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Between lake variation in the trophic ecology of an invasive crayfish

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5 Jackson, M.C.^{1,2,3*}, Evangelista, C.^{4,5*}†, Zhao, T.⁴, Lecerf, A.⁵, Britton, J.R.¹ and Cucherousset,
6 J.⁴ * joint first author

7

8 1. School of Applied Sciences, Bournemouth University, Fern Barrow, Poole, Dorset, BH12

9 5BB, UK

10 2. Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst

11 Road, Ascot, Berkshire, SL5 7PY, UK

12 3. Centre for Invasion Biology, Department of Zoology and Entomology, University of

13 Pretoria, Hatfield, Gauteng, 0028, South Africa

14 4. CNRS, Université Toulouse III Paul Sabatier, ENFA, UMR 5174 EDB (Laboratoire

15 Evolution & Diversité Biologique), 118 route de Narbonne, Toulouse F-31062, France

16 5. EcoLab (Laboratoire d'écologie fonctionnelle et environnement), Univ. de Toulouse,

17 CNRS, INPT, UPS, Toulouse, France

18 † Present address: Department of Biosciences, Centre for Ecological and Evolutionary

19 Synthesis (CEES), University of Oslo, Oslo, Norway

20

21 **Running head:** Drivers of invasive crayfish diet

22 **Corresponding author email:** m.jackson@ic.ac.uk

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24 **Summary**

25

26 1. The trophic ecology of invasive species has important implications for their impacts on
27 recipient ecosystems, with omnivorous invaders potentially affecting native species and
28 processes over multiple trophic levels. The trophic ecology of invaders might be affected by both
29 their body size and the characteristics of their habitat due to variation in energy requirements and
30 resource availability.

31 2. Here, using stable isotope analysis, we investigated the trophic ecology of the invasive
32 crayfish *Procambarus clarkii* in 15 populations in Southwest France over a gradient of
33 individual (crayfish body size), population (crayfish abundance) and ecosystem (lake size,
34 productivity and predation pressure) characteristics. We predicted that population niche width,
35 level of omnivory and trophic position of individuals would change with abiotic and biotic
36 conditions but that these relationships would vary with lake size.

37 3. The trophic position of individual crayfish increased with body size in lakes with low
38 productivity, but decreased with body size in more productive lakes. As crayfish abundance
39 increased (and therefore potential intraspecific competition), individual trophic position and
40 population niche width decreased. This was most apparent in smaller lakes, suggesting it related
41 to an increase in encounter rates with conspecifics.

42 4. Body size, population abundance, lake size and lake productivity influenced the trophic
43 ecology of invasive crayfish, which can affect their interactions with native species. Our results
44 demonstrated that the trophic ecology of invasive species can be variable across invaded
45 landscapes, with implications for their ecological impacts on native communities. This

46 emphasises the importance of characterising the diet of invasive species across their non-native
47 range and environmental gradients to better predict and manage their impacts.

48

49 **Introduction**

50

51 The trophic ecology of invasive species has strong implications for their establishment
52 success, their invasive distribution, and their impacts on native organisms and recipient
53 ecosystems (Zhang *et al.* 2010; Griffen *et al.* 2012; Dick *et al.* 2013). The addition of invasive
54 species to an established food web creates novel trophic links and modifies energy pathways,
55 potentially resulting in altered food web structure (Vander Zanden, Casselman & Rasmussen
56 1999; Woodward *et al.* 2008; Cucherousset, Blanchet & Olden 2012). This is important, as food
57 web structure is a fundamental ecological attribute that underlies species diversity, mediates
58 community dynamics, and influences ecosystem processes (Thompson *et al.* 2012; Thompson,
59 Dunne & Woodward 2012). Understanding the trophic role of invaders in food webs is therefore,
60 essential for understanding the mechanisms driving their ecological impacts.

61 As trophic plasticity and omnivory are typical traits of successful invaders (Clavel,
62 Julliard & Devictor 2011), their trophic ecology may differ across their invasive range in a
63 complex manner (Tillberg *et al.* 2007; Cucherousset *et al.* 2012). Omnivorous species (i.e.
64 species that forage across trophic levels) are important for food web structure through their
65 bridging of multiple trophic levels (Parkyn, Collier & Hicks 2001; Moore *et al.* 2012). Invasive
66 omnivores can have disproportionate impacts on native communities via direct and indirect
67 effects that cascade across trophic levels (e.g. Moore *et al.* 2012; Klose & Cooper 2013). Indeed,
68 some omnivorous species have the potential to act as detritivores, herbivores, predators or
69 scavengers in different habitats, implying that habitat characteristics have a disproportionately
70 strong influence on diet. In addition, the diet of conspecific omnivores can vary with body size
71 (García-Berthou & Moreno-Amich 2000; Bondar *et al.* 2005), but this is usually explored

72 through ontogenetic diet shifts, neglecting that individuals of the same developmental stage
73 could potentially differ in their foraging strategy. An understanding of the mechanisms that drive
74 omnivory will allow better assessment of the impacts of omnivorous invaders on recipient
75 ecosystems (Stenroth *et al.* 2008; Griffen *et al.* 2012).

76 Environmental factors directly affect food production and population dynamics and are
77 therefore key drivers of the trophic attributes of animal populations, with the trophic ecology of
78 omnivores expected to vary with these environmental variables (Araújo, Bolnick & Layman
79 2011). Environmental factors that limit resource availability, such as high levels of competition
80 or low productivity, are expected to reduce the level of diet variability within populations by
81 decreasing the range of resources available to consumers (e.g. Jackson *et al.* 2012).
82 Alternatively, evidence also suggests that intraspecific competition can increase population diet
83 variability as individuals consume alternative prey items to maintain their energy requirements
84 (e.g. Svanbäck & Bolnick 2007). Predation pressure could also be a potential driver of the
85 trophic ecology of individuals through its ability to modify the density and foraging strategy of
86 consumers (e.g. Eklöv & Svanbäck 2006). However, competitive and predator-prey interactions
87 are affected by habitat characteristics such as ecosystem size, which can influence resource
88 quantity and encounter rates between individuals. For instance, small lakes often have
89 proportionally larger inputs of allochthonous subsidies and higher availability of littoral
90 resources (as food and habitat) than larger lakes, but their restricted size might result in relatively
91 intense intra-specific interactions (Stenroth *et al.* 2008). In combination, this suggests that
92 complex interactions between ecosystem size and other environmental factors could potentially
93 play an important role in driving the trophic ecology of consumers.

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

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

115 (1) Individual trophic position will increase with increasing carapace length, given that larger
116 individuals are more likely to be carnivorous (Stenroth *et al.* 2008). In addition, we predicted that

117 size-related shift in trophic position would be affected by environmental parameters. For
118 instance, we hypothesised that population abundance (and therefore potential intraspecific
119 competition) would enhance this size-related shift in trophic position due to increasing
120 cannibalism by largest individuals at high densities (Houghton *et al.* 2017).

121 (2) Population niche width and the level of omnivory will increase with lake productivity,
122 reflecting the wider diversity of available resources. This relationship will be less evident in
123 larger lakes where littoral and allochthonous resources are restricted (Stenroth *et al.* 2008).

124 (3) Population niche width and the level of omnivory will decrease as predation pressure and/or
125 crayfish abundance increase due to reduced access to resources (Araújo, Bolnick & Layman
126 2011; Jackson *et al.* 2012), and that this relationship will be less evident in larger lakes due to
127 reduced encounter rates (and therefore, reduced competitive and predation pressures; Stenroth *et*
128 *al.* 2008).

129

130 **Materials and Methods**

131

132 *Study area and model species*

133 The sampled crayfish populations were in 15 lakes that provided gradients of abiotic
134 (lake productivity and size) and biotic (predation pressure and population abundance)
135 environmental conditions (Table 1). All lakes were located south of Toulouse (southwest France)
136 in the Garonne floodplain and were created from gravel extraction. The model crayfish species,
137 *P. clarkii*, is one of the most invasive crayfish species worldwide (Capinha, Leung & Anastacio
138 2011; Grey & Jackson 2012). Native to southern North America and parts of Central America, it
139 is a large-bodied benthic omnivorous invertebrate that is highly flexible in diet choice (Gherardi

140 2006; Grey & Jackson 2012). The species was introduced in France in 1976 (Laurent 1997) and
141 has since spread throughout the country (Gherardi 2006).

142

143 *Data collection*

144 All lakes were sampled from mid-September to early October 2012 so that stable isotope
145 analysis would reflect their summer feeding when crayfish reach maximal activity (Stenroth *et*
146 *al.* 2005). In six lakes, *P. clarkii* coexisted with another invasive crayfish species, *Orconectes*
147 *limosus*, with the latter representing only a small proportion of the crayfish population (number
148 of individuals per trap per hour ranged from 0.005 to 0.049 versus the mean number of *P. clarkii*
149 per trap per hour of 1.51 ± 0.43 SE) and thus was not included in the subsequent analyses.
150 Sexually mature individuals of *P. clarkii* (hereafter referred to as crayfish) were sampled in the
151 littoral area using traps baited with fishmeal pellets (trap size = 62 cm \times 34 cm \times 34 cm). Sexual
152 maturity was visually checked by examining the development of external sexual characteristics
153 (i.e. first and second pairs of abdominal appendages). Traps were set during the day (mean
154 number 12.19 ± 1.64 SD) and night (mean number 4.25 ± 0.58 SD), to account for diel
155 differences in trapping efficiency. Population abundance was estimated using catch per unit
156 effort (CPUE) which was determined from numbers of crayfish caught in these traps over a 24-
157 hour period ($\text{ind.trap}^{-1}.\text{h}^{-1}$). Where required, additional individuals were collected for stable
158 isotope analyses using seine and pond nets in the littoral habitat. Following their removal from
159 traps and counting, crayfish were measured for carapace length using a calliper to the nearest 0.1
160 mm, euthanized using an overdose of eugenol (2-methoxy-4-(2-propenyl)-phenol), and then a
161 subsample of muscle collected from the abdomen was taken for subsequent stable isotope
162 analyses. In addition, putative food resources, including aquatic invertebrates, macrophytes and

163 terrestrial leaves, were collected using a pond net and by hand. Periphyton was collected by
164 gently brushing stones. For each studied lake, these resources were collected in three different
165 locations along the shoreline to account for spatial variability and were then stored on ice until
166 processing in the laboratory (see details in *Stable isotope analysis*).

167 The fish assemblages of the lakes were sampled using an identical protocol in each lake,
168 with a combination of gillnetting and electrofishing by point abundance sampling (PASE;
169 Cucherousset *et al.* 2006). These complementary approaches enabled capture of a wide range of
170 fish species and life stages across different types of lake substrates and habitats (see details in
171 Zhao *et al.* 2016). Gillnets were deployed in the pelagic (n = 2 gillnets; mesh size: 20 and 50
172 mm) and littoral (n = 4 to 6 depending upon lake size; mesh size: 12, 20, 30 and 60 mm) habitats
173 in the morning for approximately 1 hour to limit mortality. Electrofishing (Deka 7000; Deka,
174 Marsberg, Germany) was performed using point abundance sampling (PASE; mean = $30.50 \pm$
175 6.10 SD) using a boat working along the shoreline. The total number of point sampled per lake
176 ranged from 20 to 42 (mean = 30.6 ± 5.9), depending upon lake size (i.e. less sampling points in
177 smaller lakes) and, importantly, covered the entire lake perimeter.

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

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

190

191 *Stable isotope analysis*

192 The carbon and nitrogen stable isotope ratios ($^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$) of crayfish ($n = 11$ to
193 15 individuals per lake; mean = 14.5 ± 1.06 SD; see Table A1 in the Supporting Information)
194 and their putative food resources were used to infer crayfish diet and calculate associated trophic
195 metrics. Carbon ratios reflect consumer diet with typical enrichment of 0-1‰ whereas nitrogen
196 ratios indicate trophic position and show greater enrichment of 2-4‰ from resource to consumer
197 (Post 2002; McCutchan Jr *et al.* 2003). At each site, the putative food resources sampled
198 consisted of mixed terrestrial leaves ($n = 3$), common aquatic macrophytes ($n = 3$), periphyton (n
199 = 3), molluscs (Corbiculidae and Lymneidae; $n = 2-3$ where present), arthropods
200 (Chironomidae, Ephemeroptera, Assellidae and Sialidae; $n = 5-10$) and young-of-the-year or
201 juveniles of common fish species (except lake 10, which had no fish; *Lepomis gibbosus* at lakes
202 1, 7, 8 and 12; *Micropterus salmoides* at lake 15; and *Rutilus rutilus* at all other sites; $n = 3$ in all
203 cases). Although it is unlikely that the crayfish were actively catching fish, they will readily
204 scavenge dead fish and there is also evidence that they prey upon juveniles and eggs (Reynolds
205 2011). Isotope analyses for molluscs and fish were performed on the soft muscle tissue and fin
206 sample, respectively.

207 Once in the laboratory, periphyton samples were frozen using lyophilizer while the other
208 samples were oven dried (60 °C for 48 h). All samples were then ground to a fine powder and

209 analyzed for stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) at the Cornell Isotope Laboratory (COIL,
210 Ithaca, NY). Carbon and nitrogen stable isotope ratios were expressed relative to standards as
211 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. As the C:N ratio of molluscs and arthropods were high (4.00 ± 0.05
212 SD and 4.79 ± 0.09 SD, respectively), their stable isotope values were lipid corrected before
213 subsequent analyses (following Post *et al.* 2007).

214

215 *Data analyses*

216 The food resources that were sampled were then categorized into four groups of isotopic
217 and taxonomic similarity (Figure A1): (1) leaf litter, (2) primary producers (mixture composed of
218 macrophyte and periphyton), (3) invertebrates (mixture composed of molluscs and arthropods)
219 and (4) fish. These groups were not confounded by baseline variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and,
220 therefore we were able to compare crayfish diet between lakes. Moreover, to ensure comparison
221 of diet variability between populations, stable isotope values were corrected using resource
222 baseline values (following Jackson & Britton 2014). For $\delta^{13}\text{C}$, values were converted to a
223 corrected carbon isotope ratio ($\delta^{13}\text{C}_{\text{cor}}$) adjusted for between-population variation using the
224 following equation:

$$225 \quad \delta^{13}\text{C}_{\text{cor}} = (\delta^{13}\text{C}_c - \delta^{13}\text{C}_{\text{litter}}) / (\delta^{13}\text{C}_{\text{primprod}} - \delta^{13}\text{C}_{\text{litter}})$$

226 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
227 stable isotope values of leaf litter and primary producers for the specific lake from which the
228 crayfish were sampled (Figure A1). Likewise, the trophic position of each crayfish (TP_c) was
229 calculated using the following equation:

$$230 \quad \text{TP}_c = 2 + (\delta^{15}\text{N}_c - \delta^{15}\text{N}_{\text{inv}}) / 3.8$$

231 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
232 (average $\delta^{15}\text{N}$ of invertebrates), 3.8 is the fractionation between trophic levels (the average of the
233 below studies, see details further) and 2 is the trophic position of the baseline organism (Post
234 2002; Olsson *et al.* 2009).

235 These corrected isotope values were then used to calculate the isotopic niche of each
236 population using SIBER in the SIAR package (R Core Team 2015; Jackson *et al.* 2011; Jackson
237 *et al.* 2012). Bayesian standard ellipse areas (SEA_b) were calculated as a measure of the isotopic
238 niche width using 10,000 replicates. This measure of niche width is based on the distribution of
239 individuals in the isotopic space and is calculated from the variance and covariance of $\delta^{13}\text{C}$ and
240 $\delta^{15}\text{N}$ values. As it is based on a Bayesian framework, studies on simulated data have indicated
241 that a sample size of 15 individuals per population is sufficient for calculating trophic niche
242 width using SEA (Jackson *et al.* 2011; Brind'Armour & Dubois 2013).

243 We quantified the relative dietary contribution (%) of each resource to the diet of
244 individual crayfish using the Bayesian mixing model SIAR in R (R Core Team 2015; Parnell *et*
245 *al.* 2010). Isotope mixing models were run with the unconverted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of
246 resource groups (mean and standard deviation values) and individual crayfish. Fractionation
247 factors between consumers and resources were calculated using data from crustacean feeding
248 experiments in the literature (Rudnick & Resh 2005; Yokoyama *et al.* 2005; Suring & Wing
249 2009; Carolan *et al.* 2012); 1.32 ± 1.53 ‰ and 2.04 ± 0.11 ‰ for $\delta^{13}\text{C}$, and 3.40 ± 2.23 ‰ and
250 4.24 ± 0.99 ‰ for $\delta^{15}\text{N}$ for animal and plant matter respectively. The mean estimated
251 proportional contribution of each resource to the diet of each individual was then used to
252 calculate an index of individual omnivory (IO) using the following equation:

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

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

257

258 *Statistical analyses*

259 Linear and linear mixed effects models (package lme4 v.1.1.10; Bates *et al.* 2015) were
260 used to examine the effects of lake characteristics (productivity, population abundance, predation
261 and lake size) on population trophic niche width (SEA_b) and individual diet metrics (trophic
262 position [*Model 1*] and index of omnivory), respectively. The variance inflation factor (VIF) was
263 applied and absence of collinearity between explanatory variables was observed ($VIF < 10$; Zuur
264 *et al.* 2009). Explanatory variables were measured on different scales and thus were standardised
265 to have a mean of zero and a standard deviation of one. Linear mixed effects models included
266 lake identity as a random factor and crayfish carapace length as a covariate. Population
267 abundance was square-root transformed to ensure more even dispersion between lakes. All full
268 models were initially run with two-way interactions between both abiotic and biotic factors and
269 lake size. A linear model [*Model 2*] was also used to test the potential effects of environmental
270 parameters on size-related shift in trophic position. This model was initially run with two-way
271 interaction between carapace length and environmental parameters. The best models were
272 selected using Akaike's information criterion using the dredge function in the MuMIn R package
273 v.1.15.1 which performed automated model selection (Barton 2015). Then a model averaging
274 approach, the *importance* function in the MuMIn R package, was used across all models with
275 $\Delta AIC_C < 2$ to assess the relative importance of each predictor variable calculated based on AIC-

276 weights (Burnham & Andersson 2002). Importance ranged from 0 (parameter not given
277 explanatory weight) to 1 (parameter in all top models). Assumptions of linearity and
278 homogeneity of variances on residuals from all models were checked visually and both trophic
279 position and omnivory index were \log_{10} transformed. Analyses of the Cook's distance (D) plot
280 revealed that lakes F and I had larger D values than the rest when testing for an effect of lake
281 variables on SEA_b (Bollen & Jackman 1990). Consequently, the isotope data from these lakes
282 could be considered as too influential with the potential to skew the results, therefore we
283 removed these lakes from the niche width analyses. For each linear mixed effect model, both the
284 marginal (R^2_M , effect of the fixed variables) and conditional (R^2_C , effect of the fixed and random
285 variables) R^2 were calculated (Nakagawa & Schielzeth 2013). All statistical analyses were
286 performed using R v.3.2.2 (R Development Core Team 2015).

287

288 **Results**

289

290 The trophic niche width (SEA_b) of crayfish varied across the 15 lakes, ranging between
291 0.44 and 0.72 ‰² (mean = 0.52 ± 0.08 SD; Figure A2). Analyses performed on 13 lakes (*cf.*
292 *Statistical analyses*) revealed that SEA_b was significantly affected by population abundance ($z =$
293 2.11, $P = 0.035$; Table 2 and Table B1). Specifically, population niche width decreased with
294 increasing abundance (Fig. 1).

295 The trophic position of individual crayfish (mean = 2.49 ± 0.48 SD) was significantly and
296 positively affected by carapace length ($z = 2.38$, $P = 0.017$; Fig. 2a, Table 3). However, analyses
297 performed within each lake revealed that this relationship was only found in lakes I and M (Fig.
298 B3). In addition, the shift in trophic position with carapace length was significantly affected by

299 lake productivity ($z = 2.00$, $P = 0.045$; Table 3 and Table B2). Specifically, trophic position
300 increased with carapace length in lakes with low productivity while it decreased with carapace
301 length in highly productive lakes (Fig. 2b). Individual trophic position was also significantly and
302 negatively affected by crayfish abundance ($z = 2.10$, $P = 0.036$; Table 3), with this interaction
303 varying significantly with lake size (interaction term: $z = 1.96$, $P = 0.05$; Table 3 and Table B2),
304 although this interaction had a low relative importance (RI = 0.33; Table 3). Specifically, these
305 results indicated that the trophic position of crayfish decreased with increasing abundance in
306 small lakes but did not change with abundance in large lakes (Fig. 2c).

307 Crayfish omnivory varied over a 10-fold range (mean = 0.95 ± 0.41 SD) but was not
308 significantly affected by carapace length ($P = 0.09$; Table 3) or any environmental conditions (P
309 > 0.14 ; Table 3 and Table B2).

310

311 **Discussion**

312

313 Understanding the drivers of the diet of invasive species can be an effective tool in
314 predicting their impacts on recipient ecosystems (e.g. Alexander *et al.* 2014; Jackson *et al.*
315 2015). Here, the trophic ecology of a global omnivorous invader was influenced by both
316 individual and environmental characteristics. Specifically, population abundance was an
317 important driver of crayfish trophic ecology by influencing both population niche width and the
318 trophic position of individuals. The effect of crayfish abundance on trophic position also varied
319 with lake size, and trophic position increased with crayfish size, but only in lakes of low
320 productivity.

321 Our results revealed that crayfish population niche width decreased with increasing
322 population abundance, which may be related to increased intraspecific competition. This could
323 be due to a decrease in between-individual variation, or a decrease in individual specialisation
324 (Bolnick *et al.* 2003; Araújo *et al.* 2011). Individual specialisation is a widespread occurrence in
325 natural populations (Araújo, Bolnick & Layman 2011), but few studies have quantified its
326 importance, particularly in invasive species where it may play a central role in the persistence of
327 invasive populations by opening niche opportunities (Shea & Chesson 2002; Cucherousset *et al.*
328 2012). Regardless of the mechanism, our results indicated that the crayfish foraged on a diverse
329 range of resources when their abundance was low, but converged on the same resources when
330 abundance was high. This resulted in a relatively uniform diet and a smaller isotopic niche in
331 lakes with high abundances. This may be due to increased competition for resources when they
332 become less available as abundance increased (Araújo, Bolnick & Layman 2011; Jackson *et al.*
333 2012). However, it is important to note that we did not directly measure resource availability and
334 instead assumed that it was reduced when lake productivity was low, and/or potential
335 competition was high.

336 Contrasting theories suggest that competition can either (1) decrease population niche
337 width by decreasing the range of resources available to consumers (e.g. Jackson *et al.* 2012); or
338 (2) increase population niche width as individuals consume alternative prey items to maintain
339 their energy requirements (e.g. Svanbäck & Bolnick 2007). Our results appear to support the first
340 theory, especially since it was found that individual trophic position also decreased with crayfish
341 population abundance (as a measure of competition). As abundance increases, changes in
342 crayfish behaviour to reduce the risk of antagonistic interactions with conspecifics might cause a
343 shift in habitat use or time spent foraging (Svanbäck & Bolnick 2007), causing individuals to

344 consume resources at lower trophic levels. However, a recent study suggested that cannibalism
345 in crayfish increases with population density (Houghton *et al.* 2017). The negative effect of
346 population abundance on trophic position was only evident in smaller lakes which might be
347 linked to an increase in encounter rates between conspecific individuals, since these are likely to
348 increase in smaller areas if abundance remains the same. Our results suggest that individual
349 crayfish in small lakes consume less animal resources when crayfish abundance (and therefore,
350 potential competition) is high. In larger lakes, this relationship is absent which might be due to a
351 lower chance of encounters between conspecifics and/or increases in resource availability.

352 Ontogenetic dietary shifts have been described in many crayfish species where juvenile
353 crayfish preferentially feed on aquatic invertebrates and adults mainly feed on vegetal detritus
354 (e.g. Guan & Wiles 1998). This ontogenetic shift is particularly associated with differences in the
355 nutrient requirements for growth and the inability of larger crayfish to forage on fast moving
356 aquatic invertebrates (Momot 1995; Nyström, Brönmark & Granelo 1999). Here, however, it was
357 detected that the trophic position of sexually mature crayfish increased with their carapace length
358 in lakes of low productivity, suggesting that the invasive crayfish incorporated more animal
359 material in their diet as they grew larger. Larger individuals are likely to be more competitive for
360 access to nutrient rich animal prey, even when their size difference with a competitor is small
361 (e.g. Correia 2002). This trait may be specific to invasive crayfish, which tend to be both more
362 flexible in diet choice and more predatory than their native counterparts (Grey & Jackson 2012;
363 Olsson *et al.* 2009; but see Lagrue *et al.* 2014). Stenroth *et al.* (2008) revealed that the trophic
364 position of invasive signal crayfish was higher in eutrophic lakes, but we detected no direct
365 influence of lake productivity. This is contrary to the productivity hypothesis that suggests that
366 food chain length and therefore, the trophic level of consumers, increases with increasing

367 ecosystem productivity (Post 2002; Takimoto & Post 2013). In contrast, we found that the
368 positive relationship between trophic position and body size was only evident in lakes of low
369 productivity. In highly productive lakes the effect of body size was reversed, which might be a
370 result of increased resource choice at lower trophic levels.

371 Variation in crayfish diet across gradients of lake characteristics is likely to influence the
372 effect of crayfish on community structure and ecosystem functioning. For example, when
373 crayfish occupy lower trophic levels and consume more plant material they may increase
374 decomposition rates and decrease macrophyte cover (Twardochled, Olden & Larson 2013;
375 Jackson *et al.* 2014; Alp *et al.* 2016). If crayfish become more important predators then they
376 might affect invertebrate community structure and, potentially, modify the intensity of trophic
377 cascades that subsequently change decomposition rates and macrophyte cover (Jackson *et al.*
378 2014; Lagrue *et al.* 2014, Alp *et al.* 2016). Therefore, future studies should focus on aspects of
379 ecosystem functioning because invasive crayfish have the potential to modify numerous trophic
380 interactions. Importantly, in previous studies, impacts were generally associated with trophic
381 differentiation between crayfish species (Twardochleb, Olden & Larson 2013; Jackson *et al.*
382 2014), whereas here we argue that strong differences in trophic ecology can also be found
383 between populations of a single species, and this may drive context-dependent impacts on
384 recipient ecosystems. Consequently, it is also recommended that the relative importance of intra-
385 versus inter-specific variability would be investigated to determine the ecological effects of
386 invasive consumers on ecosystems (Palkovacs *et al.* 2015).

387 Increasingly, evidence indicates that individuals within species differ in their diet and
388 therefore their functional role, notably through variations in body size (Miller & Rudolf 2011;
389 Sato & Watanabe 2013). This intraspecific variability can exceed variability between species and

390 result in changes in the functioning of ecosystems (Rudolf & Rasmussen 2013a; Rudolf &
391 Rasmussen 2013b). Therefore, an understanding of intraspecific variability in resource use of
392 invaders, and how this varies across the invaded landscape, is essential to measure impact and
393 best direct management practices. We found that the trophic ecology of an invasive crayfish
394 varied with individual (body size), population (abundance) and environmental (lake size) traits.
395 Variation in crayfish diet will influence which native species in the food web are negatively
396 affected by the invasion, and ecosystem processes such as leaf litter decomposition. Furthermore,
397 these variations in trophic ecology may influence invasion success and future invasion spread
398 throughout the landscape. Future research on invasive species should therefore consider the
399 complex and reciprocal relationships between invasion success and impact, trophic ecology, and
400 variations in environmental conditions; all which influence, and are influenced by, one another.

401

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403

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414

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614 **Tables**

615

616 **Table 1** Environmental characteristics of the fifteen studied lakes. Predation pressure was

617 calculated as the total biomass (g) of fish predators captured using gillnetting and electrofishing.

618 Density was based on CPUE which was determined from number of crayfish caught in traps over

619 a 24-hour period (ind. trap⁻¹ h.⁻¹). Productivity (TSI) was calculated using measures of Secchi

620 disc, chlorophyll-a concentration and total phosphorus concentration. Lake size (ha) was

621 calculated from aerial pictures and geographic information system (GIS) analyses.

Lake	Longitude (E)	Latitude (N)	Predation (e.g. fish predators; g)	Density (CPUE crayfish; ind.trap ⁻¹ .h ⁻¹)	Lake productivity (Secchi disk depth; m)	Lake size (ha)
A	1.202	43.322	12259	3.2	2.80	8.69
B	1.203	43.317	28205	3.2	2.41	9.50
C	1.290	43.530	15564	1.5	0.64	20.53
D	1.274	43.454	2398	0.0	0.97	17.54
E	1.355	43.519	16120	0.2	0.67	1.84
F	1.337	43.506	36658	0.8	1.64	4.24
G	1.266	43.386	26794	5.7	1.88	20.75
H	1.227	43.343	3099	0.0	0.64	20.39
I	1.194	43.320	0	2.4	2.43	13.25
J	1.258	43.372	14103	3.1	1.60	10.18
K	1.251	43.365	1327	1.2	1.40	16.50
L	1.040	43.206	18749	0.2	2.37	8.65
M	1.047	43.208	16294	0.2	2.37	21.16
N	1.039	43.209	13323	0.8	2.74	14.65
O	1.262	43.552	1739	0.3	1.09	0.75

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624

625 **Table 2** Summary results after model averaging of the final linear model with biotic (predation
626 [g. fish predators], density [CPUE crayfish; ind.trap⁻¹.h⁻¹; square-root transformed],) and abiotic
627 (lake productivity [Secchi disk depth; m], lake size [ha]) parameters as factors affecting crayfish
628 population niche width (SEA_b; n = 13, *see details in Statistical analyses*). All explanatory
629 variables are standardized. The relative importance value (RI) of each explanatory variable and
630 the 95% CI are presented. Significant *P*-values are highlighted in bold.

631

Response variable	Predictor	Estimate (SE)	z	P	95% CI	RI
Trophic niche width	Intercept	0.55 (0.04)	12.04	< 0.001	0.459, 0.637	NA
	Density	-0.08 (0.03)	2.11	0.035	-0.155, -0.006	0.70
	Predation	0.03 (0.02)	1.81	0.071	-0.003, 0.068	0.39
	Lake productivity	-0.03 (0.01)	1.62	0.105	-0.055, 0.005	0.29

632

633

634 **Table 3** Summary results after model averaging of the linear mixed effects models with
635 environmental characteristics (predation [g. fish predators], density [CPUE crayfish; ind.trap⁻¹.h⁻¹;
636 ¹; square-root transformed], productivity [Secchi disk depth; m] and lake size [ha]) and carapace
637 length (mm) as factors affecting individual crayfish trophic niche (trophic position [\log_{10}
638 transformed] and index of omnivory [\log_{10} transformed]; n = 218). Lake identity was included as
639 a random effect. All explanatory variables are standardized. The relative importance value (RI)
640 of each explanatory variable and the 95% CI are presented. Significant *P*-values are highlighted
641 in bold. Marginal (R^2_M , effect of the fixed effects) and conditional (R^2_C , effect of the fixed and
642 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 [‡]	Intercept	0.45 (0.04)	10.81	< 0.001	NA	3.70e-01, 0.53	0.39 - 0.73
	Carapace length	0.01 (0.003)	2.38	0.017	1	1.43e-03, 0.01	
	Lake productivity	0.03 (0.02)	1.63	0.102	0.63	-5.76 e-03, 0.06	
	Density	-0.08 (0.04)	2.10	0.036	0.88	-1.61 e-01, -0.01	
	Lake size	-0.03 (0.04)	0.92	0.357	0.43	-1.05 e-01, 0.04	
	Density × Lake size	0.07 (0.03)	1.96	0.050	0.33	6.05, 0.13	
	Lake productivity × Lake size	0.03 (0.02)	1.38	0.167	0.19	-1.06 e-02, 0.06	
	Predation	0.02 (0.02)	0.94	0.347	0.24	1.73 e-02, 0.05	
Trophic position [†]	Intercept	0.45 (0.04)	12.78	< 0.001	NA	0.38, 0.52	0.24 - 0.74
	Carapace length	0.01 (0.01)	0.95	0.341	1	-0.01, 0.02	
	Lake productivity	0.02 (0.02)	1.33	0.184	0.75	-0.01, 0.06	
	Density	-0.07 (0.04)	2.03	0.043	1	-0.15, -0.002	
	Carapace length × Lake productivity	0.01 (0.003)	2.00	0.045	0.75	0.0001, 0.01	
	Predation	0.02 (0.02)	1.13	0.259	0.18	-0.01, 0.05	
	Carapace length × Density	0.01 (0.01)	1.19	0.232	0.30	-0.01, 0.02	
	Lake size	-0.01 (0.02)	0.42	0.677	0.11	-0.04, 0.02	
Index of omnivory	Intercept	0.05 (0.05)	1.19	0.236	NA	-0.14, 0.04	0.10 - 0.68
	Carapace length	0.01 (0.01)	1.69	0.092	0.72	-0.002, 0.03	
	Lake size	0.05 (0.03)	1.48	0.140	0.50	-0.02, 0.12	
	Lake productivity	-0.02 (0.04)	0.51	0.610	0.16	-0.09, 0.05	
	Desnsity	-0.03 (0.07)	0.46	0.644	0.16	-0.18, 0.11	

643 [‡]Model 1 and [†] Model 2, see details in *Statistical analyses*

644 **Figures legends**

645

646 **Figure 1.** Relationship between density (crayfish CPUE; $\text{ind.trap}^{-1}.\text{h}^{-1}$; square-root transformed)
647 and crayfish population niche width (SEA_b). $n = 13$ (*see details in Statistical analyses*).

648

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

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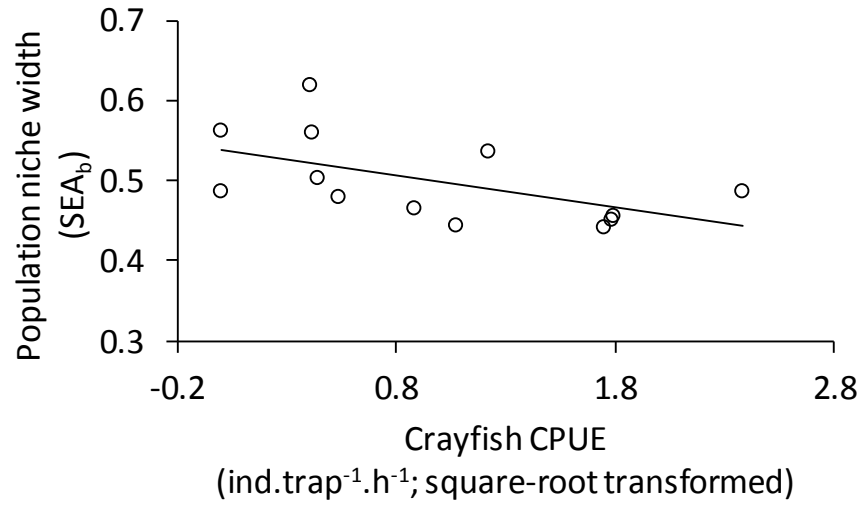
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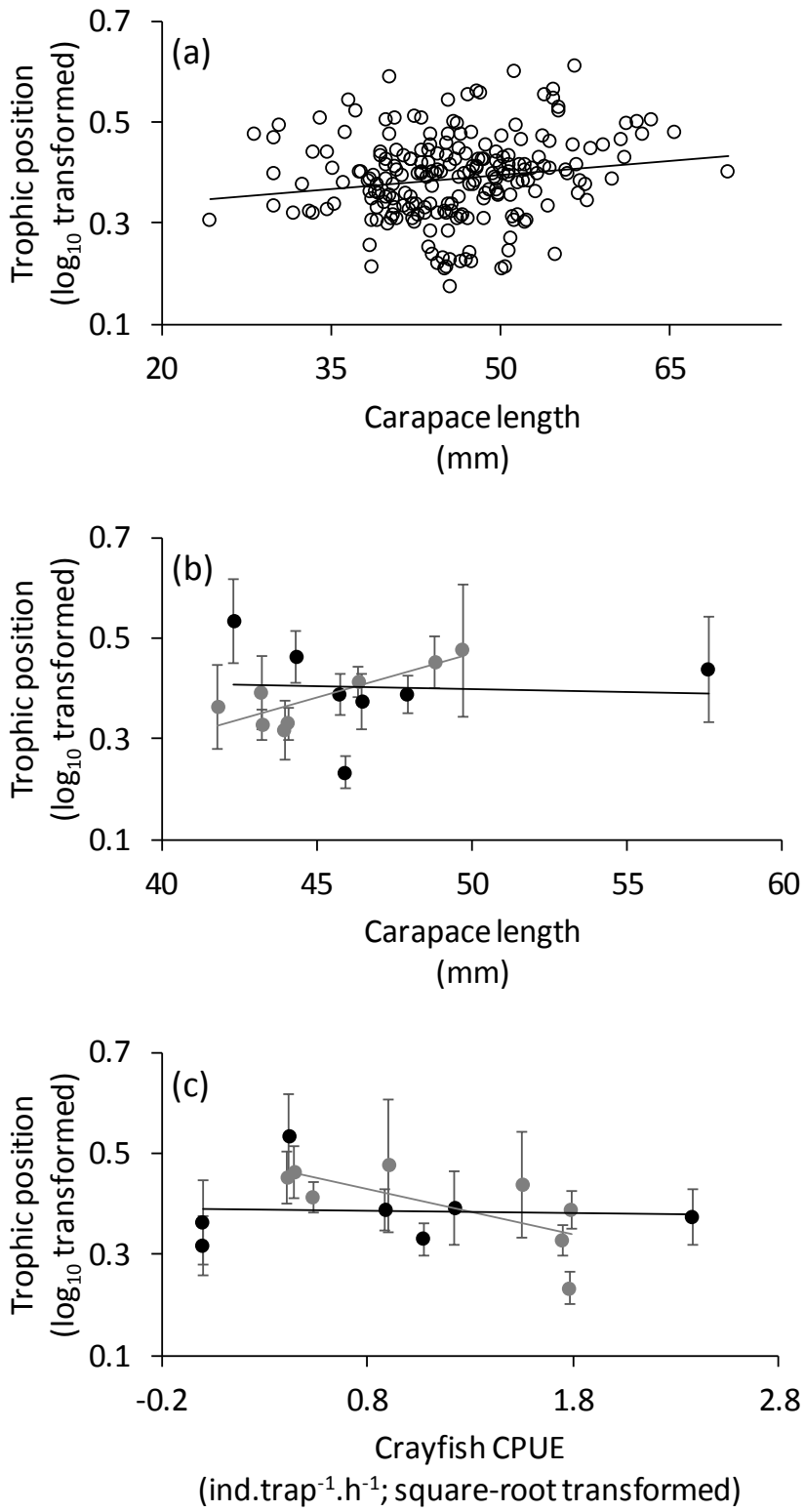
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Figure 1



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Figure 2