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1 Narrower isotopic niche size in fish infected by the intestinal
2 parasite *Pomphorhynchus* sp. compared to uninfected ones

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20

21

22 **Abstract:**

23 Examples of parasite-related effects on intermediate crustacean hosts are numerous but their
24 ecological consequences on their vertebrate hosts are scarce. Here, we address the role of
25 macroparasite infections on the trophic niche structure of definitive hosts and its potential
26 physiological consequences using wild fish populations infected with an acantocephalan
27 parasite *Pomphorhynchus* sp., a trophically-transmitted intestinal worm. Infected and
28 uninfected fish were sampled from six populations on the Marne River, France and the
29 prevalence of intestinal parasites in the host populations ranged from 50% to 90%. Although
30 the isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) did not differ between infected and uninfected fish, we
31 found a consistent pattern of isotopic niche size being considerably smaller in infected hosts
32 when compared with non-infected ones. This was not explained by interindividual differences
33 in intrinsic factors such as length/age or body condition between infected and uninfected fish.
34 These results suggest a potential niche specialization of infected fish, which did not impair
35 their energetic status.

36 **Keywords:** Body condition, Carbon, European chub, Host-parasite system, Intestinal worms,
37 Nitrogen

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44 **1. Introduction**

45 Parasites are ubiquitous components of biological systems, found virtually in all free-
46 living organisms on earth (Strona, 2015). By definition, parasites live at the expense of their
47 hosts and this interdependence of parasites is known to cause considerable changes in the
48 physiology and metabolism of hosts (Shinagawa *et al.*, 2001; Hicks *et al.*, 2018), leading to
49 potential reduced outcomes in host individuals (Johnson and Dick, 2001; Östlund-Nilsson *et*
50 *al.*, 2005). Parasites are therefore recognized as important stress factors in all ecosystems.

51 In the last decade, stable isotopes have become popular in stress ecology studies (Wolf
52 *et al.*, 2009), to assess stress-induced changes on the interactions between organisms and
53 between organisms and their environment. Changes in isotope signatures may, indeed, vary
54 depending on various endogenous and environmental pressures *via* metabolic alterations
55 (Bowes *et al.*, 2014; Yohannes *et al.*, 2017; Karlson *et al.*, 2018). Because stable isotopes
56 measures integrate dietary information over long timescales, they are useful tools to
57 investigate the impact of parasite infections on individual hosts (Sánchez *et al.*, 2013;
58 Knudsen *et al.*, 2014), especially since some parasites are known to accumulate and survive in
59 their hosts over several weeks or months (Sandground, 1936). In addition, isotopic niche
60 being tightly correlated with trophic niche, stable isotopes are ecologically valuable for
61 quantifying changes in the trophic structure of communities and populations (Layman *et al.*,
62 2007; Jackson *et al.*, 2011). Consequently, stable isotopes could provide insight into parasite-
63 related effects on the ecology of their host. Yet few studies have assessed the effects of
64 macroparasite infections on isotopic signature and niche structure of definitive hosts as well
65 as its functional significance (Britton and Andreou 2016; Gilbert *et al.*, 2020; Riekenberg *et*
66 *al.*, 2021).

67 Recent works suggest that the host's feeding behaviour, or diet, is likely to be a crucial
68 factor in shaping host–parasite interactions (Britton and Andreou 2016; Hite *et al.*, 2020),

69 especially for trophically transmitted parasites such as parasitic worms (i.e., helminths:
70 acanthocephalans, nematodes, cestodes and trematodes). The breadth of a host's trophic niche
71 has long been associated with structuring helminth infections. For instance, greater diet
72 breadth increases potential encounter with parasite intermediate hosts, therefore leading to
73 higher parasite abundance and taxon richness (Lagrue *et al.*, 2011; Paterson *et al.*, 2019). In a
74 recent metanalysis, Gutiérrez *et al.* (2019) found positive associations between trophic niche
75 breadth and trophically transmitted helminths in birds. On the other hand, parasites could
76 affect the trophic niche of infected organisms through impairment of host phenotypic traits or
77 behavioural alterations (Lefèvre *et al.*, 2009; Weinersmith and Faulkes, 2014; Parker *et al.*,
78 2015). The latter has been documented in manipulative parasites, which alter host habitat
79 preferences, foraging activity, and antipredator behaviours (Loot *et al.*, 2001; Poulin, 2007;
80 Friesen *et al.*, 2018). Still, the relationship between trophic niche and trophically-transmitted
81 helminth infection is complex and not yet well understood, with contrasting results reported in
82 the literature (Tierney, 2016; Pegg *et al.*, 2017). The outcomes usually depend on several key
83 traits such as the life cycles, infection or feeding sites and modes of parasites.

84 Among parasites relying on trophic transmission to reach the definitive host,
85 acanthocephalans are ubiquitous obligatory intestinal worms encountered in a range of
86 taxonomically diverse host species, from aquatic to terrestrial habitats. These intestinal
87 parasites are commonly transmitted to vertebrate definitive hosts by aquatic crustacean preys
88 serving as intermediate hosts (Kennedy, 2006). In intermediate hosts, seemingly odd
89 behaviours of parasitized individuals have been reported, from reverse phototaxis (Franceschi
90 *et al.*, 2008) to changes in habitat and resource use (Fielding *et al.*, 2003; Médoc *et al.*, 2011).
91 These parasite-altered behaviours render hosts more susceptible to predation and increase the
92 likelihood of reaching the definitive host (Moore, 2002). Because parasite survival and
93 transmission in intermediate host depends on the survival of the host itself, behavioural

94 responses to predation have been reported to switch from “predation suppression” during non-
95 infective phase to “predation enhancement” when transmission is optimal, that is, when the
96 parasite reaches the stage infective to a definitive host (Dianne *et al.*, 2011). In predatory final
97 hosts, parasites are likely to minimize pathogenicity to increase their own reproductive output
98 and/or avoid multiple infections with other parasite species that may be harmful for the host.
99 One way to limit or avoid co-infections may occur by altering the trophic niche through
100 changes in the host feeding behaviour, which remains understudied for vertebrate definitive
101 hosts.

102 The objective of this study was to investigate interindividual variations in bivariate
103 $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space between infected and uninfected fish cohorts and assess its potential
104 physiological consequence. To this purpose, we used a well-known and widespread host-
105 parasite system, being composed of a freshwater fish the European chub, *Squalius cephalus*,
106 and its acanthocephalan parasite *Pomphorhynchus* sp., a thorny-headed worm living within
107 the small intestines of vertebrates. Stable isotope data were used to calculate trophic niche
108 metrics and overlap using the Bayesian stable isotope approach. The Fulton’s condition factor
109 provided relevant information on the energetic status and overall health of host individuals.
110 We hypothesized that, under natural conditions, acanthocephalan parasites would prevent
111 multiple infection of their host with other parasite species through a reduction of the host
112 trophic niche, hence closing the encounter filter for parasites acquired by ingestion, leading to
113 different host body condition according to their infection status. While controlling for
114 potential confounding factors such as age and body length of host individuals, we expected *i*)
115 altered isotopic signatures between infected and uninfected fish, *ii*) decreased health status in
116 infected host, reflected by a poorer body condition, and *iii*) smaller isotopic niche in infected
117 cohorts as an evolutionary strategy in parasitism.

118

119 2. Materials and Methods

120 2.1 Ethic statement

121 Fish sampling was conducted in accordance with the relevant national and European
122 guidelines (L436-9, EN14011). The authorization for the scientific fish capture was delivered
123 by local administration authorities (Departmental Direction of Territories of Seine-et-Marne,
124 Val de Marne, Aisne, and Marne).

125

126 2.2 Sample collection

127 In September 2016, sampling was conducted on six stations of the Marne River and its
128 tributaries, France, along a 290-km-long stretch of the river (Table 1 and Table S1). Fish were
129 captured using a DEKA 3000 portable electrofishing unit (“Martin-pêcheur”) in an upstream
130 direction, within a period of twelve days to limit temporal variations. Given the relatively
131 short-range movements of chubs (Penczak, 2006), fish from different sampling sites were
132 considered distinct populations. A total of 118 acanthocephalan-infected and uninfected
133 European chub, *Squalius cephalus*, from 8.8 to 41.5 cm in length were captured (Table 1) and
134 fish were euthanized in 1 g/L MS222 solution. Total length (L_T ; nearest mm) and whole-fish
135 wet weight (W_T ; ± 0.1 g) were recorded. Prior tissue sampling, the Fulton’s condition factor
136 (K , $n = 118$) was calculated according to the following equation: $K = (W_T / L_F^3) \times 100$. Note
137 that parasite mass was considered negligible to fish mass when estimating its body condition
138 as *Pomphorhynchus* sp. represented less than 1% of fish mass even for heavily parasitized
139 ones (unpublished data). Scales were collected from each specimen above the lateral line and
140 age determination was independently made by two different operators to limit interpretation
141 bias (see Molbert *et al.*, 2020 for additional information). Chub intestine and body cavity were
142 examined for the presence of parasitic worms. For ectoparasites, external examination of fish
143 surface (skin and gills) was carried out. In our study, chub harbored only one parasite species,

144 which was initially identified as *Pomphorhynchus laevis* based on morphological
145 characteristics. However, without molecular identification to distinguish with other closely
146 related acanthocephalan species (e.g., *Pomphorhynchus tereticollis*), parasites were reported
147 as *Pomphorhynchus* sp. All parasites were found within the host intestine. A sample of dorsal
148 muscle was collected on each individual for isotopic measurements. These samples were then
149 lyophilized (Alpha1- 4LD plus; Martin Christ) for 48h, ground to obtain a fine powder and
150 weighed into aluminium capsules.

151

152 *Isotopic measurements.* Isotopic measurements were performed on 0.20–0.25 mg of freeze-
153 dried and powdered muscle samples (n = 113, some samples were lost because of combustion
154 issues) and analyzed by means of a Flash HT elemental analyzer (ThermoFisher) coupled to a
155 Delta V mass spectrometer (ThermoFisher) at the IRD laboratory in Bondy (France). Stable
156 isotope abundances are expressed as the deviation from international standards in parts per
157 thousand (δ , ‰) as follow: $\delta X\text{‰} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000$, with X corresponding
158 to ^{13}C or ^{15}N and R representing $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios. Atmospheric N_2 and Pee Dee
159 Belemite were used as standards for nitrogen and carbon, respectively. The analytical
160 precision was found to be 0.1‰ and 0.7‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. There was no lipid
161 correction applied to the data.

162

163 2.3 Data analyses

164 Infection levels of *Pomphorhynchus* sp. in *S. cephalus* were described as their prevalence
165 (*i.e.*, number of infected fish/total number of fish x 100). Stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)
166 from infected and uninfected fish cohorts were used to characterize isotopic signature and
167 trophic structure from wild fish host populations in the Marne River. Two metrics of standard
168 ellipse areas (SEAs) were calculated with the R package SIBER (Jackson *et al.*, 2011) to

169 assess the distribution of individuals in isotopic space, which enclose approximately 40% of
170 the data within groups (Jackson *et al.*, 2011). SEA_C , which stand for sample size corrected
171 standard ellipse, gives a single estimate of ellipse area whereas SEA_B , a Bayesian-estimated
172 standard ellipse area, gives a distribution of estimates that reflects variability in the data. Both
173 metrics, SEA_C and SEA_B , were calculated for infected and uninfected fish hosts and the
174 isotopic niche width was compared between groups (infected vs uninfected) by calculating the
175 probability that the distributions of SEA_B differed from one another. The overlap in the
176 isotopic niches of infected and uninfected host cohorts was calculated through the area of
177 overlap between two fitted ellipses based on the maximum likelihood and then as the
178 proportion overlap (%). Note that we did not obtain sufficient samples of uninfected hosts to
179 explore isotopic space across all locations.

180

181 2.4 Statistical analyses

182 All statistical models were performed in R v. 3.3.2 software (R Core Team, 2016). All data
183 were tested for normality and homogeneity before further statistical analyses and a
184 significance level of $\alpha < 0.05$ was used for all tests. Since age and body length were highly
185 correlated ($F_{(1,109)} = 484.5$, $p < 0.001$), we only used body length in our models to avoid
186 collinearity. Linear Mixed Models (LMMs) with site as random effects, to account for
187 different fish populations and environmental conditions, were used to assess *i*) the effect of
188 infection and body length on isotopic ratios ($\delta^{15}N$ and $\delta^{13}C$) and *ii*) the effect of parasite
189 infection and $\delta^{15}N$ (as a proxy of trophic position) on condition factor. Analyses were
190 performed using the *lmer* statistical procedure available in the *lme4* and *lmerTest* packages for
191 linear mixed models (Pinheiro and Bates, 2000; Kuznetsova *et al.*, 2017). Variance
192 components were estimated using a restricted maximum likelihood (REML) function and all
193 models had normal error structures. Data are presented as mean (β) \pm standard error (SE).

194

195 **3. Results**

196 Data and descriptive statistics are summarized in Table 1. The prevalence of intestinal worms
197 *Pomphorhynchus* sp, ranging from 50% to 90%, did not significantly differ among sampling
198 sites (Fisher-exact, $p = 0.072$). The probability of infection by acanthocephalan parasites was
199 not significantly correlated with body length (binomial GLMM: $Z = 4.476$, $p=0.064$) or age
200 ($Z = 4.645$, $p=0.067$), and similarly, the body weight of infected and uninfected chub did not
201 significantly differ when the effect of body length was controlled (Gaussian GLMM:
202 $F_{(1,112)}=1.490$, $p>0.05$). Importantly, the body condition was not significantly altered by
203 intestinal parasites *Pomphorhynchus* sp. (K ; LMM: $F_{(1,98,6)}=0.152$, $p>0.05$), but was positively
204 correlated to $\delta^{15}\text{N}$ (LMM: $F_{(1,53,9)}=4.471$, $p=0.039$, $\beta \pm \text{SE}$: 0.018 ± 0.009).

205 The isotopic signature of chub varied among the different populations studied (LMM; $\delta^{15}\text{N}$:
206 $F_{(5,105)}=8.688$, $p<0.001$ and $\delta^{13}\text{C}$: $F_{(5,105)}=9.152$, $p<0.001$) and ranged from 5.92 to 12.9 ‰ for
207 and -30.2 to -22.8 ‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ respectively (Table 1). Interestingly, there were no
208 significant effects of parasite infection by *Pomphorhynchus* sp. on stable isotopes ratios
209 (LMM; $\delta^{15}\text{N}$: $F_{(1,106,1)}=0.411$, $p=0.522$ and $\delta^{13}\text{C}$: $F_{(1,106,4)}=0.963$, $p=0.329$). There was
210 however a consistent pattern of isotopic niche size (SEA_B and its sample-corrected version,
211 SEA_C) being considerably smaller in infected cohorts when compared with their non-infected
212 conspecifics (Table 2 and Figure 1), with niche width of uninfected groups being up to 3
213 times larger than that of infected ones. Overall, there were various degrees of isotopic overlap
214 between infected and uninfected cohorts among chub populations. Specifically, the isotopic
215 niche of infected hosts has some overlap with uninfected conspecifics, ranging from 60% to
216 97% (*i.e.*, infected niche within that of uninfected conspecifics; Table 2 and Figure 1).

217

218 **4. Discussion**

219 Parasitism is among the most common stress factors affecting free-living animals and how
220 parasites affect their host varies greatly, from causing minor alteration to death. One
221 understudied topic, albeit of greater ecological significance, is to evaluate potential shifts that
222 occur in trophic ecology of hosts following parasite infections, especially by trophically
223 transmitted parasites. In this study, the use of a widespread chub-acanthocephalan system
224 revealed different patterns in the isotopic niche of infected and non-infected chub cohorts, as
225 measured by the standard ellipse area (*i.e.*, the isotopic niche) in the bivariate $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$
226 space. Apart from two fish populations, infected subgroups showed a more restricted isotopic
227 breadth compared to uninfected ones, although the extent of divergence between infected and
228 uninfected niches differed between populations. Additionally, the isotopic niches of infected
229 chub sat within that of uninfected ones for half of the populations under study. This illustrates
230 a potential trophic specialization, with infected fish consuming specific food items that are
231 also within the dietary range of uninfected chub, and this non-lethal consequence of parasite
232 infection may have strong implications for the feeding ecology of the host.

233 There are empirical examples of an association between parasite infection and
234 shifts in host trophic niche, but they remain somewhat restricted for macroparasites (Bernardo
235 and Singer, 2017). Parasite-mediated shifts in trophic niche can be associated to the cost
236 exerted by parasites or modifications of the host phenotype, which can influence diet
237 preferences or prey selectivity (Britton and Andreou, 2016; Vivas Muñoz *et al.*, 2021). These
238 changes, which can limit hosts' niche usage, are either adaptative for the host or the parasite
239 as they redress physiological deficits imposed by parasite infections (Britton, Pegg and
240 Williams, 2011; Sánchez *et al.*, 2013; Pegg *et al.*, 2015), provide nutritional requirements for
241 parasites growth, reproduction and survival (Esch and Fernández, 1993) or limit co-infection
242 which might be detrimental for the established parasite (direct competition for space and
243 resources, or indirect through the release of toxic products; Ferrari *et al.*, 2009). For instance,

244 the tapeworm *Schistocephalus solidus* causes infected sticklebacks, *Gasterosteus aculeatus*, to
245 eat smaller prey (Milinski, 1984), or selectively preyed on larger items than uninfected
246 individuals, which compensated for the energy cost of infection (Ranta, 1995). Similarly,
247 Pegg *et al.* (2017) reported a consistent niche specialization in two cyprinid fish species
248 infected by a copepod gill parasite. They speculated that infected fishes increased their
249 predation on prey requiring relatively low-energy expenditure to capture (*i.e.*, abundant and/
250 or relatively slow moving) as a consequence of parasite-associated energetic costs. In wild
251 common carp *Cyprinus carpio*, individuals infected with cestodes shifted to lower trophic
252 status prey items as a result of pathological damage to the gastrointestinal tract (Britton, Pegg
253 and Williams, 2011). Despite the variation in isotopic niche between chub cohorts, the
254 absence of differences in relative body condition (as measured by the Fulton's condition
255 factor) between infected and uninfected fish may suggest that hosts maintained their energetic
256 requirements. While adult acanthocephalans are usually less virulent in the final host, thorny-
257 headed parasites are known to perforate the gut wall with their proboscis and, under heavily
258 infection, obstruct the digestive tube and cause severe local inflammation (Taraschewski,
259 2000). Cases of serious illness, enhanced mortality or altered reproduction in
260 acanthocephalan-infected fish are seldom, although fitness cost for the vertebrate host has
261 already been observed in fish in the face of infection by acanthocephalan parasites (Salal *et*
262 *al.*, 2001; Rajeshkumar *et al.*, 2013; Sakthivel, 2014; Atalabi *et al.*, 2018). Here, the low
263 abundance of *Pomphorhynchus* sp. might explain the absence of pathological effects on the
264 host.

265 Interestingly, trophic niche use at the study sites showed different trends for
266 infected and uninfected cohorts among chub populations. This result suggests that parasite
267 infection on niche specialization is context-dependent (Thorburn *et al.*, 2022). There is
268 mounting evidence that stress factors, other than parasite infection, can alter physiological

269 performance and affect interindividual variability of the isotopic signature (Karlson *et al.*,
270 2018). Chub populations were, among other things, exposed to various contaminants from
271 industrial, agricultural, and urban activities along the Marne River (Molbert *et al.*, 2020). A
272 previous study, based on the same host-parasite system, evidenced enhance oxidative stress in
273 non-infected chubs exposed to high contaminant levels, which could drive fitness costs for the
274 host (Molbert *et al.*, 2021). Although the body condition did not differ with the infection
275 status, alteration in metabolic pathways through differential exposure to contaminants could
276 explain interpopulation variations in trophic niches between infected and non-infected
277 cohorts. In fact, the lack of evidence at higher biological scale could be explained by the
278 “selection hypothesis”, stating that less fit animals are sampled less frequently as a result of
279 more efficient predation on sick and weak animals.

280 Since our study only reveals association, we cannot ascertain causation between
281 niche specialization and parasite infection. Alternatively, dietary specialization could be a
282 driver of *Pomphorhynchus* sp. infection (Britton and Andreou, 2016, Gutiérrez *et al.*, 2017),
283 as specialized feeding behavior can lead to large variations in exposure to parasites among
284 individual hosts. Infection in chub populations at the study sites, was solely explained by a
285 single genus, which suggests intense feeding on gammarid intermediate hosts or infected
286 paratenic fish hosts. Smaller SEAc in infected chub cohorts compared to uninfected ones also
287 support that infected fish had more selective diet, while uninfected conspecifics appeared to
288 be more generalist feeders. In line with those findings, Costa- Pereira *et al.* (2019)
289 demonstrated that thin-toed frogs, *Leptodactylus* spp, with lower helminth parasite load
290 adopted a more flexible feeding strategy and suggested that diet consistency may lead to
291 increase infection rates. Although parasite infection may lead to smaller niches formed by
292 groups of trophically specialised individuals (Bolnick *et al.*, 2003; Quevedo *et al.*, 2009; Pegg
293 *et al.*, 2017), Tierney (2016) showed an opposite trend, with infected cohorts of brown trout,

294 *Salmo trutta*, having greater SEAc than non-infected ones. Where brown trout were infected
295 by seven species of helminth parasites, including the acanthocephalan *Pomphorhynchus*
296 *tereticollis*, we only found one acanthocephalan genus among 6 populations along a 290-km-
297 long stretch of the Marne River. These results support the hypothesis that higher parasite
298 species richness is associated with greater niche breadth, and thus higher probability to
299 encounter parasite intermediate hosts.

300 Last but not least, isotopic turnover rates are important for understanding how
301 parasite infection affects stable isotope fractionation. While carbon and nitrogen half-lives in
302 fish muscle are ca. 50 and 100 days, respectively (Church *et al.*, 2009; Buchheister and
303 Latour, 2010; Busst and Brittons, 2018), the lifespan of most fish acanthocephalans in the
304 intestine of fish host does usually not exceed 7–8 months (Nachev and Sures, 2016). In this
305 study, however, the dynamics of current and past infection by *Pomphorhynchus* sp., or other
306 parasitic worms, is unknown. As a result, parasite infection could be confounded given the
307 slow turnover rate of stable isotope in muscle. With naturally infected fish, parasite effect on
308 the isotopic niche or composition should therefore be treated with caution. Overall, future
309 challenges lie in the determination of the influence of trophic niche on helminth infection (or
310 vice versa) and its functional significance, especially for host-parasite systems composed of
311 macroparasites with complex life cycle and vertebrate hosts. To this purpose, emphasis should
312 be placed on studies combining field studies and experimental approaches, and parasite effect
313 on host trophic niche should be considered within a comprehensive framework rather than in
314 isolation.

315

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318 analyses.

319

320 **Conflicts of interest**

321 The authors declare no conflict of interest.

322

323 **Contributions**

324 A.G. acquired the funding, conceived the idea, designed the methodology and captured the
325 fish. N.M. carried out stable isotope analyses, ran statistical analyses and drafted the
326 manuscript. Both authors contributed critically to the manuscript draft and gave final
327 accordance for publication.

328

329 **Reference**

330 Atalabi, T. E., Awharitoma, A. O., & Akinluyi, F. O. (2018). Prevalence, intensity, and
331 exposed variables of infection with Acanthocephala parasites of the gastrointestinal
332 tract of *Coptodon zillii* (Gervais, 1848) [Perciformes: Cichlidae] in Zobe Dam, Dutsin-
333 Ma Local Government Area, Katsina State, Nigeria. *The Journal of Basic and Applied*
334 *Zoology*, **79**, 29.

335 Bernardo, M. A., & Singer, M. S. (2017). Parasite-altered feeding behavior in insects:
336 integrating functional and mechanistic research frontiers. *Journal of Experimental*
337 *Biology*, **220**, 2848–2857.

338 Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., &
339 Forister, M. L. (2003). The Ecology of Individuals: Incidence and Implications of
340 Individual Specialization. *The American Naturalist*, **161**, 1–28.

341 Bowes, R. E., Holliday Lafferty, M., & Thorp, J. H. (2014). Less means more: nutrient stress
342 leads to higher $\delta^{15}\text{N}$ ratios in fish. *Freshwater Biology*, **59**, 1926–1931.

343 Britton, J. R., Pegg, J., & Williams, C. F. (2011). Pathological and ecological host
344 consequences of infection by an introduced fish parasite. *PLoS ONE*, **6**, e26365.

345 Britton, J. R., & Andreou, D. (2016). Parasitism as a driver of trophic niche specialisation.
346 *Trends in Parasitology*, **32**, 437–445.

347 Buchheister, A., & Latour, R. J. (2010). Turnover and fractionation of carbon and nitrogen
348 stable isotopes in tissues of a migratory coastal predator, summer flounder
349 (*Paralichthys dentatus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **67**,
350 445–461.

351 Busst, G. M. A., & Britton, J. R. (2018). Tissue-specific turnover rates of the nitrogen stable
352 isotope as functions of time and growth in a cyprinid fish. *Hydrobiologia*, **805**, 49–60.

353 Church, M. R., Ebersole, J. L., Rensmeyer, K. M., Couture, R. B., Barrows, F. T., & Noakes,
354 D. L. G. (2009). Mucus: a new tissue fraction for rapid determination of fish diet
355 switching using stable isotope analysis. *Canadian Journal of Fisheries and Aquatic
356 Sciences*, **66**, 1–5.

357 Costa- Pereira, R., Toscano, B., Souza, F. L., Ingram, T., & Araújo, M. S. (2019). Individual
358 niche trajectories drive fitness variation. *Functional Ecology*, **33**, 1734–1745.

359 Dianne, L., Perrot-Minnot, M. J., Bauer, A., Gaillard, M., Léger, E., & Rigaud, T. (2011).
360 Protection first then facilitation: a manipulative parasite modulates the vulnerability to
361 predation of its intermediate host according to its own developmental stage. *Evolution*,
362 **65**, 2692–2698.

363 Esch, G. W., & Fernández, J. C. (1993). A functional biology of parasitism: ecological and
364 evolutionary implications. Chapman and Hall, London, England.

365 Ferrari, N., Cattadori, I., Rizzoli, A., & Hudson, P. (2009). *Heligmosomoides polygyrus*
366 reduces infestation of *Ixodes ricinus* in free-living yellow-necked mice, *Apodemus*
367 *flavicollis*. *Parasitology*, **136**, 305–316.

368 Fielding, N. J., MacNeil, C., Dick, J. T. A., Elwood, R. W., Riddell, G. E., & Dunn, A. M.
369 (2003). Effects of the acanthocephalan parasite *Echinorhynchus truttae* on the feeding
370 ecology of *Gammarus pulex* (Crustacea: Amphipoda). *Journal of Zoology*, **261**, 321–
371 325.

372 Franceschi, N., Bauer, A., Bollache, L., & Rigaud, T. (2008). The effects of parasite age and
373 intensity on variability in acanthocephalan-induced behavioural
374 manipulation. *International Journal of Parasitology*, **38**, 1161–1170.

375 Friesen, O. C., Poulin, R., & Lagrue, C. (2018). Parasite-mediated microhabitat segregation
376 between congeneric hosts. *Biology Letters*, **14**, 20170671–20170671.

382 Gilbert, B. M., Nachev, M., Jochmann, M. A., Schmidt, T. C., Köster, D., Sures, B., &
383 Avenant-Oldewage, A. (2020). Stable isotope analysis spills the beans about spatial
384 variance in trophic structure in a fish host – parasite system from the Vaal River
385 System, South Africa. *International Journal for Parasitology: Parasites and Wildlife*,
386 **12**, 134–141.

387 Gutiérrez, J. S., Rakhimberdiev, E., Piersma, T., & Thieltges, D. W. (2017). Migration and
388 parasitism: Habitat use, not migration distance, influences helminth species richness in
389 Charadriiform birds. *Journal of Biogeography*, **44**, 1137–1147.

390 Hicks, O., Burthe, S. J., Daunt, F., Newell, M., Butler, A., Ito, M., Sato, K., & Green, J. A.
391 (2018). The energetic cost of parasitism in a wild population. *Proceedings of the Royal*
392 *Society B*, **285**, 20180489–20180489.

393 Hite, J. L., Pfenning, A. C., & Cressler, C. E. (2020). Starving the enemy? Feeding behavior
394 shapes host-parasite interactions. *Trends in Ecology & Evolution*, **35**, 68–80.

395 Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche
396 widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in
397 R. *Journal of Animal Ecology*, **80**, 595–602.

398 Johnson, M. W., & Dick, T. A. (2001). Parasite effects on the survival, growth, and
399 reproductive potential of yellow perch (*Perca flavescens* Mitchell) in Canadian shield
400 lakes. *Canadian Journal of Zoology*, **79**, 1980–1992.

401 Karlson, A. M. L., Reutgard, M., Garbaras, A., & Gorokhova, E. (2018). Isotopic niche
402 reflects stress-induced variability in physiological status. *Royal Society open science*,
403 **5**, 171398–171398.

404 Kennedy, C. R. (2006). *Ecology of the Acanthocephala*. Cambridge University Press, New
405 York, New York, 249 pp.

406 Knudsen, R., Siwertsson, A., Adams, C. E., Newton, J., & Amundsen, P. A. (2014). Similar
407 patterns of individual niche use are revealed by different time-integrated trophic
408 tracers (stable isotopes and parasites). *Ecology of Freshwater Fish*, **23**, 259–268.

409 Kuznetsova, A., Brockhoff, P. B., & Christensen R. H. B. (2017). lmerTest Package: Tests in
410 Linear Mixed Effects Models. *Journal of Statistical. Software*, **82**.

411 Lagrue, C., Kelly, D. W., Hicks, A., & Poulin, R. (2011). Factors influencing infection
412 patterns of trophically transmitted parasites among a fish community: host diet, host–
413 parasite compatibility or both? *Journal of Fish Biology*, **79**, 466–485.

414 Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope
415 ratios provide for community-wide measures of trophic structure? *Ecology*, **88**, 42–48.

416 Lefèvre, T., Lebarbenchon, C., Gauthier-Clerc, M., Missé, D., Poulin, R., & Thomas, T.
417 (2009). The ecological significance of manipulative parasites. *Trends in Parasitology*,
418 **24**, 41–48.

419 Loot, G., Brosse, S., Lek, S., & Guégan, J. F. (2001). Behaviour of roach (*Rutilus rutilus* L.)
420 altered by *Ligula intestinalis* (Cestoda: Pseudophyllidea): A field demonstration.
421 *Freshwater Biology*, **46**, 1219–1227.

422 Médoc, V., Piscart, C., Maazouzi, C., Simon, L., & Beisel, J. N. (2011). Parasite-induced
423 changes in the diet of a freshwater amphipod: Field and laboratory evidence.
424 *Parasitology*, **138**, 537–546.

425 Milinski, M. (1984). Parasites determine a predator's optimal feeding strategy.
426 *Behavioral Ecology and Sociobiology*, **15**, 35–37.

427 Molbert, N., Alliot, A., Leroux-Coyau, M., Médoc, V., Biard, C., Meylan, S., Jacquin, L.,
428 Santos, R. & Goutte, A. (2020). Potential benefits of acanthocephalan parasites for
429 chub hosts in polluted environments. *Environmental Science and Technology*, **54**,
430 5540–5549.

431 Molbert, N., Agostini, S., Alliot, F., Angelier, F., Biard, C., Decencière, B., Leroux-Coyau, M.,
432 Millot, A., Ribout, C. & Goutte, A. (2021). Parasitism reduces oxidative stress of fish
433 host experimentally exposed to PAHs. *Ecotoxicology and Environmental Safety*, **219**,
434 112322.

435 Moore, J. (2002). *Parasites and the Behavior of Animals*. Oxford Univ. Press, Oxford, U.K

436 Nachev, M., & Sures, B. (2016). Seasonal profile of metal accumulation in the
437 acanthocephalan *Pomphorhynchus laevis*: a valuable tool to study infection dynamics
438 and implications for metal monitoring. *Parasites Vectors*, **9**, 300.

439 Östlund-Nilsson, S., Curtis, L., Nilsson, G. E., & Grutter, A. S. (2005). Parasitic isopod
440 *Anilocra apogonae*, a drag for the cardinal fish *Cheilodipterus quinquelineatus*.
441 *Marian Ecology Progress Series*, **287**, 209–216.

442 Parker, G. A., Ball, M. A., & Chubb, J. C. (2015). Evolution of complex life cycles in
443 trophically transmitted helminths. I. Host incorporation and trophic ascent. *Journal of*
444 *Evolutionary Biology*, **28**, 267–291.

445 Paterson, R. A., Nefjodova, J., Salis, R. K., Knudsen, R. (2019). Exploring trophic niches and
446 parasite communities of sympatric Arctic charr and brown trout populations of
447 southern Norway. *Hydrobiologia*, **840**, 271–280.

448 Pegg, J., Andreou, D., Williams, C. F., & Britton, J. R. (2015). Head morphology and
449 piscivory of European eels, *Anguilla anguilla*, predict their probability of infection by
450 the invasive parasitic nematode *Anguillicoloides crassus*. *Freshwater Biology*, **60**,
451 1977–1987.

452 Pegg, J., Andreou, D., Williams, C. F., & Britton, J. R. (2017). Consistent patterns of trophic
453 niche specialization in host populations infected with a non-native copepod parasite.
454 *Parasitology*, **144**, 945–953.

455 Penczak, T. (2006). Movement pattern and growth ratio of tagged fish in two lowland rivers
456 of central Poland. *Polish Journal of Ecology.*, **54**, 267–282.

457 Pinheiro, J., & Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS* (1st ed). New York:
458 Springer-Verlag. Retrieved from //www.springer.com/gp/book/9780387989570.

459 Poulin, R. (2007). *Evolutionary Ecology of Parasites*. Princeton Univ. Press., Princeton, New
460 Jersey, 2nd ed.

461 Quevedo, M., Svanbäck, R. & Eklöv, P. (2009). Intrapopulation niche partitioning in a
462 generalist predator limits food web connectivity. *Ecology*, **90**, 2263–2274.

463 R Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation
464 for Statistical Computing, Vienna, Austria.

465 Rajeshkumar, S., Gomathinayagam, S., Ansari, A., & Munuswamy, N. (2013). Infection of
466 acanthocephalan parasite *Neoechinorhynchus agilis* sp. in the grey mullet (*Mugil*

467 *cephalus*) a candidate species from Corentyne coast, Berbice, Guyana. *International*
468 *Journal of Current Research and Review*, **5**, 53–62.

469 Ranta, E. (1995). Schistocephalus infestation improves prey-size selection by 3-spined
470 sticklebacks, *Gasterosteus aculeatus*. *Journal of Fish Biology*, **46**, 156–158.

471 Riekenberg, P. M., Joling, T., IJsseldijk, L. L., Waser, A. M., van der Meer, M. T. J., &
472 Thieltges, D. W. (2021). Stable nitrogen isotope analysis of amino acids as a new tool
473 to clarify complex parasite–host interactions within food webs. *Oikos*, **130**, 1650–
474 1664.

475 Sakthivel, A. (2014). Acanthocephalan (*Echinorhynchus* sp.) infection of yellowfin tuna
476 (*Thunnus albacares*) from Nagapattinam, south east coast of India. *Journal of Coastal*
477 *Life Medicine*, **2**, 596–600.

478 Sánchez, M. I., Varo, N., Matesanz, C., Ramo, C., Amat, J. A., & Green, A. J. (2013).
479 Cestodes change the isotopic signature of brine shrimp, *Artemia*, hosts: Implications
480 for aquatic food webs. *International Journal for Parasitology*, **43**, 73–80.

481 Sandground, J. H. (1936). On the potential longevity of various helminths with a record for a
482 species of *Trichostrongylus* in man. *The Journal of Parasitology*, **22**, 464–470.

483 Salal, P., Faliex, E., De Buron, I., & Morand, S. (2001). Sex discriminatory effect of the
484 Acanthocephalan *Acanthocephaloides propinquus* on a gobiid fish *Gobius Bucchichii*.
485 *Parasite*, **8**, 231–236.

486 Shinagawa, K., Urabe, M., & Nagoshi, M. (2001). Effects of trematode infection on
487 metabolism and activity in a freshwater snail, *Semisulcospira libertina*. *Diseases of*
488 *Aquatic Organisms*, **45**, 141–144.

489 Strona, G. (2015). Past, present and future of host–parasite co-extinctions. *International*
490 *Journal of Parasitology*, **4**, 431–441.

- 491 Taraschewski, H. (2000). Host-parasite interactions in Acanthocephala: a morphological
492 approach. *Advance in Parasitology*, **46**, 1–179.
- 493 Thorburn, D., Bal, T., Deflem, I., Volckaert, F., Eizaguirre, C., & Raeymaekers, J. (2022).
494 Context-dependent parasite infection affects trophic niche in populations of sympatric
495 stickleback species. *Parasitology*, **149**, 1164–1172.
- 496 Tierney, P. A. (2016). The role of helminth parasites in host invasion: a freshwater fish
497 system. Thesis. The University of Dublin, 212pp.
- 498 Vivas Muñoz, J. C., Feld, C. K., Hilt, S., Manfrin, A., Nachev, M., Köster, D., Jochmann, M.
499 A., Schmidt, T. C., Sures, B., Ziková, A., & Knopf, K. (2021). Eye fluke infection
500 changes diet composition in juvenile European perch (*Perca fluviatilis*). *Scientific*
501 *Report*, **11**, 3440.
- 502 Weinersmith, K., & Faulkes, Z. (2014). Parasitic Manipulation of Hosts' Phenotype, or How
503 to make a zombie—An introduction to the Symposium. *Integrative and Comparative*
504 *Biology*, **54**, 93–100.
- 505 Wolf, N., Carleton, S. A., & Martínez del Rio, C. (2009). Ten years of experimental animal
506 isotopic ecology. *Functional Ecology*, **23**, 17–26.
- 507 Yohannes, E., Grimm, C., Rothhaupt, K. O., & Behrmann-Godel, J. (2017). The effect of
508 parasite infection on stable isotope turnover rates of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ in multiple
509 tissues of Eurasian perch *Perca fluviatilis*. *PLoS ONE*, **12**, e0169058.