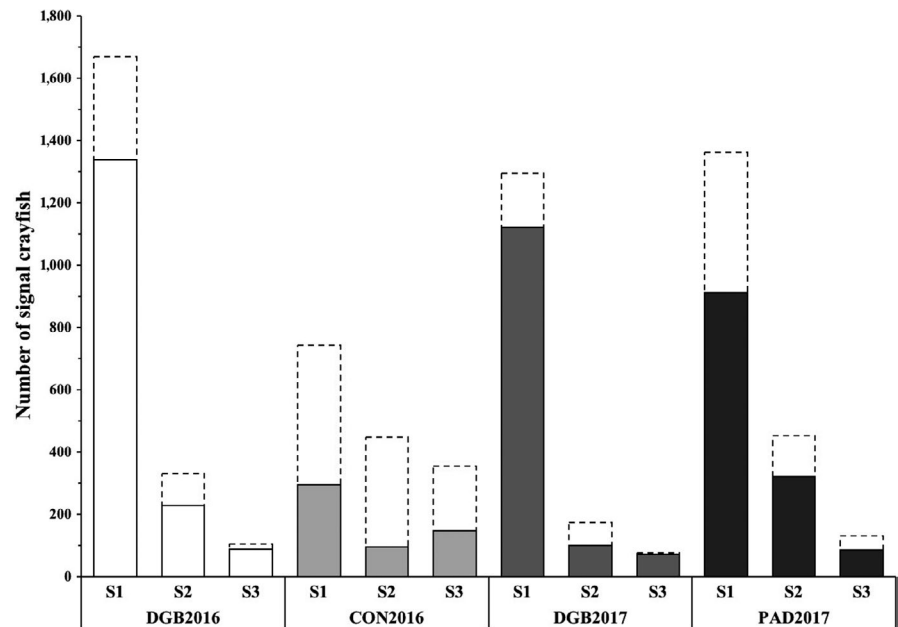
TABLE 2 Total population density estimates for each triple drawdown (TDD) with associated population capture efficiency estimates

Site	Total population density estimate (crayfish/m^2)	Lower confidence interval (95%; crayfish/m^2)	Upper confidence interval (95%; crayfish/m^2)	Estimated percentage of total population captured in TDD
DGB2016	111.3 (*SE* 4.74)	110.7 (*SE* 0.77)	112.0 (*SE* 0.81)	99.2
CON2016	28.3 (*SE* 50.1)	24.6 (*SE* 0.28)	32.1 (*SE* 0.42)	72.5
DGB2017	86.3 (*SE* 2.64)	86.0 (*SE* 0.82)	86.7 (*SE* 0.86)	99.6
PAD2017	45.5 (*SE* 9.35)	44.9 (*SE* 0.65)	46.1 (*SE* 0.71)	96.8

FIGURE 6 Bean plot (i.e. probability density of the catch data) of signal crayfish size-class distribution (mm CL) captured through triple drawdown, handsearching and trapping techniques across all study sites. Dotted lines represent the four key size groups (≤12, 13–25, 26–34, ≥35 mm CL)
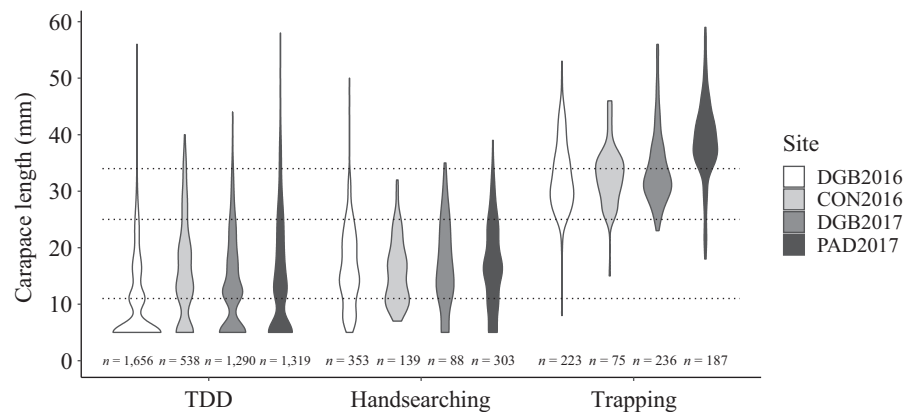
drawdown-derived density estimates (e.g. 0.6 CPUE at CON2016—density 20.5 crayfish/m^2 and 0.7 CPUE at PAD2017—density 86.0 crayfish/m^2). Male:female ratios were 39:61, 44:56, 54:46 and 43:57 at DGB2016, CON2016, DGB2017 and PAD2017, respectively. Handsearching captured crayfish between a size range of 5–50 mm CL, with a median size of 15–16 mm CL (Figure 6). Handsearch samples were dominated by juvenile crayfish (29%–39% of total catch) and sub-adults (49%–63% of total catch), with a small proportion of sexually viable (4%–12%) and trappable adults (0%–1%, Figure 3), respectively.

A total of 721 signal crayfish were captured by trapping across the four sites. CPUEs ranged from 3 to 5.9 crayfish per trap (Table 1).

Consistent with the drawdown results, the lowest CPUE was found at CON2016. However, the remaining trapping CPUE values were also incongruent with the drawdown-derived density estimates (Table 1). Male:female ratios were 39:61, 52:48, 44:56 and 52:48 at DGB2016, CON2016, DGB2017 and PAD2017, respectively. Trap-caught individuals ranged from 8 to 59 mm CL, with a median CL of 30–40 mm (Figure 6). Very few sub-adults and a single juvenile individual were caught, with the majority of the catch of adult size (≥26 mm CL, 92.8%–98.8%, Figure 3), despite the 5 mm mesh.

Based on depletion results (Figures 4 and 5), we believe that the TDD sampled the vast majority of the true population (Table 2).

When comparing the TDD, handsearch and trap data (Figure 6), the TDD appeared to provide robust insights into crayfish population structure across all size classes (5–58 mm CL). The TDD had a median size of 12 mm CL (Figure 6), and of the total TDD catch ($n = 4,803$), 50% of individuals were <11 mm CL and 90% of individuals were <25 mm CL.

4 | DISCUSSION

4.1 | Invasive crayfish population structure

The range of crayfish densities (20.5–110.4 individuals/m^2) established using our TDD method along the invasion gradient at BGB are extremely high, and far exceed most published field estimates (e.g. <1–8/m^2, Ibbotson & Furse, 1995). Indeed, the density reported from the CON2016 TDD of 20.5 individuals/m^2 falls within the upper range of densities previously recorded from UK rivers invaded by signal crayfish (3–20/m^2 in Guan & Wiles, 1997; 20/m^2 in Bubb, Thom, & Lucas, 2004). However, the highest density of at least 110.4 signal crayfish individuals/m^2 observed in this study at DGB exceeds previous density estimates by more than a factor of 5.

The high density values for signal crayfish might relate to the population along BGB being well established (10–20+ years), and because BGB provides highly suitable habitat conditions and minimal predation pressure on signal crayfish. In the absence of fish from PAD and DGB, predation was limited to conspecific cannibalism and riparian predators such as European otter *Lutra lutra* and grey heron *Ardea cinerea*. As such, the population densities at PAD2017 and both DGB2016/17 may not necessarily represent a standard baseline for England, but instead could represent highly successful populations thriving under potentially optimal conditions. The fish species present at CON2016 are known to directly predate crayfish, as well as indirectly compete for food and habitat (e.g. European bullhead in Dahl, 1998 and Guan & Wiles, 1997; brown trout, Atlantic salmon and European eel in Freeman, Turnbull, Yeomans, & Bean, 2010; Reynolds, 2011). Further research is required to establish if the relatively lower densities of signal crayfish reported at CON2016 are linked to fish-related predation pressure. Overall, the evidence that signal crayfish can achieve such high densities in its non-native range is of great concern.

The male:female ratio from the TDD is broadly consistent with the available literature for signal crayfish (see Almeida et al., 2013). However, what is clear from all sites is the large number and overall dominance of juveniles in all the populations (36%–72%), with the relatively smaller population of juveniles at CON2016 potentially linked to greater predation pressure from fish. Based on kick sampling, Wooster, Snyder, and Madsen (2012) reported that, in its native range (northeastern Oregon), 58% of the catch of signal crayfish were juveniles (0–14 mm CL in their study, >85% of which were 4–8 mm CL), suggesting that the population

structures observed within our study are similar to native population demographics.

4.2 | Implications for crayfish survey and management

The TDD method has proven to be an effective technique for surveying crayfish in situ while highlighting limitations of two 'common practice' survey methods—handsearching and baited funnel trapping. The drawdown consistently sampled crayfish of all size classes, providing more robust and representative information on the signal crayfish populations including estimates of density, biomass, male:female ratios and size-class distribution. In contrast, both handsearching and trapping generated semi-quantitative CPUE values affording only a broad indication of crayfish abundance, and consistently failing to sample full population demographics (5–59 mm CL in this study). In addition, the incongruence between the trapping and handsearching-derived CPUEs and TDD-derived density data prevent meaningful correction factors from being applicable. While handsearching and trapping provide some utility for confirming crayfish presence, these established techniques missed key aspects of invasive population structure and density that drive interactions between crayfish and native biota (Bubb, O'Malley, Gooderham, & Lucas, 2009), thus greatly limiting their applicability in scientific studies of invasive crayfish ecology and impacts. At present, the TDD technique is the only method that can generate reliable quantitative assessments of crayfish populations.

The TDD approach performed well in the small, low-order stream system selected for this study, characterised by reduced summer flows and abundant removable in-channel refuges. In principle, the TDD could be adapted and modified to operate in multiple habitat types and freshwater systems. For TDD surveys, the ability to isolate a section of the desired watercourse or waterbody, and to remove and search the available substrates and refugia effectively is paramount. As such, systems that maintain a gradient across the site to facilitate dewatering, are dominated by cobble or boulder substrates that are easily removed, or produce a low discharge that can be overcome with pumps, are likely to be highly suitable survey sites. TDDs may be less effective in aquatic systems where crayfish construct complex, riparian burrows (Guan, 1994; Peay & Dunn, 2014) or habitats where refuges cannot be removed nor searched efficiently, such as dense macrophytes. Retention of crayfish in unsearchable refuges during dewatering is likely and may last several days (Peay & Dunn, 2014), thus affecting the robustness of population density and structure estimates. However, this problem is at least partially addressed by conducting multiple dewatering 'sweeps', as sequential rewetting encourages crayfish to leave exposed refugia (Peay & Dunn, 2014). Crucially, in each scenario where the TDD approach is applied, the efficiency of the method can be evaluated through the multiple depletion analyses.

Dewatering requires extensive pumping equipment and a number of skilled operatives. This becomes increasingly problematic

as the scale or inaccessibility of the TDD site increases. As such, many large or remote systems become unsuitable for TDD due to access, equipment and safety considerations, where contemporary methods may be suitable. However, industrial scale equipment is regularly used to dewater segments of river channels during infrastructure and civil engineering projects. Such approaches could allow the TDD to be undertaken in larger watercourses if sufficient funding and operatives are available. A further consideration is the welfare of non-target organisms, with sustained dewatering of the benthos potentially leading to localised negative impacts. As such, precautions should be taken to safeguard fauna, such as localised fish removals, and prolonged dewatering should be avoided during TDD application by increasing sweep or operative numbers.

Due to the considerable resources and labour considerations and the obvious difficulties of re-routing entire invaded watercourses needed for TDD, we also suggest that TDD is better suited as a survey method as opposed to a control option. Nevertheless, when employed in suitable systems, the TDD could advance our understanding of invasive crayfish biology, for example through highlighting specific environmental parameters supporting high-density populations such as substrate conditions (Hein et al., 2006), fish communities (Reynolds, 2011) or presence of other invasive species (Simberloff & Von Holle, 1999). Considering the successes and limitations of the TDD, it is clear that a great need exists in the field of applied crayfish ecology for novel quantitative sampling methodologies to be developed. The TDD is well suited to evaluate their efficiency, and is currently the only method capable of ground-truthing sampling methods in situ.

The TDD has strong implications for the evaluation of management techniques for invasive crayfish. Our study clearly demonstrated that the use of conventional funnel baited traps to control invasive signal crayfish would be highly unsuccessful for our system, with only 2.3% of the entire population large enough to be readily trapped (≥35 mm CL). Even with an additional 5-mm mesh attached to the traps, only 10.1% of the total population becomes 'trappable'. Furthermore, due to the cannibalistic tendencies of crayfish (Houghton, Wood, & Lambin, 2017), extractive trapping that preferentially removes large adults most likely reduces already limited predation pressure on the remaining population. Thus, trapping does not represent an effective, viable management or control method in invaded systems that have a juvenile-dominated population structure, as in this study. Further limitations, consequences and risks associated with conventional baited funnel trapping for control highlighted in previous studies include an increased fitness of remaining animals (Moorhouse & Macdonald, 2011), early onset of sexual maturity (Holdich et al., 2014), intentional anthropogenic spread (Edsman, 2004) and bycatch of non-target species (De Palma-Dow et al., 2020). Thus, our research adds to mounting evidence suggesting that trapping of invasive crayfish is both an ineffective and potentially damaging activity.

In recent years, in a drive to develop additional methodologies to increase the efficacy of invasive crayfish control efforts, traps have been modified, with male sterilisation also trialled (Stebbing et al., 2016). These approaches reportedly decreased CPUE for adult signal crayfish populations. Long-term trapping combined with fisheries management resulted in substantial reductions in modelled populations of rusty crayfish, with the increased predatory fish population providing effective control of juveniles (Hein et al., 2006). Furthermore, artificial refuge traps (ARTs) have been investigated as a management tool for signal crayfish in an upland river of south-west England (Green et al., 2018). ARTs appeared to show promise in catching berried females of high reproductive value (2% of those captured) and intermediate size classes (75.7% of total crayfish caught were 21–39 mm CL), but showed limited potential in the capture of juvenile individuals (1.2% of total catch was <13 mm CL). Control methods with the highest potential of success are those that target the whole population equally. The evaluation of the success of any control approach requires robust population demographic data prior and post-intervention. Our study shows that such data can now be obtained, where appropriate, through the use of the TDD method. For example, a TDD could be performed before and after a control trial and used to calculate the reduction in crayfish density and identify which size classes have been targeted. Therefore, the ability of the TDD to accurately describe all aspects of the population is fundamental to assessing the efficiency of the control and management of invasive crayfish.

5 | CONCLUSIONS

The TDD method has enabled collection of the first fully quantitative data on signal crayfish population density and demographics within its invasive range. Based on the strong depletions evidencing high catch efficiency, this method was proven effective at sampling crayfish across all size classes. Our study also highlights severe limitations of survey data from commonly used crayfish handsearching and trapping methods. We show, unequivocally, that trapping cannot be used as an effective control method for invasive crayfish populations at least in conditions resembling our study system. The TDD affords an ability to ground-truth and hence evaluate the efficiency of future crayfish survey methods. Knowledge of the structure and density of crayfish populations derived from a TDD approach will allow more detailed future assessments of invasive crayfish impacts and of the effectiveness of crayfish removal and control methods.

AUTHORS' CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

ORCID

Eleri G. Pritchard https://orcid.org/0000-0003-2391-6946

Carl D. Sayer https://orcid.org/0000-0001-6075-4881

Michael A. Chadwick https://orcid.org/0000-0003-4891-4357

Lawrence J. B. Eagle https://orcid.org/0000-0003-0252-8450

Jan C. Axmacher https://orcid.org/0000-0003-1406-928X

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