

**RESEARCH ARTICLE**

# Thermal sensitivity of feeding and burrowing activity of an invasive crayfish in UK waters

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**Abstract**

Climate change and invasive species are among the biggest threats to global biodiversity and ecosystem function. Although the individual impacts of climate change and invasive species are commonly assessed, we know far less about how a changing climate may impact invading species. Increases in water temperature due to climate change are likely to alter the thermal regime of UK rivers, and this in turn may influence the performance of invasive species such as signal crayfish (*Pacifastacus leniusculus*), which are known to have deleterious impacts on native ecosystems. We evaluate the relationship between water temperature and two key performance traits in signal crayfish—feeding and burrowing rate—using thermal experiments on wild-caught individuals in a laboratory environment. Although water temperature was found to have no significant influence on burrowing rate, it did have a strong effect on feeding rate. Using the thermal performance curve for feeding rate, we evaluate how the thermal suitability of three UK rivers for signal crayfish may change as a result of future warming. We find that warming rivers may increase the amount of time that signal crayfish can achieve high feeding rate levels. These results suggest that elevated river water temperatures as a result of climate change may promote higher signal crayfish performance in the future, further exacerbating the ecological impact of this invasive species.

**KEYWORDS**

climate change, invasive species, signal crayfish, thermal performance curves, water temperature

**1 | INTRODUCTION**

Climate change and invasive species are global threats to biodiversity and ecosystem function (Bellard, Cassey, & Blackburn, 2016; WWF, 2020). Invasive species can alter food webs, outcompete natives and engineer ecosystems in ways that disrupt the provision of

ecosystem services (Gallardo, Clavero, Sánchez, & Vilà, 2016; Pyšek et al., 2020). Climate change may raise organisms' body temperatures, altering activity times, ecological performance and evolutionary fitness (Peñuelas et al., 2013). Although threats of climate change and invasive species are commonly assessed, the effect of climate change on the invaders themselves remains relatively unexplored (Rahel &

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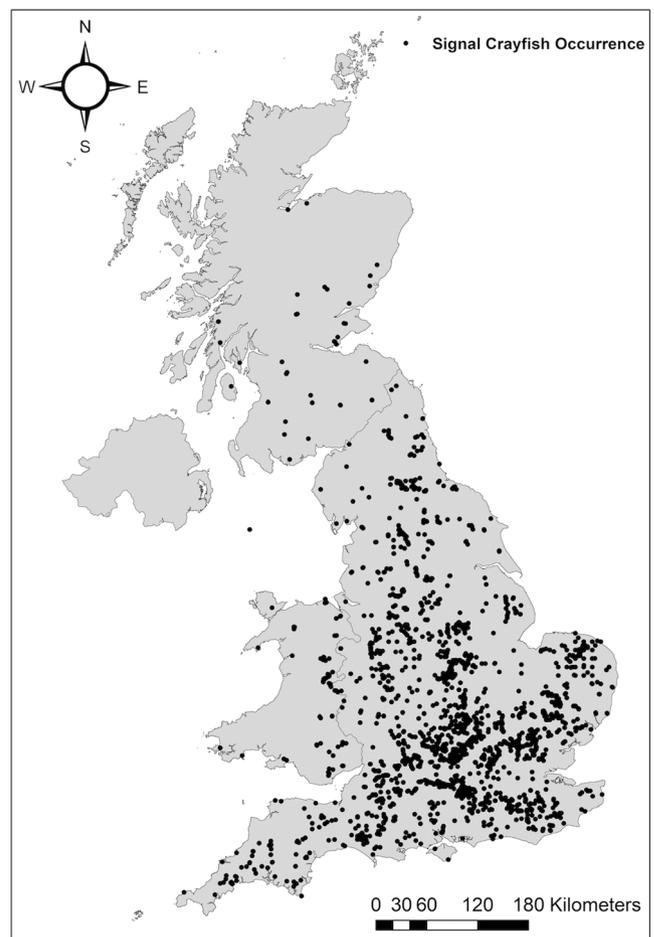
Olden, 2008). This is despite the potential of warming to increase key ecological rates, potentially accelerating invaders' spread and exacerbating their impacts (Hulme, 2017).

Research on river temperature has increased in the last few decades as scientists and environmental managers alike have recognized its importance in fluvial systems (Garner, Hannah, Sadler, & Orr, 2014). Although the physical controls of water temperature in rivers are varied and complex (e.g., see Dugdale, Hannah, & Malcolm, 2017), there is a general agreement that climate change will increase water temperature in rivers (Paul, Coffey, Stamp, & Johnson, 2019).

Temperature has pervasive influences on the physiology, distribution and behaviour of organisms (Brown, Gillooly, Allen, Savage, & West, 2004). Temperature is especially important for ectotherms because their internal body temperature is determined primarily by their environment (Angilletta, 2009). As most aquatic species are ectotherms, rising water temperature may result in major changes to their performance (Sinclair et al., 2016), timing of major life history events (Everall, Johnson, Wilby, & Bennett, 2015; Harper & Peckarsky, 2006) and geographic distribution (Liu, Guo, Ke, Wang, & Li, 2011). The physiological and ecological thermal sensitivities of ectotherms typically adopt a consistent form, whereby the performance of an organism increases slowly to an optimum, before falling sharply (Angilletta, 2009). The shape of these thermal performance curves (TPCs) has been commonly used in terrestrial systems by comparing them with spatial and temporal variations in environmental temperature to determine how thermal variation affects ecological performance (Gunderson & Leal, 2012; Sinclair et al., 2016). Aquatic ecologists are increasingly utilizing TPCs to gain a better understanding of the thermal sensitivity of different organisms, including crayfish and shrimp (Ern et al., 2015). TPCs can also provide information regarding how species may respond to future warming as a result of climate change (Simcic, Pajk, Jaklic, Brancelj, & Vrezec, 2014).

Due to increases in the frequency and magnitude of their introductions, invasive species are altering freshwater ecosystems around the world (Gallardo et al., 2016; Reid et al., 2019). The impacts of invasive species in freshwater ecosystems are exacerbated by the strong trophic interactions in these systems, which can lead to direct and indirect ecological effects on native species and, ultimately, a loss of biodiversity (Gallardo et al., 2016). There is also now a much wider appreciation that invasive species can be potent ecosystem engineers, conducting biogeomorphological activity that modulates environmental processes (e.g., turbidity and sediment transport) and impacts other species (Rice, Johnson, Mathers, Reeds, & Extence, 2016). As well as potentially influencing their rate of establishment and their interactions with natives, novel thermal regimes in freshwater environment as a result of climate change may alter the performance of key activities in invasive species (Rahel & Olden, 2008).

Signal crayfish (*Pacifastacus leniusculus*) are native to the north-western United States and were introduced to the United Kingdom for aquaculture in the 1970s (Holdich, James, Jackson, & Peay, 2014). Following the release and escape of individuals from aquaculture facilities, signal crayfish have spread throughout much of the United Kingdom (Figure 1), and evidence suggests that their range is still



**FIGURE 1** Map showing detected signal crayfish occurrence in the United Kingdom. Occurrence data are from the National Biodiversity Network Atlas (available from <https://species.nbnatlas.org/species/NHMSYS0000377494>)

expanding (Robinson, Uren Webster, Cable, James, & Consuegra, 2018). Signal crayfish threaten the survival of the native white-clawed crayfish (*Austropotamobius pallipes*) through competition and the spread of crayfish plague (*Aphanomyces astaci*), a fungal infection that they themselves are immune to (James et al., 2017). These factors have all contributed to the white-clawed crayfish becoming endangered in the United Kingdom (Holdich et al., 2014). Signal crayfish are also known to be adverse ecosystem engineers (Harvey et al., 2011). In particular, signal crayfish activities, such as burrowing into river beds and banks, foraging and movement, have been shown to alter sediment transport and induce bank collapse (Rice et al., 2016). Geomorphic activity by signal crayfish can also threaten economically valuable salmonid species such as Atlantic salmon (*Salmo salar*), as increases in fine-sediment transport can reduce the survival rate of their incubating eggs (Harvey et al., 2011). Additionally, the polytrophic feeding habits of signal crayfish can reduce the abundance and diversity of macrophytes (Nystrom & Strand, 1996) and invertebrates in rivers (Mathers et al., 2020). The ecological and environmental impacts of invasive signal crayfish can also indirectly impact other trophic levels, including native fish (Wood, Hayes, England, & Grey, 2017).

As with other ectotherms, signal crayfish are influenced by water temperature (Bohman et al., 2016; Simcic et al., 2014). For example, activity levels show clear seasonal variability, with declining movement during colder months (Johnson, Rice, & Reid, 2014). Therefore, it is important to understand how the detrimental impacts of crayfish, such as burrowing, are influenced by temperature. Previous work has suggested that processes related to overall metabolism in signal crayfish, such as oxygen consumption, can remain high over a broad range of temperatures (Simcic et al., 2014). Although this suggests that other performance traits in signal crayfish may also share this relationship with temperature, it is also possible that other traits are more temperature dependent. It is therefore important to assess how different ecological traits (particularly those associated with signal crayfishes' detrimental impacts) are influenced by temperature, in order to better understand potential impacts of their invasion on rivers already threatened by climate change.

Here, we aim to increase our understanding of crayfish thermal performance and whether higher future river temperatures may promote (or hinder) invasive signal crayfish performance in the United Kingdom. We quantify thermal sensitivity for two key ecological rates—feeding and burrowing—and compare the resulting TPCs to check for thermal alignment between traits. We focus on these two traits as they are directly associated with many ecological and environmental impacts of invasive signal crayfish. Finally, we compare TPCs with current temperatures in several UK rivers to illustrate whether warming may hinder or enhance the ecological performance of invasive signal crayfish.

## 2 | METHODS

### 2.1 | Thermal performance curves

#### 2.1.1 | Sampling and acclimation

In order to remove the potential confounding effects of sex and size, which can influence activities such as feeding habits and activity level in crayfish (Holdich et al., 2014; Lewis, 2002), we selected 12 adult male signal crayfish with carapace lengths ranging from 41.3 to 58.0 mm for the performance tests. These were the largest males captured. Tests were conducted in two batches (six individuals per batch). Performance trials for Batch 1 were begun on 3 October 2018 and on 6 November 2018 for Batch 2. Although signal crayfish typically have lower activity levels in the United Kingdom during these cooler months compared with warmer periods of the year, they remain active during these periods (Johnson et al., 2014). Animals were trapped in Gaddesby Brook, Leicestershire, using Trappy Funnel Crayfish traps baited with cat food. After capture, animals were placed in individual 75-L tanks filled with dechlorinated tap water to a depth of approximately 28 cm. Water was circulated continuously through the entire system into a sump reservoir, which was aerated and maintained at 16°C using an aquarium cooler (Hailea HC-500A). Each tank contained a gravel bottom and a refuge (ceramic pot). The

walls of adjacent tanks were shielded to ensure animals could not see each other. Tanks were subject to a natural light : dark cycle based on ambient light. Crayfish were fed with King British catfish pellets on Mondays, Wednesdays and Fridays between 16:00 and 17:00. Animals were acclimated at 16°C for 21 days. None of individuals used were injured or underwent moulting during the period when performance tests were conducted.

#### 2.1.2 | Initial experimental conditions

Following the acclimation period, animals were placed in individual experimental tanks with a 30 × 22 cm base covered with 6 cm of gravel with a maximum grain size of 10 mm. Tanks were filled with 2.5 L of water (~15 cm depth), covered and placed in a temperature controlled chamber (Lovibond Thermostatic Cabinet) with dividers so animals could not see each other. Tanks were continuously aerated and initially set at 15°C. Animals were transferred to experimental tanks at 17:00 and fed as per their normal schedule. After 16 h (9:00 the following morning) at 15°C, chamber temperature was reduced to 10°C. At 18:00, freeze-dried carrot—a commonly used food source in crayfish experiments (Nylund & Westman, 2000; Statzner, Peltret, & Tomanova, 2003)—was added to a feeding spike embedded in the gravel of each tank to ensure it remained secured on the gravel bottom. This allowed animals to become familiar with the experimental food prior to performance tests. Carrot was left in the tank for 15 h (until 9:00 the following morning) then removed. This mimicked the exposure to carrots during the experimental period to help equalize animals' satiation/starvation state at the beginning of the experiment. At 10:00 (1 h after carrot removal), chamber temperature was reduced to 5°C to begin experimental trials. The rate of temperature change in this initial period, and subsequently during experimental trials, is similar to the rates of temperature change recorded in UK rivers (e.g., Wilby, Johnson, & Toone, 2014). The timing of initial acclimation and experimental trials is given in Table S1.

### 2.2 | Experimental procedures

Crayfish performance was measured at 5°C intervals, from 5°C to 30°C, by quantifying food consumed and the amount of burrowing activity taking place in a 15-h period (from 18:00 to 9:00) at each temperature. At each temperature, the procedure was as follows: on Day 1, at 10:00, the temperature chamber was set to the target temperature (water temperature took 5 h to reach the target temperature). At 18:00, on Day 2 (after 32 h), the gravel bed was smoothed and levelled using guides drawn on tank sides, and a preweighed piece of freeze-dried carrot was placed on the feeding spike and secured on the gravel bed. At the end of the trial period, 9:00 on Day 3, the carrot was removed and placed in the freezer. Each animal was then placed in an individual plastic container with water at the current experimental temperature. Water was drained from the experimental tank

without disturbing the gravel bed. The surface of the gravel bed was then scanned using an Einscan S (Shining 3D) 3D scanner. We used a static, vertical scan with the scanner located in a fixed position from the gravel surface to obtain a 3D point cloud of the gravel surface. After scanning, the tank was refilled with the drained water, and the animals were placed back in the same tank. At 10:00, the chamber temperature was raised to the next treatment temperature and the process repeated. Our procedure measured performance at progressively warmer temperature. Although this induced temporal autocorrelation, it reduced the chance of animals experiencing thermal shock due to large changes in temperature (e.g., 5°C to 30°C and back to 10°C). At the end of the experiments, including the 21-day acclimation period, animals had been in captivity for 35 days.

### 2.2.1 | Quantifying TPCs

To measure the mass of food consumed, we re-freeze-dried and reweighed the partially consumed carrots to the nearest 0.1 mg using a Fisherbrand PS-200 balance. We used freeze-drying to reduce effects of water absorption during feeding trials on estimates of food consumed. Feeding activity was quantified as the difference between preconsumption and postconsumption masses. We measured relative burrowing activity ( $B_{rel}$ ) using the following equation:

$$B_{rel} = 0.5 * \sum(\text{abs}(z_i - \text{mean}(z))) / N,$$

where  $z$  is the elevation of the  $i$ th pixel in the gravel scan (in pixels) and  $N$  is the number of pixels. The equation first finds the summed absolute deviations from the mean gravel level across all pixels. This is then multiplied by 0.5 because gravel displaced from one area of the tank must increase the gravel height in another. Results are presented per pixel because variation in the completeness of scans mean pixel number varied across scans. Although some variation in elevation will arise from differences in initial gravel smoothing, this will be independent of temperature and thus will add noise but not bias to our results. It was not possible to scan tank beds prior to burrowing as refilling tanks with water disturbed the gravel.

We found no interaction between crayfish batch and the relationship between performance and temperature for feeding (two-way analysis of variance [ANOVA],  $F = 0.51$ ,  $df = 5.60$ ,  $p = 0.77$ ) or burrowing (two-way ANOVA,  $F = 2.18$ ,  $df = 5.60$ ,  $p = 0.07$ ), so we pooled the data from the two batches to fit TPCs. We characterized curves using a Gompertz  $\times$  Gaussian equation (Frazier, Huey, & Berrigan, 2006; Frishkoff, Hadly, & Daily, 2015), with individual crayfish as a random effect on maximum performance to account for overall differences in activity among individuals. We tested whether curves were significant using a likelihood-ratio test relative to an intercept-only mixed-effects model. We estimated the strength of this relationship as the  $R^2$  of the regression of observed feeding activity against the fitted values based solely on fixed effects. All analyses were conducted using R v3.6.3 (R Core Team, 2019), including the nlme (Pinheiro, Bates,

DebRoy, Sarkar, & R Core Team, 2020) and lme4 (Bates, Maechler, Bolker, & Walker, 2014) packages.

For significant TPCs, their optimal temperature ( $T_{opt}$ ), the temperature of maximum performance, and thermal performance breadth ( $T_{br}$ ) were calculated. As in other studies (Huey & Stevenson, 1979),  $T_{br}$  was defined as the temperatures in which performance was at least 80% of the calculated maximum. In order to calculate  $T_{br}$ , we assumed that the lowest recorded performance intensity of the trait during the experiments was its minimum.

### 2.3 | Signal crayfish performance and stream temperature

Water temperature data at three UK sites (River Aire, Lancashire, River Dee, Gwynedd, and River Stour, Dorset) for the whole of 2007 were collated from the Environment Agency Surface Water Archive (Figure 2; sites IDs KELBROOK\_ON\_AIRE,



**FIGURE 2** Location of the three river sites from which water temperature data for 2007 were collated using the Environment Agency Surface Water Archive. KELBROOK\_ON\_AIRE was the site used for the River Aire, BALA\_GS\_ON\_DEE was used for the River Dee and HAMOON\_ON\_STOUR\_MIDDLE\_(DOR) was used for the River Stour

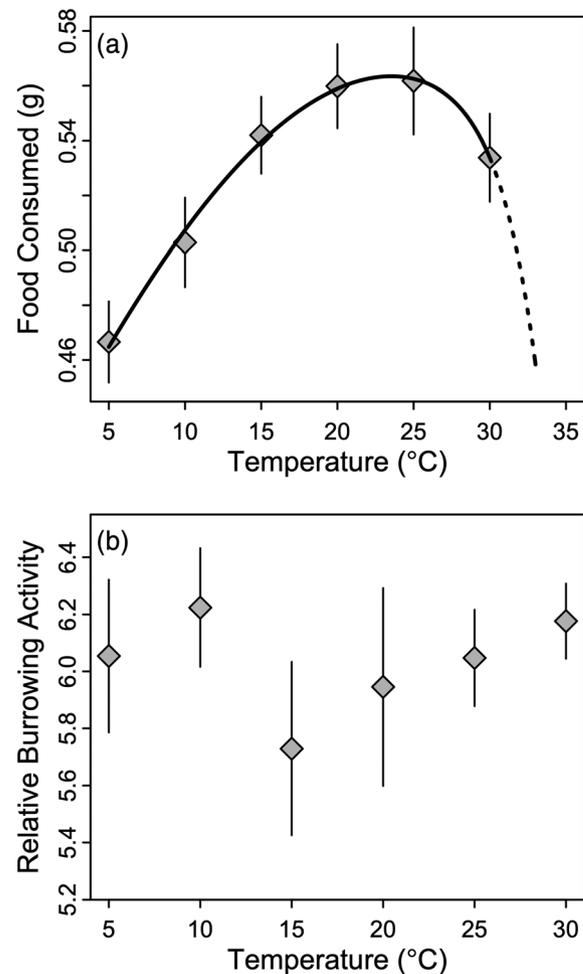
BALA\_GS\_ON\_DEE and HAMOON\_ON\_STOUR\_MIDDLE). We selected these rivers for three reasons. Firstly, although most of the data in the archive are collected opportunistically during water quality sampling campaigns (Orr et al., 2014), these three sites had at least one water temperature reading every hour for the whole of 2007. Secondly, they cover a broad geographical extent in England and Wales. And thirdly, examination of records in the National Biodiversity Network's Gateway ([www.nbn.org.uk](http://www.nbn.org.uk)) showed that signal crayfish have been recorded in all three rivers. Data for 2007 were used to represent water temperature as this was the most recent year with full records in the archive; water temperatures in 2007 from the Rivers Stour and Dee were not exceptional relative to previous years (Figure S1); earlier data were not available for the River Aire. Temperature series were checked visually and cleaned for obviously spurious values. Subsequently, we calculated averaged hourly water temperature values for each site for the whole calendar year of 2007 and used these to determine the proportion of water temperature values that were within the calculated  $T_{br}$  of signal crayfish for all three rivers.

In order to gain some broad context of how warming may affect performance metrics, three temperature values were uniformly added to all hourly measurements of the study rivers: +1.3°C, +2.8°C and +3.6°C. These values were derived from warming scenarios based on modelling of global river temperatures (van Vliet, Ludwig, Zwolsman, Weedon, & Kabat, 2011). The goal of this analysis was to illustrate how general warming may influence performance, not to accurately represent the complex and heterogeneous nature of the impact climate change is expected to have on river temperature. In the absence of a river-scale assessment of future climate impacts on water temperature in the United Kingdom, our method offers a simplistic, but useful, starting point for determining how warming may affect the ecological performance of invasive crayfish in the United Kingdom.

### 3 | RESULTS

#### 3.1 | Thermal performance curves

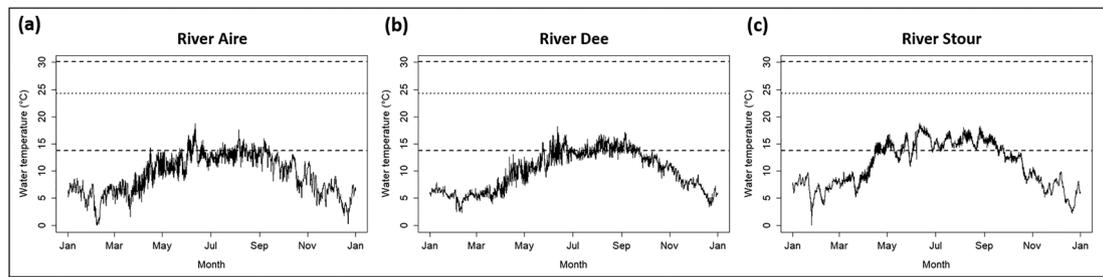
We found that signal crayfish feeding activity (Figure 3) varies with temperature in a manner consistent with classic TPCs (Angilletta, 2009), with a gradual rise to an optimum, followed by a sharper decline as temperature approaches upper thermal limits. The Gompertz × Gaussian model (Frishkoff et al., 2015) fits the data significantly better than a null model (likelihood ratio test statistic: 25.4,  $df = 3$ ,  $p = 1 \times 10^{-5}$ ), with an estimated  $R^2$  of 0.28. The TPC revealed an optimum feeding rate at  $24.3 \pm 0.02^\circ\text{C}$ , with  $T_{br}$  between  $13.7^\circ\text{C}$  and  $30.1^\circ\text{C}$ . Although signal crayfish burrowed extensively in experimental tanks, we found no relationship between burrowing activity and temperature (Figure 2, likelihood ratio test statistic: 1.35,  $df = 3$ ,  $p = 0.72$ , estimated  $R^2 = 0.02$ ). Data are available from Rodriguez Valido et al. (2020).



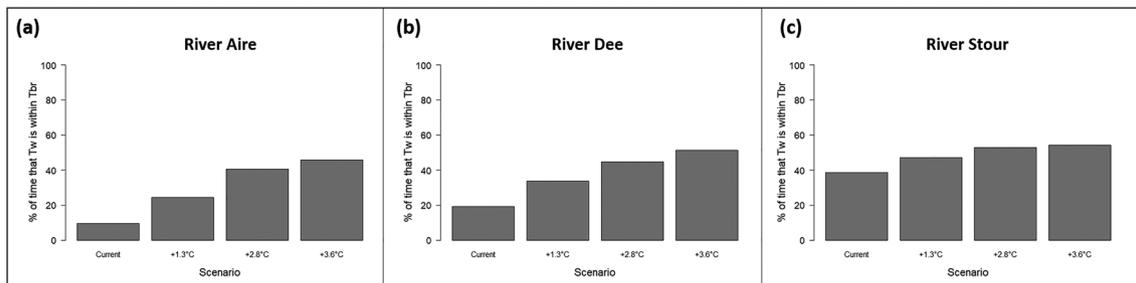
**FIGURE 3** Thermal performance curves for feeding (a) and burrowing (b) activity in signal crayfish. The solid line for the feeding curve covers the range of experimental values. Values are means and standard errors across 12 individuals. Curve was fitted using a Gompertz × Gaussian function, and the dashed line reflects extrapolation beyond the range of the training data. Whereas the relationship between feeding rate and water temperature was significant (likelihood ratio test statistic: 25.4,  $df = 3$ ,  $p = 1 \times 10^{-5}$ ,  $R^2 = 0.28$ ), the relationship between burrowing and temperature was not (likelihood ratio test statistic: 1.35,  $df = 3$ ,  $p = 0.72$ ,  $R^2 = 0.02$ )

#### 3.2 | Signal crayfish performance and UK river temperature

Current water temperature in all three rivers generally only reached the  $T_{br}$  for feeding rate in signal crayfish during warm summer days (Figure 4). Current water temperature in the River Stour tended to be within the  $T_{br}$  of signal crayfish feeding rate more (38.6%) than for the other two rivers (9.6% for River Aire and 19.2% for River Dee). We found that the proportion of water temperature values within the  $T_{br}$  for feeding rate increased in all three rivers under the warming scenarios (Figures 5 and S2). Under the most extreme scenarios of a uniform warming of 3.6°C, this proportion rose to 45.9% for the River Aire, 51.4% for the River Dee and 54.1% for the River Stour



**FIGURE 4** Hourly averaged water temperature for the River Aire, River Dee and River Stour for 2007 in relation to the thermal niche of signal crayfish. Dashed lines indicate the thermal performance breadth ( $T_{br}$ ) for the feeding rate in signal crayfish, and the dotted line represents its thermal optimum ( $T_{opt}$ ).  $T_{br}$  is the range of temperatures where feeding rates is at least 80% of the maximum, that is, the rate at  $T_{opt}$



**FIGURE 5** The proportion of hourly water temperature ( $T_w$ ) values during a year within the feeding rate thermal performance breadth ( $T_{br}$ ) of signal crayfish for the River Aire (a), River Dee (b) and River Stour (c) under current water temperatures and future, uniform, increases in water temperature.  $T_{br}$  reflects temperatures where feeding rate is at least 80% of the maximum

(Figures 5 and S2). Even under the most extreme warming considered here (+3.6°C), water temperature did not surpass the  $T_{opt}$  of feeding rate in any of the three rivers.

## 4 | DISCUSSION

We found that the two performance traits of signal crayfish, feeding and burrowing rate, exhibited markedly different responses to water temperature. Feeding rate in individuals was significantly influenced by water temperature, with performance rising to its optimum at  $24.3 \pm 0.02^\circ\text{C}$  before falling. On the other hand, burrowing activity showed no clear relationship with the water temperature. This difference in responses to temperature between feeding and burrowing activity suggests that the former is more closely linked to underlying, temperature-dependent physiological processes; as metabolism increases with temperature, increased feeding rates are needed to meet energy demands (Brown et al., 2004). In contrast, our results suggest burrowing is not metabolically limited but rather reflects behavioural decisions based on nonthermal cues. This difference suggests that impacts of ecosystem engineering by signal crayfish may be less predictable under future climate change than competitive and predatory interactions with other species. The lack of thermal alignment between feeding and burrowing rate found in this study is consistent with the idea that different performance traits in organisms can vary markedly in their relationship with temperature (Schulte,

Healy, & Fanguie, 2011). This highlights the need for studies analysing thermal alignment in multiple traits in order to more accurately characterize the effect of changing thermal conditions. As with many laboratory studies analysing organisms, our analysis of performance may have been influenced by factors such as the necessary simplification of environmental conditions, lack of biological interactions and the impact of captivity on individuals. However, laboratory approaches such as these are essential to provide consistent, replicated conditions and provide information on the ecology of organisms that is otherwise difficult to determine. Future work focused on thermal performance of signal crayfish in the wild would be highly beneficial.

The feeding rate results in our study match those observed by Simcic et al. (2014), which found that optimum food-consumption rate in signal crayfish occurred at  $26^\circ\text{C}$  and  $20^\circ\text{C}$  for females and males, respectively. Feeding rate in signal crayfish varied with water temperature in a manner consistent with classical TPCs (Angilletta, 2009), rising with temperature until it reached its optimum at  $24.3 \pm 0.02^\circ\text{C}$  and then declining sharply. Although animals were exposed to the experimental food prior to experimental trials, we cannot completely discount the possibility that changes in feeding may reflect growing familiarity with the food source. However, if changes in feeding rate were due to this, rather than temperature effects, then we would not expect to see the observed declines at higher temperatures. Our results are also consistent with the optimal temperature for growth ( $22.8^\circ\text{C}$ ) in signal crayfish (Firkins & Holdich, 1993). The similarity between our results and others suggests that, as well as

feeding rate, overall individual fitness in signal crayfish may be greatest around this temperature. Furthermore, the broad thermal niche of signal crayfish may promote their invasion success. Their feeding rate  $T_{br}$  between 13.7°C and 30.1°C suggests that signal crayfish have the capacity to maintain high ecological functioning across a broad range of thermal conditions, a niche dimension that could facilitate their ability to outcompete native species, such as the white-clawed crayfish.

Burrowing by signal crayfish increases sediment transport in some invaded UK rivers and modifies their bed topography (Johnson, Rice, & Reid, 2010; Rice et al., 2016). Although our findings suggest that signal crayfish burrowing is not directly influenced by temperature, their contribution to sediment transport may still increase due to warming of rivers. This could be as a result of greater population growth due to increases in other important traits that are influenced by temperature, including feeding rate. Traits such as burrowing and feeding in invasive signal crayfish may also change under future warming in response to nonthermal behavioural cues, such as shifts in abundance of prey and or hydrological change (Rahel & Olden, 2008). This highlights the complexity of predicting how a species may respond to climate change. It also demonstrates the importance of expanding our focus beyond temperature to identify nonthermal drivers of behaviours important for ecosystem functioning.

Although the effects of future climate change on river temperatures in the United Kingdom are highly uncertain (Hannah & Garner, 2015), increases in ecological performance are predicted under three simplistic, hypothetical, amounts of warming (+1.3, +2.8 and +3.6°C; van Vliet et al., 2011). Although values varied across rivers, in general, present-day river temperatures were too low for signal crayfish to maximize their performance and only reached  $T_{br}$  during the warmest periods of summer. However, under the warming scenarios, it is possible that there will be large increases in the amount of time that water temperatures are favourable for signal crayfish. Even under the most extreme warming scenario of 3.6°C,  $T_{opt}$  for feeding rate (24.3°C) was not surpassed, suggesting there is little to no risk of overheating and diminished performance of these invaders in the future. Instead, warming is likely to increase performance, that is, feeding rate, potentially allowing signal crayfish to capture more food resources. This in turn may enable signal crayfish to expand their invasive range in the United Kingdom to currently uninhabited areas faster than otherwise possible under current river temperatures. Analysing the thermal sensitivity of native species alongside that of invasive species would increase our understanding of how rising temperature will affect their future interactions. Future research quantifying TPCs for white-clawed crayfish would greatly improve our understanding of how suggested increases in signal crayfish performance under warming will influence the health of their remaining populations in the United Kingdom and in turn provide crucial information for conservation strategies to aid this important native species.

The warming scenarios considered here were purposefully simplistic. Given that water temperature in parts of the United Kingdom is estimated to be warming by 0.3°C per decade (Orr et al., 2014), the scenarios represent relatively extreme changes to

water temperature, at least in the short term. We stress that the resultant values are not intended to be accurate predictions of future temperature but instead have heuristic value in demonstrating that increases in water temperature are likely to enhance, rather than impede, signal crayfish performance. Our work also highlights the need for improved models of future river water temperature as accurate predictions of animal body temperatures are central to understanding the effects of climate change on ecological performance and functioning (Sinclair et al., 2016). Additionally, although higher performance in feeding rate is predicted in signal crayfish under climate change, this may not automatically translate into an increase in their overall fitness. This is because it is notoriously difficult to assess how an increase in performance of a trait influences classical measures of fitness, such as lifetime reproductive success or intrinsic population growth, and requires observation during the entire lifespan of the organism (Sinclair et al., 2016). The intrinsic complexity of climate change and its impacts on ecosystems makes predicting the way individual species may respond to its impacts very difficult (Gunderson & Leal, 2012). However, determining the TPC of key traits in invasive species can improve our understanding of whether future warming is likely to promote or hinder their invasion.

## 5 | CONCLUSION

Our results suggest that river warming will not alter burrowing activity in a predictable way, suggesting that crayfish-induced sediment transport from this activity will not increase under future climate change and that effects of signal crayfish on physical and biotic dimensions of river systems may become decoupled under future temperature change. However, feeding rate in signal crayfish was closely related to the water temperature. Signal crayfish appear to maintain this key ecological rate at a relatively high level over a broad range of temperatures, which may help explain their highly successful invasion in the United Kingdom and elsewhere. The differential relationships between these two traits and water temperature acts as another example that different traits in organisms can vary markedly in their response to environmental conditions.

Analysis of water temperature from three rivers across the United Kingdom showed that current temperatures in those sites were generally too low for signal crayfish to maximize their feeding rate. As a result, increases in water temperature due to climate change are expected to increase the performance of this invasive species. Further studies analysing the relationship between signal crayfish and thermal habitat in rivers will enable us to get a better understanding of how this invasive species will respond to continued warming of rivers.

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## AUTHOR CONTRIBUTIONS

CARV, MFJ, SJD and ACA designed the study. All authors collected data. CARV and ACA led the manuscript writing with input from MFJ, SJD and the remaining authors.

## DATA AVAILABILITY STATEMENT

All data on crayfish burrowing and feeding activity have been deposited on Figshare (DOI: 10.6084/m9.figshare.13043111). UK river water temperature data are freely available from: <https://data.gov.uk/dataset/d1f77818-9cc4-430e-a970-f386c5d835eb/surface-water-temperature-archive-up-to-2007>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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