

Between-lake variation in the trophic ecology of an invasive crayfish

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Abstract

1. The trophic ecology of invasive species has important implications for their impacts on recipient ecosystems, with omnivorous invaders potentially affecting native species and processes over multiple trophic levels. The trophic ecology of invaders might be affected by both their body size and the characteristics of their habitat due to variation in energy requirements and resource availability.
2. Here, using stable-isotope analysis, we investigated the trophic ecology of the invasive crayfish *Procambarus clarkii* in 15 populations in southwest France over a gradient of individual (crayfish body size), population (crayfish abundance) and ecosystem (lake size, productivity and predation pressure) characteristics. We predicted that population niche width, level of omnivory and trophic position of individuals would change with abiotic and biotic conditions, but that these relationships would vary with lake size.
3. The trophic position of individual crayfish increased with body size in lakes with low productivity, but decreased with body size in more productive lakes. As crayfish abundance increased (and therefore potential intraspecific competition), individual trophic position and population niche width decreased. This was most apparent in smaller lakes, suggesting it related to an increase in encounter rates with conspecifics.
4. Body size, population abundance, lake size and lake productivity influenced the trophic ecology of invasive crayfish, which can affect their interactions with native species. Our results demonstrated that the trophic ecology of invasive species can be variable across invaded landscapes, with implications for their ecological impacts on native communities. This emphasizes the importance of characterising the diet of invasive species across their non-native range and environmental gradients to better predict and manage their impacts.

KEYWORDS

food web, niche width, omnivory, *Procambarus clarkii*, stable isotope

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1 | INTRODUCTION

The trophic ecology of invasive species has strong implications for their establishment success, their invasive distribution, and their impacts on native organisms and recipient ecosystems (Dick et al., 2013; Griffen, Altman, Bess, Hurley, & Penfield, 2012; Zhang et al., 2010). The addition of invasive species to an established food web creates novel trophic links and modifies energy pathways, potentially resulting in altered food web structure (Cucherousset, Blanchet, & Olden, 2012; Vander Zanden, Casselman, & Rasmussen, 1999; Woodward, Papantoniou, Edwards, & Lauridsen, 2008). This is important, as food web structure is a fundamental ecological attribute that underlies species diversity, mediates community dynamics, and influences ecosystem processes (Thompson, Dunne, & Woodward, 2012; Thompson, Brose et al., 2012). Understanding the trophic role of invaders in food webs is therefore, essential for understanding the mechanisms driving their ecological impacts.

As trophic plasticity and omnivory are typical traits of successful invaders (Clavel, Julliard, & Devictor, 2011), their trophic ecology may differ across their invasive range in a complex manner (Cucherousset, Boulétreau et al., 2012; Tillberg, Holway, LeBrun, & Suarez, 2007). Omnivorous species (i.e. species that forage across trophic levels) are important for food web structure through their bridging of multiple trophic levels (Moore et al., 2012; Parkyn, Collier, & Hicks, 2001). Invasive omnivores can have disproportionate impacts on native communities via direct and indirect effects that cascade through the food web (e.g. Klose & Cooper, 2013; Moore et al., 2012). Indeed, some omnivorous species have the potential to act as detritivores, herbivores, predators or scavengers in different habitats, implying that habitat characteristics have a disproportionately strong influence on diet. In addition, the diet of conspecific omnivores can vary with body size (Bondar, Bottriell, Zeron, & Richardson, 2005; García-Berthou & Moreno-Amich, 2000), but this is usually explored through ontogenetic diet shifts, neglecting that individuals of the same developmental stage could potentially differ in their foraging strategy. An understanding of the mechanisms that drive omnivory will allow better assessment of the impacts of omnivorous invaders on recipient ecosystems (Griffen et al., 2012; Stenroth et al., 2008).

Environmental factors directly affect food production and population dynamics and are therefore key drivers of the trophic attributes of animal populations, with the trophic ecology of omnivores expected to vary with these environmental variables (Araújo, Bolnick, & Layman, 2011). Environmental factors that limit resource availability, such as high levels of competition or low productivity, are expected to reduce the level of diet variability within populations by decreasing the range of resources available to consumers (e.g. Jackson et al., 2012). Alternatively, evidence also suggests that intraspecific competition can increase population diet variability as individuals consume alternative prey items to maintain their energy requirements (e.g. Svanbäck & Bolnick, 2007). Predation pressure could also be a potential driver of the trophic ecology of individuals through its ability to modify the density and foraging strategy of consumers (e.g. Eklöv & Svanbäck, 2006). However, competitive and

predator-prey interactions are affected by habitat characteristics such as ecosystem size, which can influence resource quantity and encounter rates between individuals. For instance, small lakes often have proportionally larger inputs of allochthonous subsidies and higher availability of littoral resources (as food and habitat) than larger lakes, but their restricted size might result in relatively intense intra-specific interactions (Stenroth et al., 2008). In combination, this suggests that complex interactions between ecosystem size and other environmental factors could potentially play an important role in driving the trophic ecology of consumers.

Freshwater non-native crayfish are important and successful invaders, with some species now widely distributed across a number of continents (Capinha, Leung, & Anastacio, 2011). Invasive crayfish often dominate the invertebrate biomass of freshwater systems, leading to substantial impacts on native organisms and ecosystem functioning (Alp, Cucherousset, Buoro, & Lecerf, 2016; Lodge et al., 2012; Twardochleb, Olden, & Larson, 2013). Crayfish are opportunistic omnivores that rely on terrestrial plant litter, aquatic primary producers, and animal prey (Jackson et al., 2014). While their trophic ecology in their invasive range has been assessed in several ecosystems (e.g. Jackson et al., 2012, 2014; Olsson, Stenroth, Nyström, & Granéli, 2009; Rudnick & Resh, 2005), variation across their adult body size range is often overlooked, and their diet has rarely been characterised in relation to environmental determinants. Where it has, results are contradictory, with Stenroth et al. (2008) reporting that crayfish diet was influenced by productivity and not ecosystem size, whilst Larson, Olden, and Usio (2011) detected a significant effect of ecosystem size and the level of urbanisation around lake shorelines. Thus, there remains some uncertainty around how the trophic ecology of crayfish varies over gradients of interacting environmental conditions and body size.

Here, our aim was to investigate how the effects of environmental conditions on the trophic ecology of an invasive omnivore can be influenced by ecosystem size. Using red swamp crayfish *Procambarus clarkii* (Cambaridae) as the model species and stable-isotope analysis to analyse their trophic ecology, populations in 15 invaded waterbodies in southwest France were studied to assess their population trophic niche width, and trophic position and level of omnivory in each individual. We hypothesised that:

1. Individual trophic position will increase with increasing carapace length, given that larger individuals are more likely to be carnivorous (Stenroth et al., 2008). In addition, we predicted that size-related shift in trophic position would be affected by environmental parameters. For instance, we hypothesised that population abundance (and therefore potential intraspecific competition) would enhance this size-related shift in trophic position due to increasing cannibalism by largest individuals at high densities (Houghton, Wood, & Lambin, 2017).
2. Population niche width and the level of omnivory will increase with lake productivity, reflecting the wider diversity of available resources. This relationship will be less evident in larger lakes where littoral and allochthonous resources are restricted (Stenroth et al., 2008).

3. Population niche width and the level of omnivory will decrease as predation pressure and/or crayfish abundance increase due to reduced access to resources (Araújo et al., 2011; Jackson et al., 2012), and that this relationship will be less evident in larger lakes due to reduced encounter rates (and therefore, reduced competitive and predation pressures; Stenroth et al., 2008).

2 | MATERIALS AND METHODS

2.1 | Study area and model species

The sampled crayfish populations were in 15 lakes that provided gradients of abiotic (lake productivity and size) and biotic (predation pressure and population abundance) environmental conditions (Table 1). All lakes were located south of Toulouse (southwest France) in the Garonne floodplain and were created from gravel extraction. The model crayfish species, *P. clarkii*, is one of the most invasive crayfish species worldwide (Capinha et al., 2011; Grey & Jackson, 2012). Native to southern North America and parts of Central America, it is a large-bodied benthic omnivorous invertebrate that is highly flexible in diet choice (Gherardi, 2006; Grey & Jackson, 2012). The species was introduced in France in 1976 (Laurent, 1997) and has since spread throughout the country (Gherardi, 2006).

2.2 | Data collection

All lakes were sampled from mid-September to early October 2012 so that stable-isotope analysis would reflect their summer feeding

when crayfish reach maximal activity (Stenroth et al., 2005). In six lakes, *P. clarkii* coexisted with another invasive crayfish species, *Orconectes limosus*, with the latter representing only a small proportion of the crayfish population (number of individuals per trap per hour ranged from 0.005 to 0.049 versus the mean number of *P. clarkii* per trap per hour of 1.51 ± 0.43 SE) and thus was not included in the subsequent analyses. Sexually mature individuals of *P. clarkii* (hereafter referred to as crayfish) were sampled in the littoral area using traps baited with fishmeal pellets (trap size = 62 cm × 34 cm × 34 cm). Sexual maturity was visually checked by examining the development of external sexual characteristics (i.e. first and second pairs of abdominal appendages). Traps were set during the day (mean number 12.19 ± 1.64 SD) and night (mean number 4.25 ± 0.58 SD), to account for diel differences in trapping efficiency. Population abundance was estimated using catch per unit effort (CPUE) which was determined from numbers of crayfish caught in these traps over a 24-hr period ($\text{ind.trap}^{-1}.\text{hr}^{-1}$). Where required, additional individuals were collected for stable isotope analyses using seine and pond nets in the littoral habitat. Following their removal from traps and counting, crayfish were measured for carapace length using a calliper to the nearest 0.1 mm, euthanised using an overdose of eugenol (2-methoxy-4-(2-propenyl)-phenol), and then a subsample of muscle collected from the abdomen was taken for subsequent stable isotope analyses. In addition, putative food resources, including aquatic invertebrates, macrophytes and terrestrial leaves, were collected using a pond net and by hand. Periphyton was collected by gently brushing stones. For each studied lake, these resources were collected in three different

TABLE 1 Environmental characteristics of the fifteen studied lakes. Predation pressure was calculated as the total biomass (g) of fish predators captured using gillnetting and electrofishing. Density was based on CPUE which was determined from number of crayfish caught in traps over a 24-hr period ($\text{ind. trap}^{-1} \text{hr}^{-1}$). Productivity (TSI) was calculated using measures of Secchi disc, chlorophyll-a concentration and total phosphorus concentration. Lake size (ha) was calculated from aerial pictures and geographic information system (GIS) analyses

Lake	Longitude (E)	Latitude (N)	Predation (e.g. fish predators; g)	Density (CPUE crayfish; $\text{ind.trap}^{-1}.\text{hr}^{-1}$)	Lake productivity (Secchi disk depth; m)	Lake size (ha)
A	1.202	43.322	12,259	3.2	2.80	8.69
B	1.203	43.317	28,205	3.2	2.41	9.50
C	1.290	43.530	15,564	1.5	0.64	20.53
D	1.274	43.454	2,398	0.0	0.97	17.54
E	1.355	43.519	16,120	0.2	0.67	1.84
F	1.337	43.506	36,658	0.8	1.64	4.24
G	1.266	43.386	26,794	5.7	1.88	20.75
H	1.227	43.343	3,099	0.0	0.64	20.39
I	1.194	43.320	0	2.4	2.43	13.25
J	1.258	43.372	14,103	3.1	1.60	10.18
K	1.251	43.365	1,327	1.2	1.40	16.50
L	1.040	43.206	18,749	0.2	2.37	8.65
M	1.047	43.208	16,294	0.2	2.37	21.16
N	1.039	43.209	13,323	0.8	2.74	14.65
O	1.262	43.552	1,739	0.3	1.09	0.75

locations along the shoreline to account for spatial variability and were then stored on ice until processing in the laboratory (see details in Stable-isotope analysis).

The fish assemblages of the lakes were sampled using an identical protocol in each lake, with a combination of gillnetting and electrofishing by point abundance sampling (PASE; Cucherousset, Paillisson, Carpentier, Eybert, & Olden, 2006). These complementary approaches enabled capture of a wide range of fish species and life stages across different types of lake substrates and habitats (see details in Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2016). Gillnets were deployed in the pelagic ($n = 2$ gillnets; mesh size: 20 and 50 mm) and littoral ($n = 4-6$ depending upon lake size; mesh size: 12, 20, 30 and 60 mm) habitats in the morning for approximately 1 hr to limit mortality. Electrofishing (Deka 7000; Deka, Marsberg, Germany) was performed using point abundance sampling (PASE; mean = 30.50 ± 6.10 SD) using a boat working along the shoreline. The total number of point sampled per lake ranged from 20 to 42 (mean = 30.6 ± 5.9), depending upon lake size (i.e. less sampling points in smaller lakes) and, importantly, covered the entire lake perimeter.

All the sampled fish were then identified to species level, measured for fork length to the nearest mm and categorised into one of three life-stages (young-of-the-year, juvenile or adult), based on size distribution and literature on their size at maturity (see details in Zhao et al., 2016). The body mass of each fish was then calculated using length-weight relationships for each species (Zhao et al. unpublished data). Predation pressure was calculated as the total biomass (g) of fish predators; including juveniles and adults of all piscivorous species (*Anguilla anguilla*, *Esox lucius*, *Micropterus salmoides*, *Perca fluviatilis*, *Sander lucioperca* and *Silurus glanis*), and *Cyprinus carpio*, an omnivore and known predator of crayfish (Britton et al., 2007).

Finally, in September 2012, all lakes were visited to measure water transparency using Secchi disc depth (m), subsequently used as an estimate of lake productivity (Larson et al., 2011). Lake size (ha) was calculated from aerial picture and geographic system (GIS) analyses.

2.3 | Stable-isotope analysis

The carbon and nitrogen stable isotope ratios (^{13}C : ^{12}C and ^{15}N : ^{14}N) of crayfish ($n = 11-15$ individuals per lake; mean = 14.5 ± 1.06 SD; see Table SA1 in the Supporting Information) and their putative food resources were used to infer crayfish diet and calculate associated trophic metrics. Carbon ratios reflect consumer diet with typical enrichment of 0–1‰ whereas nitrogen ratios indicate trophic position and show greater enrichment of 2–4‰ from resource to consumer (McCutchan, Lewis, Kendall, & McGrath, 2003; Post, 2002). At each site, the putative food resources sampled consisted of mixed terrestrial leaves ($n = 3$), common aquatic macrophytes ($n = 3$), periphyton ($n = 3$), molluscs (Corbiculidae and Lymnaeidae; $n = 2-3$ where present), arthropods (Chironomidae, Ephemeroptera, Assellidae and Sialidae; $n = 5-10$) and young-of-the-year or juveniles of common fish species (except lake I, which had no fish; *Lepomis*

gibbosus, *Micropterus salmoides* or *Rutilus rutilus*; $n = 3$ in all cases). Although it is unlikely that the crayfish were actively catching fish, they will readily scavenge dead fish and there is also evidence that they prey upon juveniles and eggs (Reynolds, 2011). Isotope analyses for molluscs and fish were performed on the soft muscle tissue and fin samples, respectively.

Once in the laboratory, periphyton samples were frozen using lyophiliser while the other samples were oven dried (60°C for 48 hr). All samples were then ground to a fine powder and analysed for stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) at the Cornell Isotope Laboratory (COIL, Ithaca, NY). Carbon and nitrogen stable isotope ratios were expressed relative to standards as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. As the C:N ratio of molluscs and arthropods were high (4.00 ± 0.05 SD and 4.79 ± 0.09 SD respectively), their stable isotope values were lipid corrected before subsequent analyses (following Post et al., 2007).

2.4 | Data analyses

The food resources that were sampled were then categorised into four groups of isotopic and taxonomic similarity (Figure SA1): (1) leaf litter, (2) primary producers (mixture composed of macrophyte and periphyton), (3) invertebrates (mixture composed of molluscs and arthropods) and (4) fish. These groups were not confounded by baseline variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and, therefore we were able to compare crayfish diet between lakes. Moreover, to ensure comparison of diet variability between populations, stable isotope values were corrected using resource baseline values (following Jackson & Britton, 2014). For $\delta^{13}\text{C}$, values were converted to a corrected carbon isotope ratio ($\delta^{13}\text{C}_{\text{cor}}$) adjusted for between-population variation using the following equation:

$$\delta^{13}\text{C}_{\text{cor}} = (\delta^{13}\text{C}_c - \delta^{13}\text{C}_{\text{litter}}) / (\delta^{13}\text{C}_{\text{primprod}} - \delta^{13}\text{C}_{\text{litter}})$$

where $\delta^{13}\text{C}_c$ is the carbon isotope values of crayfish, and $\delta^{13}\text{C}_{\text{litter}}$ and $\delta^{13}\text{C}_{\text{primprod}}$ are the mean stable isotope values of leaf litter and primary producers for the specific lake from which the crayfish were sampled (Figure SA1). Likewise, the trophic position of each crayfish (TP_c) was calculated using the following equation:

$$\text{TP}_c = 2 + (\delta^{15}\text{N}_c - \delta^{15}\text{N}_{\text{inv}}) / 3.8$$

where $\delta^{15}\text{N}_c$ is the isotopic value of crayfish, $\delta^{15}\text{N}_{\text{inv}}$ is the isotopic value of primary consumers (average $\delta^{15}\text{N}$ of invertebrates), 3.8 is the fractionation between trophic levels (the average of the below studies) and 2 is the trophic position of the baseline organism (Olsson et al., 2009; Post, 2002).

These corrected isotope values were then used to calculate the isotopic niche of each population using SIBER in the SIAR package (Jackson, Inger, Parnell, & Bearhop, 2011; Jackson et al., 2012; R Development Core Team, 2015). Bayesian standard ellipse areas (SEA_b) were calculated as a measure of the isotopic niche width using 10,000 replicates. This measure of niche width is based on the distribution of individuals in the isotopic space and is calculated from the variance and covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. As it is based on a Bayesian framework, studies on simulated data have indicated

that a sample size of 15 individuals per population is sufficient for calculating trophic niche width using SEA (Brind'Amour & Dubois, 2013; Jackson et al., 2011).

We quantified the relative dietary contribution (%) of each resource to the diet of individual crayfish using the Bayesian mixing model SIAR in R (Parnell, Inger, Bearhop, & Jackson, 2010; R Development Core Team, 2015). Isotope mixing models were run with the unconverted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of resource groups (mean and standard deviation values) and individual crayfish. Fractionation factors between consumers and resources were calculated using data from crustacean feeding experiments in the literature (Carolan, Mazumder, Dimovski, Diocares, & Twining, 2012; Rudnick & Resh, 2005; Suring & Wing, 2009; Yokoyama et al., 2005); $1.32 \pm 1.53\text{‰}$ and $2.04 \pm 0.11\text{‰}$ for $\delta^{13}\text{C}$, and $3.40 \pm 2.23\text{‰}$ and $4.24 \pm 0.99\text{‰}$ for $\delta^{15}\text{N}$ for animal and plant matter respectively. The mean estimated proportional contribution of each resource to the diet of each individual was then used to calculate an index of individual omnivory (IO) using the following equation:

$$\text{IO}_c = \sum (\text{Proportion}_r) \times (\text{TP}_r - (\text{TP}_c - 1))^2$$

where r is each resource group, c is an individual crayfish and TP is trophic position (Christensen & Walters, 2004). The trophic position of resources (TP_r) was assigned as 1 for primary producers, 2 for invertebrates and 3 for fish. A high value of IO indicates that the consumer feeds on prey groups characterised by multiple trophic levels.

2.5 | Statistical analyses

Linear and linear mixed effects models (package lme4 v.1.1.10; Bates, Maechler, Bolker, & Walker, 2015) were used to examine the effects of lake characteristics (productivity, population abundance, predation and lake size) on population trophic niche width (SEA_b) and individual diet metrics (trophic position [Model 1] and index of omnivory), respectively. The variance inflation factor (VIF) was applied and absence of collinearity between explanatory variables was observed ($\text{VIF} < 10$; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Explanatory variables were measured on different scales and thus were standardised to have a mean of zero and a standard deviation of one. Linear mixed effects models included lake identity as a random factor and crayfish carapace length as a covariate. Population abundance was square-root transformed to ensure more even dispersion between lakes. All full models were initially run with two-way interactions

between both abiotic and biotic factors and lake size. A linear model [Model 2] was also used to test the potential effects of environmental parameters on size-related shift in trophic position. This model was initially run with two-way interaction between carapace length and environmental parameters. The best models were selected using Akaike's information criterion using the dredge function in the MuMIn R package v.1.15.1 which performed automated model selection (Barton, 2015). Then a model averaging approach, the *importance* function in the MuMIn R package, was used across all models with $\Delta\text{AIC}_c < 2$ to assess the relative importance of each predictor variable calculated based on AIC-weights (Burnham & Andersson, 2002). Importance ranged from 0 (parameter not given explanatory weight) to 1 (parameter in all top models). Assumptions of linearity and homogeneity of variances on residuals from all models were checked visually and both trophic position and omnivory index were \log_{10} transformed. Analyses of the Cook's distance (D) plot revealed that lakes F and I had larger D values than the rest when testing for an effect of lake variables on SEA_b (Bollen & Jackman, 1990). Consequently, the isotope data from these lakes could be considered as too influential with the potential to skew the results, therefore we removed these lakes from the niche width analyses. For each linear mixed effect model, both the marginal (R^2_M , effect of the fixed variables) and conditional (R^2_C , effect of the fixed and random variables) R^2 were calculated (Nakagawa & Schielzeth, 2013). All statistical analyses were performed using R v.3.2.2 (R Development Core Team 2015).

3 | RESULTS

The trophic niche width (SEA_b) of crayfish varied across the 15 lakes, ranging between 0.44 and 0.72‰^2 (mean = 0.52 ± 0.08 SD; Figure SA2). Analyses performed on 13 lakes (cf. Statistical analyses) revealed that SEA_b was significantly affected by population abundance ($z = 2.11$, $p = .035$; Table 2 and SB1). Specifically, population niche width decreased with increasing abundance (Figure 1).

The trophic position of individual crayfish (mean = 2.49 ± 0.48 SD) was significantly and positively affected by carapace length ($z = 2.38$, $p = .017$; Figure 2a, Table 3). However, analyses performed within each lake revealed that this relationship was only found in lakes I and M (Figure SB3). In addition, the shift in trophic position with carapace length was significantly affected by lake productivity ($z = 2.00$, $p = .045$; Table 3 and SB2). Specifically, trophic

TABLE 2 Summary results after model averaging of the final linear model with biotic (predation [g. fish predators], density [CPUE crayfish; $\text{ind.trap}^{-1}.\text{hr}^{-1}$; square-root transformed],) and abiotic (lake productivity [Secchi disk depth; m], lake size [ha]) parameters as factors affecting crayfish population niche width (SEA_b ; $n = 13$, see details in Statistical analyses). All explanatory variables are standardised. The relative importance value (RI) of each explanatory variable and the 95% CI are presented. Significant p -values are highlighted in bold

Response variable	Predictor	Estimate (SE)	z	p	95% CI	RI
Trophic niche width	Intercept	0.55 (0.04)	12.04	<.001	0.459, 0.637	NA
	Density	-0.08 (0.03)	2.11	.035	-0.155, -0.006	0.70
	Predation	0.03 (0.02)	1.81	.071	-0.003, 0.068	0.39
	Lake productivity	-0.03 (0.01)	1.62	.105	-0.055, 0.005	0.29

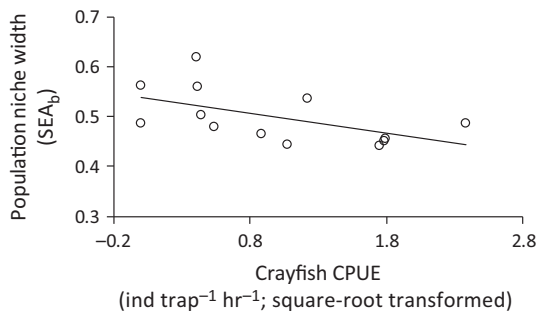


FIGURE 1 Relationship between density (crayfish CPUE; ind.trap⁻¹.hr⁻¹; square-root transformed) and crayfish population niche width (SEA_B), $n = 13$ (see details in Statistical analyses)

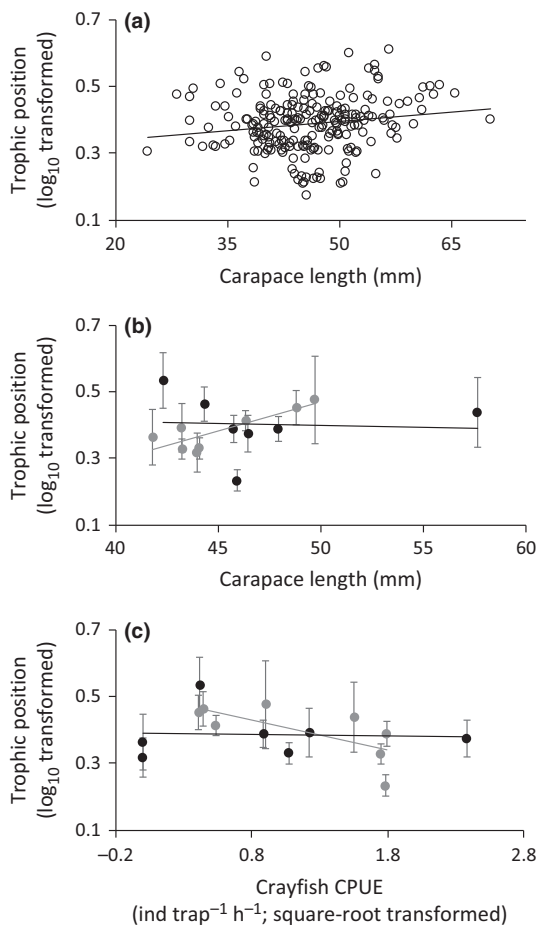


FIGURE 2 (a) Relationship between carapace length (mm) and trophic position (\log_{10} transformed). (b) Effect of lake productivity (Secchi disk depth; m) on size-related shift in trophic position (\log_{10} transformed). Based on the median threshold, grey and black circles (mean \pm SE) represent lake with low ($n = 8$) and high ($n = 7$) productivity, respectively. (c) Lake-size (ha) dependent effect of density (crayfish CPUE; ind.trap⁻¹.h⁻¹; square-root transformed) on individual trophic position (\log_{10} transformed). Based on the median threshold, grey and black circles (mean \pm SE) represent small ($n = 8$) and large lakes ($n = 7$), respectively. $n = 218$

position increased with carapace length in lakes with low productivity while it decreased with carapace length in highly productive lakes (Figure 2b). Individual trophic position was also significantly and

negatively affected by crayfish abundance ($z = 2.10$, $p = .036$; Table 3), with this interaction varying significantly with lake size (interaction term: $z = 1.96$, $p = .05$; Table 3 and SB2), although this interaction had a low relative importance (RI = 0.33; Table 3). Specifically, these results indicated that the trophic position of crayfish decreased with increasing abundance in small lakes but did not change with abundance in large lakes (Figure 2c).

Crayfish omnivory varied over a 10-fold range (mean = 0.95 ± 0.41 SD) but was not significantly affected by carapace length ($p = .09$; Table 3) or any environmental conditions ($p > .14$; Table 3 and SB2).

4 | DISCUSSION

Understanding the drivers of the diet of invasive species can be an effective tool in predicting their impacts on recipient ecosystems (e.g. Alexander, Dick, Weyl, Robinson, & Richardson, 2014; Jackson, Ruiz-Navarro, & Britton, 2015). Here, the trophic ecology of a global omnivorous invader was influenced by both individual and environmental characteristics. Specifically, population abundance was an important driver of crayfish trophic ecology by influencing both population niche width and the trophic position of individuals. The effect of crayfish abundance on trophic position also varied with lake size, and trophic position increased with crayfish size, but only in lakes of low productivity.

Our results revealed that crayfish population niche width decreased with increasing population abundance, which may be related to increased intraspecific competition. This could be due to a decrease in between-individual variation, or a decrease in individual specialisation (Araújo et al., 2011; Bolnick et al., 2003). Individual specialisation is a widespread occurrence in natural populations (Araújo et al., 2011), but few studies have quantified its importance, particularly in invasive species where it may play a central role in the persistence of invasive populations by opening niche opportunities (Cucherousset, Boulêtreau et al., 2012; Shea & Chesson, 2002). Regardless of the mechanism, our results indicated that the crayfish foraged on a diverse range of resources when their abundance was low, but converged on the same resources when abundance was high. This resulted in a relatively uniform diet and a smaller isotopic niche in lakes with high abundances. This may be due to increased competition for resources when they become less available as abundance increased (Araújo et al., 2011; Jackson et al., 2012). However, it is important to note that we did not directly measure resource availability and instead assumed that it was reduced when lake productivity was low, and/or potential competition was high.

Contrasting theories suggest that competition can either (1) decrease population niche width by decreasing the range of resources available to consumers (e.g. Jackson et al., 2012); or (2) increase population niche width as individuals consume alternative prey items to maintain their energy requirements (e.g. Svanbäck & Bolnick, 2007). Our results appear to support the first theory, especially since it was found that individual trophic position also

TABLE 3 Summary results after model averaging of the linear mixed effects models with environmental characteristics (predation [g. fish predators], density [CPUE crayfish; ind.trap⁻¹.hr⁻¹; square-root transformed], productivity [Secchi disk depth; m] and lake size [ha]) and carapace length (mm) as factors affecting individual crayfish trophic niche (trophic position [\log_{10} transformed] and index of omnivory [\log_{10} transformed]; $n = 218$). Lake identity was included as a random effect. All explanatory variables are standardised. The relative importance value (RI) of each explanatory variable and the 95% CI are presented. Significant p -values are highlighted in bold. Marginal (R^2_M , effect of the fixed effects) and conditional (R^2_C , effect of the fixed and random effects) R^2 are also provided

Response variables	Predictor	Estimate (SE)	z	p	RI	95% CI	R^2_M – R^2_C
Trophic position ^a	Intercept	0.45 (0.04)	10.81	<.001	NA	3.70 e ⁻⁰¹ , 0.53	0.39–0.73
	Carapace length	0.01 (0.003)	2.38	.017	1	1.43 e ⁻⁰³ , 0.01	
	Lake productivity	0.03 (0.02)	1.63	.102	0.63	–5.76 e ⁻⁰³ , 0.06	
	Density	–0.08 (0.04)	2.10	.036	0.88	–1.61 e ⁻⁰¹ , –0.01	
	Lake size	–0.03 (0.04)	0.92	.357	0.43	–1.05 e ⁻⁰¹ , 0.04	
	Density × lake size	0.07 (0.03)	1.96	.050	0.33	6.05, 0.13	
	Lake productivity × lake size	0.03 (0.02)	1.38	.167	0.19	–1.06 e ⁻⁰² , 0.06	
	Predation	0.02 (0.02)	0.94	.347	0.24	1.73 e ⁻⁰² , 0.05	
Trophic position ^b	Intercept	0.45 (0.04)	12.78	<.001	NA	0.38, 0.52	0.24–0.74
	Carapace length	0.01 (0.01)	0.95	.341	1	–0.01, 0.02	
	Lake productivity	0.02 (0.02)	1.33	.184	0.75	–0.01, 0.06	
	Density	–0.07 (0.04)	2.03	.043	1	–0.15, –0.002	
	Carapace length × lake productivity	0.01 (0.003)	2.00	.045	0.75	0.0001, 0.01	
	Predation	0.02 (0.02)	1.13	.259	0.18	–0.01, 0.05	
	Carapace length × density	0.01 (0.01)	1.19	.232	0.30	–0.01, 0.02	
	Lake size	–0.01 (0.02)	0.42	.677	0.11	–0.04, 0.02	
Index of omnivory	Intercept	0.05 (0.05)	1.19	.236	NA	–0.14, 0.04	0.10–0.68
	Carapace length	0.01 (0.01)	1.69	.092	0.72	–0.002, 0.03	
	Lake size	0.05 (0.03)	1.48	.140	0.50	–0.02, 0.12	
	Lake productivity	–0.02 (0.04)	0.51	.610	0.16	–0.09, 0.05	
	Desnsity	–0.03 (0.07)	0.46	.644	0.16	–0.18, 0.11	

^aModel 1 and ^bModel 2, see details in Statistical analyses.

decreased with crayfish population abundance (as a measure of competition). As abundance increases, changes in crayfish behaviour to reduce the risk of antagonistic interactions with conspecifics might cause a shift in habitat use or time spent foraging (Svanbäck & Bolnick, 2007), causing individuals to consume resources at lower trophic levels. However, a recent study suggested that cannibalism in crayfish increases with population density (Houghton et al., 2017). The negative effect of population abundance on trophic position was only evident in smaller lakes which might be linked to an increase in encounter rates between conspecific individuals, since these are likely to increase in smaller areas if abundance remains the same. Our results suggest that individual crayfish in small lakes consume less animal resources when crayfish abundance (and therefore, potential competition) is high. In larger lakes, this relationship is absent which might be due to a lower chance of encounters between conspecifics and/or increases in resource availability.

Ontogenetic dietary shifts have been described in many crayfish species where juvenile crayfish preferentially feed on aquatic invertebrates and adults mainly feed on vegetal detritus (e.g. Guan & Wiles, 1998). This ontogenetic shift is particularly associated with differences in the nutrient requirements for growth and the inability

of larger crayfish to forage on fast moving aquatic invertebrates (Momot, 1995; Nyström, Brönmark, & Graneli, 1999). Here, however, it was detected that the trophic position of sexually mature crayfish increased with their carapace length in lakes of low productivity, suggesting that the invasive crayfish incorporated more animal material in their diet as they grew larger. Larger individuals are likely to be more competitive for access to nutrient rich animal prey, even when their size difference with a competitor is small (e.g. Correia, 2002). This trait may be specific to invasive crayfish, which tend to be both more flexible in diet choice and more predatory than their native counterparts (Grey & Jackson, 2012; Olsson et al., 2009; but see Lagrue, Podgorniak, Lecerf, & Bollache, 2014). Stenroth et al. (2008) revealed that the trophic position of invasive signal crayfish was higher in eutrophic lakes, but we detected no direct influence of lake productivity. This is contrary to the productivity hypothesis that suggests that food chain length and therefore, the trophic level of consumers, increases with increasing ecosystem productivity (Post, 2002; Takimoto & Post, 2013). In contrast, we found that the positive relationship between trophic position and body size was only evident in lakes of low productivity. In highly productive lakes the effect of body size was reversed, which might be a result of increased resource choice at lower trophic levels.

Variation in crayfish diet across gradients of lake characteristics is likely to influence the effect of crayfish on community structure and ecosystem functioning. For example, when crayfish occupy lower trophic levels and consume more plant material they may increase decomposition rates and decrease macrophyte cover (Alp et al., 2016; Jackson et al., 2014; Twardochleb et al., 2013). If crayfish become more important predators then they might affect invertebrate community structure and, potentially, modify the intensity of trophic cascades that subsequently change decomposition rates and macrophyte cover (Alp et al., 2016; Jackson et al., 2014; Lagrue et al., 2014). Therefore, future studies should focus on aspects of ecosystem functioning because invasive crayfish have the potential to modify numerous trophic interactions. Importantly, in previous studies, impacts were generally associated with trophic differentiation between crayfish species (Jackson et al., 2014; Twardochleb et al., 2013), whereas here we argue that strong differences in trophic ecology can also be found between populations of a single species, and this may drive context-dependent impacts on recipient ecosystems. Consequently, it is also recommended that the relative importance of intra- versus inter-specific variability would be investigated to determine the ecological effects of invasive consumers on ecosystems (Palkovacs, Fryxell, Turley, & Post, 2015).

Increasingly, evidence indicates that individuals within species differ in their diet and therefore their functional role, notably through variations in body size (Miller & Rudolf, 2011; Sato & Watanabe, 2013). This intraspecific variability can exceed variability between species and result in changes in the functioning of ecosystems (Rudolf & Rasmussen, 2013a,b). Therefore, an understanding of intraspecific variability in resource use of invaders, and how this varies across the invaded landscape, is essential to measure impact and best direct management practices. We found that the trophic ecology of an invasive crayfish varied with individual (body size), population (abundance) and environmental (lake size) traits. Variation in crayfish diet will influence which native species in the food web are negatively affected by the invasion, and ecosystem processes such as leaf litter decomposition. Furthermore, these variations in trophic ecology may influence invasion success and future invasion spread throughout the landscape. Future research on invasive species should therefore consider the complex and reciprocal relationships between invasion success and impact, trophic ecology, and variations in environmental conditions; all which influence, and are influenced by, one another.

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