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Original Research Paper

**Distribution of *Pomphorhynchus laevis* s.l. (Acanthocephala)
among fish species at a local scale: importance of fish biomass-
density**

Marie-Jeanne Perrot-Minnot ^{a, *}, Loïc Bollache ^{b, §}, Clément Lagrue ^{c, §}

^a Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France

^b Laboratoire Chrono-environnement, UMR 6249 CNRS, Université Bourgogne Franche-Comté, 16 Route de Gray, 25000 Besançon, France

^c Department of Biological Sciences, University of Alberta, Edmonton, T6G 2E9, Alberta, Canada

§ Both authors contributed equally to this work

Running headline: Aggregation in *Pomphorhynchus* spp.

* Author for correspondance

Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté
6 Boulevard Gabriel, 21000 Dijon, France

Mail to: mjperrot@u-bourgogne.fr, Tel 33 3 80 39 63 40 / Fax33 3 80 39 62 31

1 **Summary**

2

3 Parasite distribution among hosts is a fundamental aspect of host-parasite interactions.
4 Aggregated parasite distributions within and across host species are commonly reported and
5 potentially influenced by many factors, whether host or parasite specific, or related to host-
6 parasite encounter and compatibility. Yet, the respective role of each in observed parasite
7 distributions are often unclear. Here, we documented the distribution of the acanthocephalan
8 parasite *Pomphorhynchus laevis sensu lato* in two replicate fish host populations. Aggregated
9 distributions were observed in both populations, within and across fish host species. We
10 found positive abundance-prevalence relationship across fish species, suggesting that resource
11 availability (fish host biomass-density) was the main driver of *P. laevis s.l.* distribution. This
12 was supported by further positive associations between mean parasite load and fish biomass-
13 density. We found little evidence for intensity-dependent regulation within host (i.e. intra-host
14 competition among co-infecting parasites). Furthermore, *P. laevis s.l.* infection had no
15 detectable effect on fish condition indices, except on the body condition of female barbel
16 (*Barbus barbus*). *Pomphorhynchus laevis s.l.* therefore tended to accumulate with size/age
17 within fish species, and with fish biomass density among fish species, with apparently
18 negligible limitations due to intra-host intensity-dependent regulation of parasite, or to
19 parasite-induced morbidity in fish. The relative availability of final hosts for trophic-
20 transmission thus appears to be the main driver of *P. laevis s.l.* distribution among fish.

21

22 **Key-words:** aggregation, body-condition, Cyprinid fish, complex life-cycle, freshwater,
23 gonadosomatic index, hepatosomatic index, overdispersion.

24

25

26 **Introduction**

27 The spatio-temporal distribution of parasites among hosts is a fundamental and dynamic
28 aspect of host-parasite interactions (Shaw & Dobson, 1995, Poulin, 2007a; Morand &
29 Krasnov, 2008; Poulin *et al.*, 2011). Heterogeneity in parasite distribution within and among
30 host species commonly expresses as over-dispersion (or aggregation), a pattern reported in a
31 diversity of host-parasite systems (Shaw & Dobson, 1995; Wilson *et al.*, 2002; Morand &
32 Krasnov, 2008). Aggregated parasite distribution mainly arises by chance, due to random
33 variations associated with parasite encounter and successful establishment (Poulin, 2013;
34 Gourbière *et al.*, 2015). The level of intra and interspecific parasite aggregation among hosts
35 is also expected to fluctuate with non-random variation in exposure rate and infection success
36 (i.e. the probability of encounter and host-parasite compatibility) (Anderson & Gordon, 1982;
37 Shaw & Dobson, 1995; Wilson *et al.*, 2002; Poulin, 2007a, b; Perez-del-Olmo *et al.*, 2011;
38 Poulin, 2013; Gourbière *et al.*, 2015; Johnson & Wilber, 2017). Such heterogeneity is
39 associated with host and parasite specific features, from individual to species level. For
40 instance, variation in encounter probability may arise from spatio-temporal differences in
41 foraging strategies or habitat preferences among hosts, or from differences in parasite-induced
42 alterations of host behaviour that modulate transmission success. Variations in the rate of
43 infection success may arise from differences in host physiological defence systems, and in
44 parasite exploitation or evasion strategies. Parasite species-specific features, such as life cycle
45 (direct or complex) and transmission mode (e.g. passive, active or trophic; Shaw & Dobson
46 1995; Wilson *et al.*, 2002; Poulin, 2007a), also determine parasite distribution among hosts.

47 Parasites with complex (i.e. heteroxenous) life cycles and trophic transmission rely on
48 the consumption of infected intermediate or paratenic hosts by suitable definitive hosts, to
49 complete their life cycle. They are expected to accumulate in definitive hosts, especially those
50 occupying higher trophic levels, as these hosts are likely to consume large numbers of

51 infected intermediate host prey (Shaw & Dobson, 1995; Perez-del-Olmo *et al.*, 2011; Lester
52 & McVinish, 2016). At the intraspecific level, they may also accumulate with predator size
53 and age, as prey uptake increases with predator body size. This should be especially true for
54 parasites with a prolonged use of their host for growth and reproduction, unless intensity-
55 dependent regulation occurs.

56 In this context, acanthocephalan parasites offer interesting features to test these
57 predictions (Kennedy, 2006). They have a two-host life cycle involving arthropods as
58 intermediate hosts and vertebrates as definitive hosts, occasionally incorporating paratenic
59 hosts (Crompton & Nickol, 1985; Kennedy, 2006; Médoc *et al.*, 2011). Arthropods become
60 infected when accidentally consuming eggs. In the intermediate host, the parasite grows and
61 then enters its last developmental stage (cystacanth), waiting for trophic transmission to the
62 definitive host. Upon predation of the intermediate host by the appropriate vertebrate
63 definitive host, further growth, sexual maturation and reproduction take place, and eggs are
64 released with host faeces (Crompton & Nickol, 1985). Acanthocephalans have a prolonged
65 use of their vertebrate hosts for growth, sexual maturation and continuous reproduction
66 (Crompton & Nickol, 1985). Accumulation of intestinal parasites is thus expected to occur
67 over time, although intensity-dependent regulation of parasite infra-population within
68 individual hosts may limit parasite accumulation. In addition to heterogeneity in spatial
69 distribution, abundance of adult acanthocephalans may also show marked seasonal variations
70 (Crompton & Nickol, 1985; Dudiňák and Špakulová, 2003; Kennedy, 2006

71 The goal of this study was precisely to address the distribution of the acanthocephalan
72 parasite of freshwater fish, *Pomphorhynchus laevis sensu lato* Amin *et al.*, (2003) (thereafter
73 *P. laevis s.l.*), within local fish communities. Previous records of *P. laevis s.l.* suggest a broad
74 range of fresh and brackish water fish species as definitive hosts and amphipods as
75 intermediate hosts across the Western Palearctic area (Kennedy, 2006; Špakulová *et al.*,

76 2011; Vardić Smrzlić *et al.*, 2015; Perrot-Minnot *et al.*, 2018), but also at local scales (Perrot-
77 Minnot *et al.*, 2019). Instead of comparing distribution patterns among host-parasite systems
78 (Morand & Krasnov, 2008) or among populations within a given host-parasite system
79 (Rodríguez & Valdivia, 2017), we focused on inter-host heterogeneity in parasite distribution
80 at a local scale. We considered the assemblage of local fish species as resource patches
81 structuring the parasite population into infra-populations. Specifically, we assessed parasite
82 distribution across a local range of fish species, and its consequence on fish health. We aimed
83 at answering the following questions. (1) Are the patterns of mean abundance and aggregation
84 of *P. laevis s.l.* within local fish host community assemblages consistent with some general
85 macroecological laws? We predicted that mean parasite abundance should be positively
86 correlated to prevalence (Morand & Krasnov, 2008), that parasite abundance should vary with
87 fish age (Anderson & Gordon, 1982) approximated by fish size, and that heterogeneity in
88 *Pomphorhynchus* distribution within fish host species should be consistent with the general
89 pattern of parasite aggregation (Shaw & Dobson 1995; Wilson *et al.*, 2002; Morand &
90 Krasnov, 2008). (2) Is variation in mean parasite abundance among fish species related to
91 local fish biomass-density, or density (Arneberg *et al.*, 1998, Arneberg, 2001; Poulin, 2007a;
92 Buck & Lutterschmidt, 2017)? This prediction holds if encounter rate of infected intermediate
93 host prey with a given predator species increases with predator density, with little effect of
94 other fish-specific features such as differences in diet or compatibility towards *P. laevis s.l.*
95 (3) Is variation in aggregation levels among fish species related to fish density? We expect a
96 positive association between parasite aggregation levels and fish density or biomass-density
97 across fish species, as suggested in previous studies, but also across host populations for a
98 given host-parasite system, (Rodríguez & Valdivia, 2017; Johnson & Wilber, 2017). (4) Is
99 there evidence for negative effects of infection on fish condition?

100 We documented the pattern of host use by *P. laevis s.l.* in two rivers, using standard
101 infection parameters (Shaw & Dobson, 1995; Morand & Krasnov, 2008). We conducted
102 standard analysis of abundance and distribution of *P. laevis s.l.* within the fish host network,
103 using abundance - prevalence and abundance - variance relationships (Morand & Krasnov,
104 2008). Abundance-occupancy relationship is a general pattern in free-living species (Gaston
105 *et al.*, 2000), and in parasites (Morand & Krasnov 2008). At the intraspecific level,
106 abundance-occupancy relationship is expected to be driven by temporal variations in resource
107 availability (Gaston *et al.*, 2000). For a given parasite species, variations in resource
108 availability may arise within the community of host species (Morand & Krasnov 2008),
109 driven by relative host density or biomass-density. We estimated *P. laevis s.l.* aggregation
110 among fish host species using the abundance-variance relationship known as Taylor's power
111 law (Anderson & Gordon, 1982; Shaw & Dobson, 1995; Kilpatrick & Ives, 2003; Morand &
112 Krasnov, 2008; Johnson & Hoverman, 2014). Finally, we assessed potential effects of *P.*
113 *laevis s.l.* infection on fish health, by estimating three standard body-condition metrics: body
114 condition index (BCI), hepatosomatic index (HSI, related to energy storage), and
115 gonadosomatic index (GSI, reflecting reproductive investment) (Cheppala *et al.*, 1995). These
116 metrics are commonly used to assess the impact of pollutants (Dragun *et al.*, 2013), infection
117 (Tierney *et al.*, 1996; Kalogianni *et al.*, 2013; Masson *et al.*, 2015), and habitat quality
118 (Nagrodski *et al.*, 2013) in fish.

119

120 **Material and methods**

121

122 *Localities, fish community composition and sampling*

123 One locality on the Ouche River (47°17'54.56"N 5°2'21.97"E), and one locality on the
124 Vingeanne River (47°20'51.66"N 5°27'8.76"E) were sampled in 2003 and 2005, and in 2004

125 and 2005, respectively. To avoid incorporating seasonal variation in prevalence and
126 abundance to the analysis of *P. laevis s.l.* distribution, we collected samples at the same time
127 of year (late spring / early summer). We retrieved information on the composition of local fish
128 communities in these two localities from the ONEMA database
129 (<http://www.naiades.eaufrance.fr/acces-donnees#/hydrobiologie>), based on the regular
130 monitoring of fish species richness and abundance between 2001 and 2006. The database
131 provides a full record of density and biomass-density (thereafter biomass) of each fish species
132 locally present. Thirty fish species were identified of which fourteen were present in both
133 localities (Fig. S1 in Perrot-Minnot *et al.*, 2019).

134 Fish were captured by electric fishing or netting, killed immediately, identified,
135 measured (fork length) and weighed. Upon fish dissection, we removed, opened and screened
136 intestines to collect adult *P. laevis s.l.* Since the occurrence of paratenic hosts or dead-end
137 hosts has been previously reported for *P. laevis s.l.* (Crompton & Nickol, 1985), we also
138 inspected fish body cavity and viscera for extra-intestinal infection with *P. laevis s.l.*
139 cystacanths. We included in the analyses only fish species for which at least five individuals
140 were dissected. We measured gonad and liver weights on a subset of fish to estimate GSI and
141 HSI.

142 We did not distinguish *P. tereticollis* and *P. laevis* in the present study, despite the
143 recent taxonomic revision of *P. laevis s.l.* and the erection of *P. tereticollis* as a true species
144 (Špakulová *et al.*, 2011). Both species are present in the two localities sampled here, but they
145 share the same amphipod intermediate hosts and fish definitive host species. Although they
146 seem to exhibit some specificity towards fish final hosts in terms of relative abundance rather
147 than presence/absence (Perrot-Minnot *et al.* 2019), a preliminary analysis suggested that both
148 *Pomphorhynchus* species exhibited comparable level of aggregation among fish host. This
149 subset of 815 *Pomphorhynchus* spp. required genotyping for identification, and was not large

150 enough to quantify reliably parasite distribution pattern among all fish species for each
151 *Pomphorhynchus* species. In fact, 2005 *Pomphorhynchus* that were not genotyped, and 268
152 additional individual fish (including non-infected ones), were added to the dataset used to run
153 the present analysis.

154

155 *Infection pattern of P. laevis s.l.: prevalence, abundance and aggregation across fish host*
156 *species*

157 We used multiple descriptors to characterize *P. laevis s.l.* infection patterns in each
158 fish species (Bush *et al.*, 1997): prevalence (i.e. proportion of individual hosts infected),
159 abundance (i.e. mean number of parasites per host), and intensity (i.e. mean number of
160 parasites per infected host). We estimated *Pomphorhynchus laevis s.l.* prevalence and
161 intensity for two non-exclusive categories of individual host: fish infected with intestinal adult
162 *P. laevis s.l.* and fish harbouring cystacanths in the body cavity and in viscera. We performed
163 the analysis of *P. laevis s.l.* abundance and aggregation only on intestinal adult parasites,
164 since we considered the distribution pattern of parasites among hosts in relation to population
165 stability. Indeed, the contribution of extra-intestinal parasites to the parasite life-cycle and
166 population dynamics is unclear, as it may depend on the host species considered (i.e. some
167 may act as paratenic hosts, given their inclusion into the diet of piscivorous fish, while others
168 are dead-end hosts, such as minnow and catfish, respectively) (Médoc *et al.*, 2011; Perrot-
169 Minnot *et al.*, 2019).

170 We computed the distribution of *P. laevis* abundance for each fish species within each
171 river, to illustrate its distribution pattern among individual fish for each fish species. We
172 tested the relationship between *P. laevis s.l.* abundance (log10+1 transformation) and
173 individual body size using linear regression.

174 We estimated the degree of aggregation of intestinal adult *P. laevis s.l.* within fish
175 species using the slope of the regression of variance in parasite abundance to mean parasite
176 abundance (both log₁₀-transformed), known as Taylor's power law, among fish species. To
177 get close to the sample size recommended (> 30; Shaw and Dobson 1995; Poulin 2013), we
178 removed fish species for which less than 25 individuals were sampled, and run the analysis on
179 data from the Ouche River only (N = 9 species of fish). Departure from random distribution
180 of parasites towards aggregation among fish hosts would be evidenced by a slope greater than
181 one (Morand & Krasnov, 2008; Johnson & Hoverman, 2014).

182 The variance-to-mean ratio was then used as a measure of aggregation level, in
183 preference to the other commonly used parameter k (Morand & Krasnov, 2008), because we
184 compared parasite distribution patterns among fish species differing in *P. laevis s.l.*
185 prevalence (and for some of them, with a large number of uninfected hosts) (Scott, 1987 in
186 Wilson *et al.*, 2002). We used the variance-to-mean ratio to test for a relationship between
187 aggregation level and fish biomass, across the range of fish species.

188

189 *Fish condition in relationship to P. laevis s.l. abundance*

190 Variations in fish (BCI, HSI and GSI) were analysed in relation to intestinal *P. laevis*
191 *s.l.* abundance, fish species and sex. Only fish species and sex for which at least twelve
192 individuals were screened and two infected were included in the analyses. Some individual
193 fish could not be sexed and were included as "juveniles". We measured fish body condition
194 index as the residuals of the regression of log₁₀-transformed whole body mass on log₁₀-
195 transformed body size (fork length) (Chellappa *et al.*, 1995). Since the relationship was
196 significantly different among fish species, the residuals were estimated for each fish species
197 separately. Hepatosomatic and gonadosomatic indices were calculated as the ratio of liver
198 weight and gonad weight on body mass, respectively (Chellappa *et al.*, 1995)

199

200 *Data analysis*

201 All statistical analyses were performed using R software v 3.5.1. and v. 3.6.1. (R Core
202 team, 2018). Within each fish species, the relationship between *P. laevis s.l.* abundance
203 ($\log_{10}+1$ transformation) and individual body size was tested using linear regression. We also
204 computed the 95% confidence intervals around prevalence using PropCIs package (v. 0.3.0)
205 (Scherer, 2018).

206 We run linear and generalized linear models (GLM) to analyse prevalence and
207 abundance, We performed model comparison to estimate the contribution of each predictor
208 variable to variation in the dependant variable. The approach is based on deviance comparison
209 between models fitted to the same data - the full model and the model without one predictor
210 variable- (maximum likelihood ratio test, Rpackage 'lmtest', v. 0.9-36; Zeileis & Hothorn,
211 2002). We used the associated Chi-square value and probability to assess the significance of
212 each predictor variable. We also reported the coefficient of determination R^2 , as an estimate of
213 how well variation in the dependant variable is explained by predictor ones. As we included
214 locality as a random factor, we computed both the marginal R^2_m and the conditional R^2_c ,
215 which represents the part of the variance explained by fixed effects and by the entire model
216 respectively, using R package 'MuMIn' v. 1.42.1 (Barton, 2018). We analysed differences in
217 prevalence and abundance according to fish species using GLM with binomial distribution,
218 and GLM with negative binomial link function, respectively, adding locality as a random
219 factor (package Lme4 v.1.1.19, Bates et al. 2015; and package MASS v.7.3.51; Venables &
220 Ripley 2002, respectively). We compared parasite intensity among fish species within each
221 locality using a Kruskal-Wallis test and post-hoc paired comparisons (Dunn test, Benjamini -
222 Yekutieli B-Y method of correction for multiple tests; package Dunn-test, Dinno, 2015) as
223 the distribution of intensity could not be normalized.

224 We analysed the relationship between prevalence and mean abundance across the
225 range of fish species using spearman rank correlation test. We tested the relationship between
226 mean *P. laevis s.l.* abundance and fish density or biomass across the range of fish species
227 using linear regression after log – log transformation (log10), adding locality as a random
228 factor.

229 We analysed the aggregation of *P. laevis s.l.* across the nine fish species from Ouche
230 River for which more than 25 individuals were sampled. We regressed the log10-transformed
231 variance of abundance on the log10-transformed mean abundance, applying a simple linear
232 model, Given the low sample size (9 fish species), we used ordinal nonparametric bootstrap
233 procedure (1000 replicates) to get the bootstrapped value of the regression slope and its 95%
234 confidence interval (Package boot, v.1.3-23) (Canty & Ripley, 2019). We then tested for an
235 effect of fish density- biomass on the variance-to-mean abundance ratio, using the Spearman
236 rank correlation test.

237 All three condition parameters, BCI, HIS and GSI were used as the dependent factor in
238 linear model (BCI) or GLM with gamma-distribution (HIS, GSI), including parasite
239 abundance (log10-transformed), sex, and their interaction, as fixed effects. Fish species and
240 its interaction with parasite abundance were included in the full model for HIS and GSI, while
241 separate analyses of BCI were done for each fish species.

242

243 **Results**

244 *Pomphorhynchus laevis s.l.* samples were collected from 14 species of fish, mainly cyprinids,
245 among which four species were collected in both localities (Table 1). A total of 881 fish were
246 dissected; 752 from 11 fish species sampled in the Ouche River and 129 from 9 fish species
247 sampled in the Vingeanne River. The sampling of each fish species was representative of the

248 local fish community, irrespective of whether the fish species hosted *P. laevis s.l.* or not (see
249 Table S1 in Perrot-Minnot *et al.*, 2019).

250

251 *Prevalence and abundance of P. laevis s.l.*

252 Intestinal *P. laevis s.l.* were collected from all of the eleven fish species sampled in the
253 Ouche River and from six out of the seven fish species in the Vingeanne River (Table 1; Fig.
254 1). Extra-intestinal *P. laevis s.l.* cystacanths were found in several species of fish; all but one
255 (*Chondrostoma nasus*) also harboured intestinal adults (Table 1; Fig. 1). Extra-intestinal
256 parasites were either embedded as cystacanth or attached as evaginated cystacanth on liver
257 and gonad surface or in adipose tissues.

258 Parasite distribution within each fish species was clearly over-dispersed (Fig. S1). At
259 the intra-host level, *P. laevis s.l.* abundance (log-transformed) increased significantly with
260 individual fish size in most fish species in both localities, but with a low to medium
261 coefficient of determination (0.07 to 0.62) (Fig. S2). There was no evidence for a decrease in
262 mean and variance of abundance in the upper-size category, but rather a log-linear trend for
263 parasite load to increase with body size (Fig. S2).

264 Prevalence of intestinal *P. laevis s.l.* differed among fish species ($\text{Chi}^2 = 171.3$, $\text{df} =$
265 12 , $P < 0.0001$, $\text{R}^2\text{m} = 0.21$, $\text{R}^2\text{c} = 0.37$), as well as both intestinal and extra-intestinal *P.*
266 *laevis s.l.* ($\text{Chi}^2 = 117.9$, $\text{df} = 13$, $P < 0.0001$, $\text{R}^2\text{m} = 0.34$, $\text{R}^2\text{c} = 0.49$). Half of fish species
267 harboured prevalence above 50% (Fig. 1). Infection intensity of intestinal *P. laevis s.l.*
268 differed among fish species in the Ouche River (Kruskal-Wallis chi-squared = 43.1724, $\text{df} =$
269 10 , $P < 0.0001$) but not in the Vingeanne River (chi-squared = 2.44, $\text{df} = 5$, $P = 0.79$) (Fig.
270 S3). There was no effect of sampling effort (number of individual fish sampled per fish
271 species) on prevalence or intensity (Spearman correlation test, samples from both rivers
272 pooled: $N = 18$; $S=1254$, $P = 0.24$, $\text{Rho} = -0.29$; and $S = 11.66$, $P = 0.15$, $\text{Rho} = 0.66$,

273 respectively). The abundance of intestinal *P. laevis* s.l. differed among fish species ($\text{Chi}^2 =$
274 436.4, $\text{df} = 12$, $P < 0.0001$, $R^2_{\text{m}} = 0.38$, $R^2_{\text{c}} = 0.54$). Abundance and prevalence were
275 significantly correlated across fish species and localities (Spearman correlation test: $N = 17$, S
276 $= 167.6$, $P = 0.0001$, $\text{Rho} = 0.79$; Fig. 2).

277

278 *Are differences in mean abundance among fish hosts explained by local fish biomass?*

279 We tested the hypothesis that mean parasite abundance per fish species could be
280 determined by host species abundance. The mean abundance of *P. laevis* s.l. in fish species
281 was positively correlated with local fish biomass ($N = 17$; $\text{Chi}^2 = 4.76$, $\text{df} = 1$, $P = 0.03$; R^2_{m}
282 $= R^2_{\text{c}} = 0.25$) (Fig. 3), but not with local fish density ($\text{Chi}^2 = 1.53$, $\text{df} = 1$, $P = 0.22$ (Fig. S4).
283 The roach *Rutilus rutilus*, stood as an outlier in the Ouche River but not the Vingeanne River,
284 with a lower mean abundance than expected from its biomass (Fig. 3).

285

286 *Aggregation of intestinal P. laevis s.l. across fish species*

287 The level of aggregation of intestinal *P. laevis* s.l. among fish species was estimated
288 using the relationship between variance in parasite abundance and mean abundance (log 10-
289 transformed) among nine fish species from the Ouche River. Variance in abundance of
290 intestinal parasites among fish species was strongly related to mean abundance, with a slope
291 significantly different from unity, indicative of aggregation relative to random distribution
292 (Table 2, Fig. 4). The mean abundance of intestinal *P. laevis* s.l. explained more than 95% of
293 the variance in abundance. Ouche RiverVingeanne RiverOuche RiverVingeanne River

294 The variance-to-mean abundance ratio tended to increase with biomass-density
295 although not significantly (bootstrapped estimate of Spearman rank correlation and its 95%
296 CI: $N = 9$, $\text{Rho} = 0.68$ [-0.34 – 0.97]) (Fig. S5).

297

298 *Effect of infection on fish condition indices*

299 Variations in BCI were not explained by the full model including parasite abundance, host sex
300 and their interaction as predictors in any of the fish species, except in barbel from Ouche
301 River (Table 3a), where body condition decreased with parasite load in females (Fig. S6).

302 The relationship between hepatosomatic index and parasite load differed among fish
303 species (Table 3b). Interestingly, HIS increased significantly with parasite load in barbel (Fig.
304 S7a); however, HIS increased significantly with body size in the same manner (Fig. S7b).
305 Variations in gonadosomatic index were independent of parasite load (Table 3b). GSI differed
306 according to fish species and sex (Fig. S7c, d), with females exhibiting higher size-corrected
307 weight of gonads compared to males and juveniles (Fig. S7d).

308

309 **Discussion**

310

311 *Abundance-prevalence relationship and aggregation*

312 The distribution of *P. laevis* s.l. within most fish species was aggregated, confirming the
313 pattern reported in other Acanthocephalan species, both in final hosts (Anderson & Gordon,
314 1982; Dobson & Keymer, 1985; Kennedy 2006), and in intermediate hosts (Dobson &
315 Keymer, 1985; Rodríguez & Valdivia, 2017), and more generally in macroparasites (Shaw &
316 Dobson, 1995; Poulin, 2007a, Morand & Krasnov, 2008).

317 The more abundant *P. laevis* s.l. was in a given host species, the highest was its
318 prevalence, in both localities. This pattern is equivalent to the abundance-occupancy
319 relationship in ecology. Variations in habitat availability and quality can generate such pattern
320 in free-living species (Gaston *et al.*, 2000, Freckleton *et al.*, 2006). For parasites, it
321 corresponds to variation in host availability (encounter and transmission rates) and
322 compatibility. To further understand parasite distribution across fish species, we analysed

323 aggregation using the variance – to – mean abundance relationship (Gaston *et al.*, 2000;
324 Morand & Krasnov, 2008), on a subset of fish species. A high proportion of variance in
325 parasite abundance (95%) was explained by mean abundance across fish species. This result
326 is in agreement with Shaw & Dobson (1995) and Poulin (2013), and provides evidence for a
327 nearly random process of *P. laevis s.l.* accumulation among fish species. Several factors could
328 potentially increase heterogeneity in parasite distribution among fish host species, such as
329 sample size and host mean body size (Poulin, 2013; Johnson & Wilber, 2017), and
330 behavioural or physiological differences among host species (Shaw & Dobson 1995).
331 Differences in diet choice, microhabitat and host-parasite compatibility can all influence
332 parasite distribution among hosts. However, their contribution to variation in aggregation
333 among fish hosts should be negligible compared to the process of random accumulation of *P.*
334 *laevis s.l.* This conclusion should be taken cautiously however; sample size limitations
335 restricted the number of fish species included to only nine out of the fourteen species of fish
336 hosts recorded.

337

338 *Abundance and aggregation in relation to fish biomass*

339 The process of random accumulation of *P. laevis s.l.* evidenced here was suggesting that
340 parasite distribution within and among fish species was mainly driven by the probability of
341 encounter rate of predators with infected host prey. We attempted to test this hypothesis by
342 using local fish biomass-density as a proxy for encounter rate. Interestingly, we found a
343 positive relationship between mean parasite abundance and fish biomass-density, but not fish
344 density. Most fish species prey upon amphipods, and these crustaceans are the most abundant
345 macroinvertebrates sampled in these rivers (MJPM pers. observation), Therefore, encounter
346 rate with infected prey increases with fish host density but also body mass, both leading to a
347 higher prey intake rate. The distribution of *P. laevis s.l.* among fish hosts further confirms that

348 potential variations in compatibility across fish host species have a negligible effect on the
349 distribution of *P. laevis s.l.* This interpretation holds assuming that the accumulation of adult
350 intestinal parasites in individual fish occurs at a rate proportional to encounter rate across fish
351 species, meaning low heterogeneity in compatibility, and low within-host competition among
352 co-infecting parasites. In support of this assumption, the lack of intensity-dependent
353 regulation of parasite development or fecundity has been reported previously on a subset of
354 these samples. Parasite load had no effect on parasite body size or reproductive parameters
355 (testes volume and number of eggs) (Perrot-Minnot *et al.*, 2019). It is still possible that inter-
356 individual differences within fish species in growth rate or diet choice contribute to the low to
357 medium coefficient of determination between parasite load and fish size. In addition, the
358 occurrence of extra-intestinal parasites in several fish species still suggests that some species
359 are more suitable definitive hosts than others. However, the analysis of aggregation pattern
360 using all *P. laevis s.l.* (both intra- and extra-intestinal) points to the same conclusions (data
361 not shown). We favoured the analysis of intestinal parasite distribution, since the contribution
362 of extra-intestinal parasites to the life-cycle is difficult to establish. Indeed, it may differ
363 according to fish host, either paratenic hosts (minnow), or dead-end hosts (catfish), the former
364 being part of piscivorous fish diet.

365 Given the relation of parasite distribution to local fish biomass density, a large fraction
366 of *P. laevis s.l.* population typically occurs within a few host species, mainly barbel and chub.
367 Interestingly, this pattern does not preclude narrower host range when considering *P. laevis*
368 and *P. tereticollis* separately, in particular with respect to fish feeding ecology (Perrot-Minnot
369 *et al.*, 2019).

370

371 *Effects on fish host condition/health*

372 We did not observe a decrease in the mean and variance of abundance in the upper category
373 of fish size. Following Lester (1982) and Wilson *et al.* (2002), and assuming that size
374 increases with age, this log-linear increase in abundance with age suggests negligible parasite-
375 induced mortality or acquired immunity in fish. In addition, no effect of infection on body
376 condition was evident, except in female barbel, that exhibited a decreasing body condition
377 with increasing parasite load. Since barbel exhibited the highest mean intensity of *P. laevis*
378 *s.l.*, with 25% of individuals harbouring more than 30 adult worms (Table 1; Fig. S1), it is
379 possible that *P. laevis s.l.* impacts fish body condition when reaching intensities hardly seen
380 in most fish species. In addition, parasite load did not affect HIS nor GSI. The spurious
381 positive correlation between HIS and parasite load found in barbel was likely the consequence
382 of the positive correlations of both HIS and parasite load with fish body size (or age). As such
383 positive relationship between HIS and host size has been reported before (in sharks, Hussey *et*
384 *al.*, 2009), it is important to emphasize the necessity to look for confounding variables before
385 interpreting the relationship between HIS and parasite load. In ectotherms with continuous
386 growth, this relationship is probably reflecting both the higher metabolic efficiency of larger
387 individuals within a predatory species, possibly sustained by a larger liver relative to body
388 mass or size, and the increase in parasite load with age (approximated by size). To our
389 knowledge, this hypothesis has never been addressed so far.

390

391 **Conclusion**

392 Positive relationships between abundance and occupancy, and variance and mean in
393 abundance have been regularly evidenced at the intraspecific and interspecific levels, in free-
394 living (Gaston *et al.*, 2000) and parasite species (Morand & Krasnov, 2008; Jenkins & Owens,
395 2011; Pérez-del-Olmo *et al.*, 2011). Yet, the underlying causes are not well understood, as
396 they potentially include diverse intrinsic and extrinsic factors (reviewed in Johnson &

397 Hoverman 2014, Poulin 2007a). Here, the positive association between mean *P. laevis* s.l.
398 abundance and fish biomass-density tends to suggest that resource availability, represented by
399 fish biomass-density, is the main driver of parasite distribution among hosts. It is important to
400 notice that such relationship did not hold using fish density. *Pomphorhynchus laevis* s.l.
401 therefore tends to accumulate with age within fish species, and with fish biomass-density
402 among fish species, with negligible limitations due to intra-host intensity dependent
403 regulation of parasite nor of parasite-induced morbidity in fish, respectively. It shows that
404 biomass-density, rather than density alone, has to be taken into account for trophically
405 transmitted parasites, by contrast to parasites transmitted by contact. We thereby emphasized
406 a specific feature of spatial distribution of ‘predators as resources’ for trophically-transmitted
407 parasites; and its contribution to aggregative distribution.

408

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545

546 **Figure legends**

547

548 Fig. 1: Prevalence of *P. laevis s.l.* in 14 fish species from two rivers. Individual fish were
549 harbouring adult parasites in the intestine exclusively (plain bars), both adult parasites in the
550 intestine and immature parasites (cystacanths) in body cavity or viscera (dotted bars), or
551 exclusively immature parasites (cystacanths) in body cavity or viscera (dashed bars). Total
552 prevalence is represented with its 95% confidence interval. (a), Ouche River; (b), Vingeanne
553 River; N = number of fish sampled. Asterisk: significantly lower prevalence of intestinal
554 parasites compared to the other groups of fish species. See Table 1 for abbreviations of fish
555 species.

556

557 Fig. 2: Relationship between mean abundance and prevalence of intestinal *Pomphorhynchus*
558 *laevis s.l.* across fish host species in the Ouche and Vingeanne Rivers. This relationship
559 corresponds to the “abundance–occupancy” rule for free-living species.

560

561 Fig. 3: Relationship between local fish biomass (g.100 m⁻²) and mean abundance of intestinal
562 *Pomphorhynchus laevis s.l.* per fish species, across fish species and localities (Ouche and
563 Vingeanne rivers).

564

565 Fig. 4: Relationship between variance in abundance and mean abundance of intestinal
566 *Pomphorhynchus laevis s.l.* across fish host species in the Ouche River, on a log scale.
567 Regression analysis was performed using log-transformation. A slope higher than one
568 indicates aggregation.

569

Table 1 – Abundance and intensity of *Pomphorhynchus laevis s.l.* parasites in Ouche (O; years 2003, 2005) and Vingeanne (V; years 2004 and 2005) rivers, in fish species for which at least five individuals were sampled (loach excluded for Vingeanne River). Abundance and intensity were estimated separately for adult parasites in the intestinal track and for immature parasites (cystacanths) found outside of the intestinal track, in viscera or in the body cavity. * Prevalence of intestinal *P. laevis s.l.* , and its 95% CI. BF: benthic fish, bottom feeder; BPF: benthopelagic fish.

Fish host (habitat)	River	Number of fish sampled / infected	Number of fish with <i>P. laevis s.l.</i>		Prevalence of intestinal <i>P. laevis s.l.</i> (95% CI)	<i>P. laevis s.l.</i> abundance (median-1 st and 3' quartiles)		<i>P. laevis s.l.s</i> intensity (median - 1' and 3' quartiles)	
			in intestinal tract	outside intestinal tract		Parasites in intestinal tract	Parasites outside intestinal tract	Parasites in intestinal tract	Parasites outside intestinal tract
All fish species	O	752 / 377	375	54		0 (0 - 2)	0 (0 - 0)	2 (1 - 4)	2 (2 - 6)
	V	122 / 100	83	20		2 (0 - 7)	0 (0 - 0)	5 (2 - 10.25)	2.5 (2 - 16.75)
Cypriniformes - Cyprinidae									
<i>Barbus barbus</i> (BF) Barbel, Bbs	O	26 / 16	16	0	0.61 (0.42- 0.79)	2 (0 - 9)	0 (0 - 0)	6 (2.3-31.8)	-
	V	31 / 29	29	0	0.94 (0.80- 0.99)	4 (3 - 29)	0 (0 - 0)	5 (3 - 32.5)	-
<i>Gobio gobio</i> (BF) Gudgeon, Gg	O	64 / 23	10	15	0.16 (0.08- 0.26)	0 (0 - 0)	0 (0 - 0)	1 (1 - 2.25)	2 (2 - 6)
	V	8 / 3	3	0	0.38 (0.11- 0.72)	0 (0 - 3.25)	0 (0 - 0)	4 (1 - 4)	.
<i>Squalius cephalus</i> (BPF) Chub, Sc	O	318 / 202	202	0	0.64 (0.58- 0.69)	1 (0 - 3)	0 (0 - 0)	2 (1 - 4)	-
	V	43 / 42	40	3	0.93 (0.82- 0.98)	5 (2 - 10)	0 (0 - 0)	5.5 (2 - 10)	2 (1 - 38)
<i>Rutilus rutilus</i> (BPF) Roach, Rr	O	26 / 1	1	0	0.04 (0.002-0.18)	0 (0 - 0)	0 (0 - 0)	1	-
	V	12 / 7	3	5		0 (0 - 1.5)	0 (0 - 2)	4(2 - 18)	2 (1.5 - 9)
<i>Telestes souffia</i> (BPF) Vairone, Ts	O	47 / 24	24	2	0.51 (0.37-0.65)	1 (0 - 4)	0 (0 - 0)	4 (2 - 10)	3,5 (1 - 6)

<i>Chondrostoma nasus</i> (BPF) Nase, Cn	V	15 / 7	0	7		0 (0 - 0)	0 (0 - 4)	-	4 (2 - 18)
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Table I (continued)

Fish host (habitat)	River	Number of fish sampled / infected	Number of fish with <i>P. laevis s.l.</i>		Prevalence of intestinal <i>P. laevis s.l.</i> (95% CI)	<i>P. laevis s.l.</i> abundance (median-1 st and 3' quartiles)		<i>P. laevis s.l.s</i> intensity (median - 1' and 3' quartiles)	
			in intestinal tract	outside intestinal tract		Parasites in intestinal tract	Parasites outside intestinal tract	Parasites in intestinal tract	Parasites outside intestinal tract
<i>Scardinius erythrophthalmus</i> (BPF) Rudd, Se	O	6 / 4	4	0	0.68 (0.26-0.94)	1 (0 - 2.25)	0 (0 - 0)	1.5 (1-2.75)	-
<i>Leuciscus leuciscus</i> (BPF) Common Dace, Ll	V	7 / 6	6	0	0.86 (0.47-0.99)	6 (1 - 11)	0 (0 - 0)	6.5 (1 - 13)	-
<i>Phoxinus phoxinus</i> (BPF) Minnow, Pp Cypriniformes - Balittonidae	O	68 / 40	18	31	0.24 (0.17 - 0.38)	0 (0 - 1)	0 (0 - 3)	2 (1 - 5.25)	4 (2 - 7)
<i>Barbatula barbatula</i> (BF) Loach, Bba Siluriformes - Ictaluridae	O	86 / 33	32	2	0.37 (0.28 - 0.48)	1 (0 - 1)	0 (0 - 0)	1,5 (1 -2)	1
<i>Ameiurus melas</i> (BF) Catfish, Am Perciformes - Percidae	V	6 / 6	2	5	0.18 (0.06 - 0.74)	0 (0 - 3.25)	2 (0.75-25.3)	4.5 (2 - 7)	2 (1.5 - 27.5)
<i>Perca fluviatilis</i> (BPF) Perch, Pf Scorpaeniformes - Cottidae	O	16 / 10	10	0	0.63 (0.38 - 0.83)	2 (0 - 4.75)	0 (0 - 0)	3.5 (2 - 6)	-
<i>Cottus gobio</i> (BF) Bullhead, Cg Gasterosteiformes - Gasterosteidae	O	30 / 10	10	0	0.33 (0.18-0.51)	0 (0 - 1)	0 (0 - 0)	1 (1 - 1.5)	-

<i>Gasterosteus aculeatus</i> (PF or BPF) Stickelback, Ga	O	65 / 14	12	4	0.18 (0.10-0.29)	0 (0 - 0)	0 (0 - 0)	1 (1 - 2.75)	1.5 (1 - 2.75)
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Table 2: Parameters of a power function (Taylor's power law) fitting the relationship between the logarithms of variance in abundance and mean abundance, across fish species hosts of *Pomphorhynchus laevis s.l.* from two populations. Abundance was recorded for adult intestinal parasites. The parameters a and b are from the function $\text{Var}(A) = a.M(A)^b$, with the variance in parasite abundance and mean abundance estimated for nine fish species for which at least 25 individuals were collected. The parameter b represents an index of spatial heterogeneity (or aggregation) of parasite distribution across fish species. Goodness of fit is given by the coefficient of determination r^2 , and the P -value. The slope (b) is significantly different from unity ($F_{1, 6} = 24.9, P = 0.002$) Bootsrapped values for the slope b and r^2 and their 95% intervals were calculated based on 1000 bootstrap replicates

River	Intercept (log _a)	b	Adjusted r^2	F -test statistics (df)	P	% var explained
Ouche (N = 9)	0.74	1.66 [1.39 – 1.92]	0.96 [0.80 – 0.98]	157.4 (1, 7)	< 0.0001	95.7

Table 3: Body condition metrics of fish infected with intestinal *P. laevis s.l.*, (a) Body condition index (BCI) according parasite load (log10 abundance), fish sex and their interaction, in the Ouche (OU) and Vingeanne (VI) rivers (see Fig. S6); (b) Hepatosomatic index (HSI) and gonadosomatic index (GSI), according to parasite load, fish species and sex.

(a)

BCI	Barbel (OU)	Chub (OU)	Chub (VI)	Vairone (OU)
Log10 abundance	male: Chi2 = 0.7 (1), <i>P</i> = 0.40 female: Chi2 = 16.9 (1), <i>P</i> < 0.0001	Chi2 = 4.28 (3), <i>P</i> = 0.23	Chi2 = 2.48 (3), <i>P</i> = 0.48	Chi2 = 0.52 (1), <i>P</i> = 0.47
Sex	/	Chi2 = 4.34 (4), <i>P</i> = 0.36	Chi2 = 2.50 (4), <i>P</i> = 0.64	Chi2 = 5.55 (4), <i>P</i> = 0.24
Log10abundance * sex	Chi2 = 7,51 (1), <i>P</i> = 0.006	Chi2 = 3.50 (2), <i>P</i> = 0.17	Chi2 = 1 (2), <i>P</i> = 0.61	Chi2 = 0.54 (2), <i>P</i> = 0.76
	Stone loach (OU)	Stickleback (OU)	Gudgeon (OU)	Minnow (OU)
Log10 abundance	Chi2 = 3.45 (3), <i>P</i> = 0.34	Chi2 = 0.58 (2), <i>P</i> = 0.47	Chi2 = 0.91 (2), <i>P</i> = 0.34	Chi2 = 0.52 (2), <i>P</i> = 0.47
Sex	Chi2 = 13.52 (4), <i>P</i> = 0.009	/	/	/
Log10abundance * sex	Chi2 = 2.56 (2), <i>P</i> = 0.32	/	/	/

(b)

	HSI (n=246)	GSI (n=256)
Log10 abundance	Barbel: Chi2 = 8.9 (1), <i>P</i> = 0.003 Chub: Chi2 = 5.1 (1), <i>P</i> = 0.024 all others: non signif.	Chi2 = 7.92 (9), <i>P</i> = 0.54
Fish species	/	Chi2 = 29.7 (12), <i>P</i> = 0.003
Sex	Chi2 = 18.04 (4), <i>P</i> = 0.0012	Chi2 = 77.83 (4), <i>P</i> < 0.0001
Log10 abundance * fish sp	Chi2 = 14.53 (6), <i>P</i> = 0.02	Chi2 = 5.54 (6), <i>P</i> = 0.48
Log10 abundance * sex	Chi2 = 1.43 (2), <i>P</i> = 0.49	Chi2 = 2.24 (2), <i>P</i> = 0.20

Supplementary material - Journal of Helminthology

**Distribution of *Pomphorhynchus laevis* s.l. (Acanthocephala)
among fish species at a local scale: importance of fish biomass-
density**

Marie-Jeanne Perrot-Minnot, Loïc Bollache, Clément Lagrue

Supplementary Figure S1.

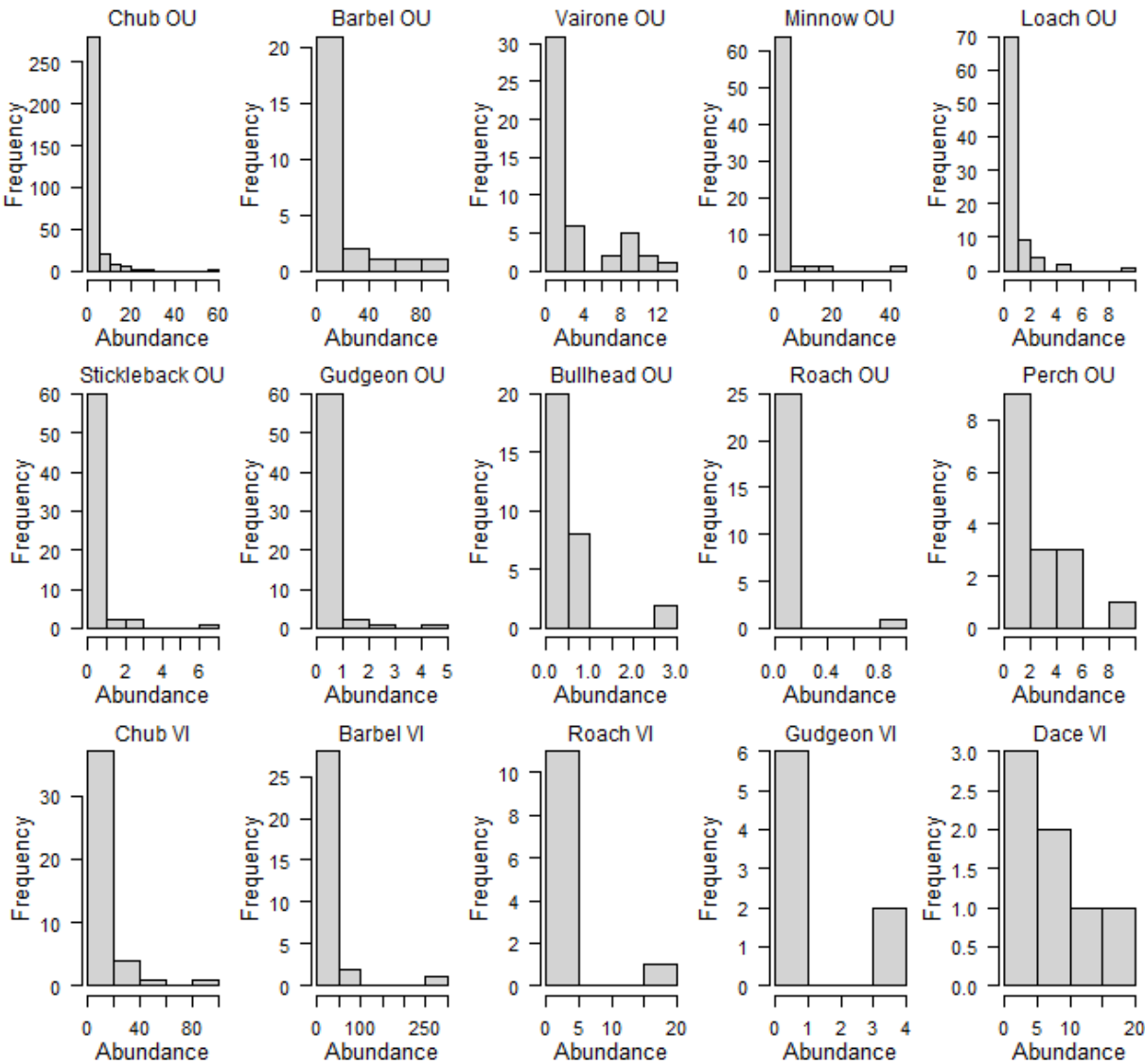


Fig. S1 Abundance distribution of intestinal *P. laevis* s.l. in different fish species sampled in the Ouche (OU) and Vingeanne rivers (VI), showing aggregate distributions of parasites among individual fish.

Supplementary Figure S2

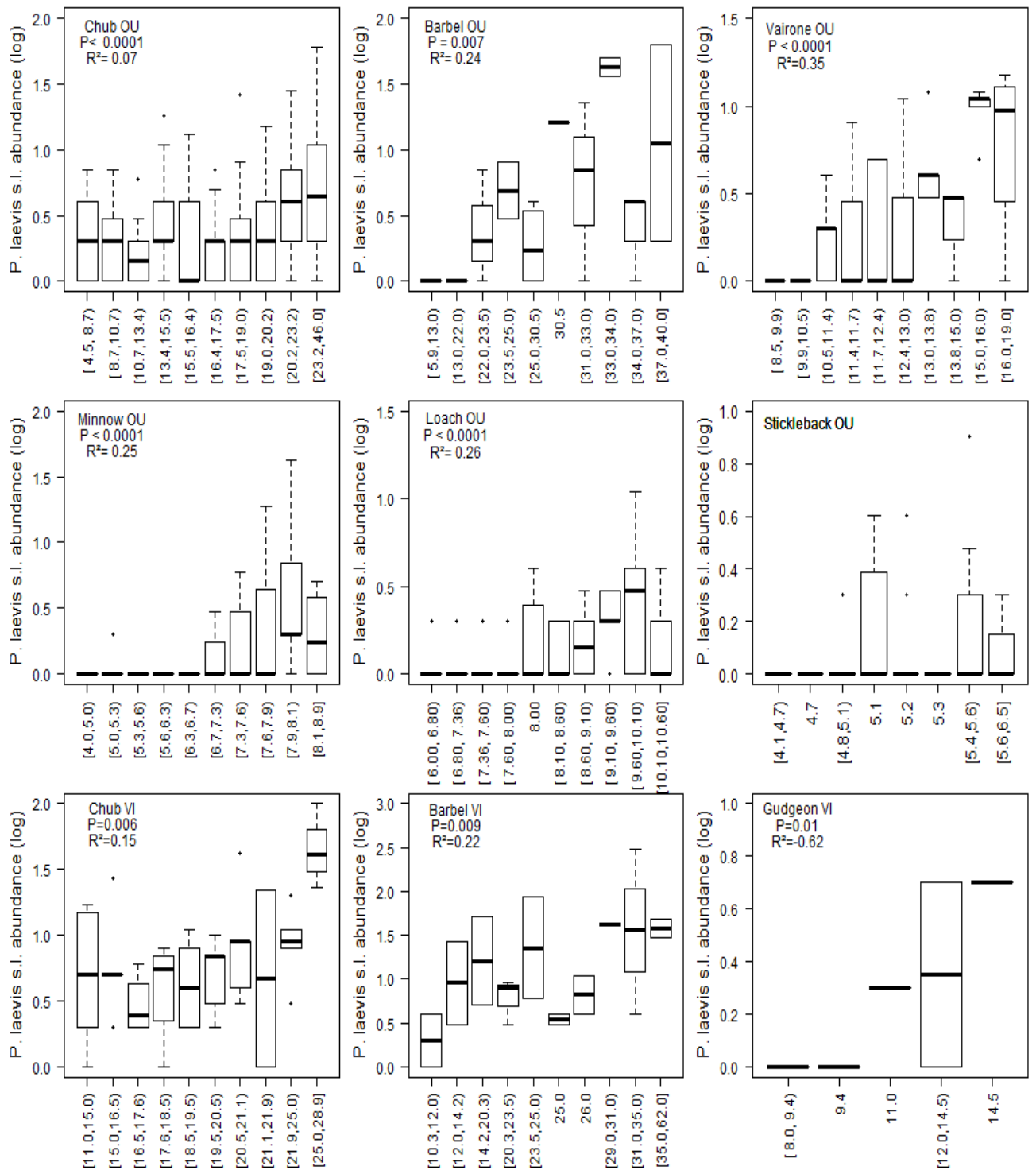


Fig. S2. Relationship between *Pomphorhynchus laevis* s.l. abundance (log₁₀+1) and individual body size in nine fish species from two localities (OU: Ouche river; VI: Vingeanne river). For illustrative purpose, we categorized fish size in deciles (equal number of

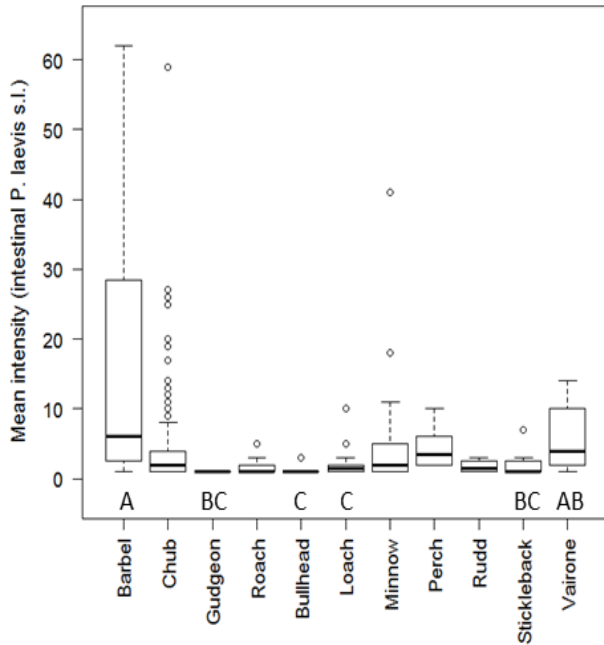
individuals per category), except for gudgeon in the Vingeanne river (quintiles), using the package Hmisc v4.2.0 (Harrell, 2019) The results of fitting the abundance of *P. laevis s.l.* to fish size using log-linear relationship are reported as *P*-value and adjusted R². Fish species for which sample size was low (< 7) are not reported.

Harrell F. E. Jr, with contributions from Charles Dupont and many others. (2019). Hmisc:

Harrell Miscellaneous. R package version 4.2-0. <https://CRAN.R-project.org/package=Hmisc>

Supplementary figure S3

(a)



(b)

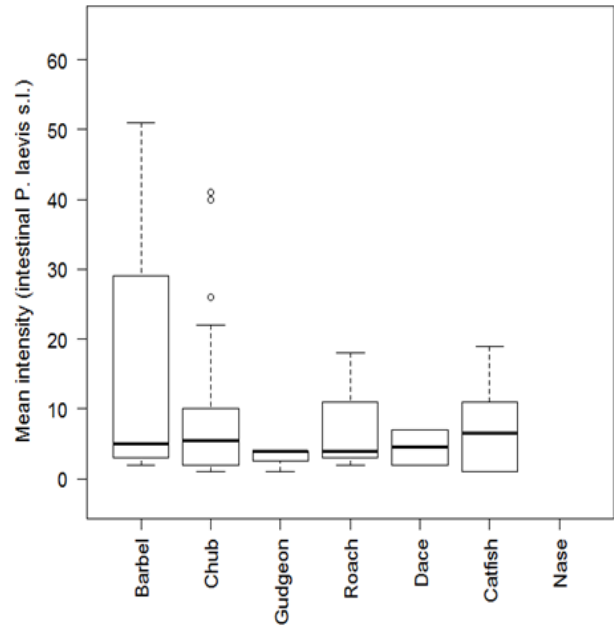


Fig. S3. Mean intensity of intestinal *Pomphorhynchus laevis s.l.* in fish host from the (a) Ouche and (b) Vingeanne rivers. Mean intensity in fish species with different letters are significantly different, after post-hoc paired comparison (Dunn tests with B–Y method), those without letter are not significantly different from any other species.

Supplementary Figure S4

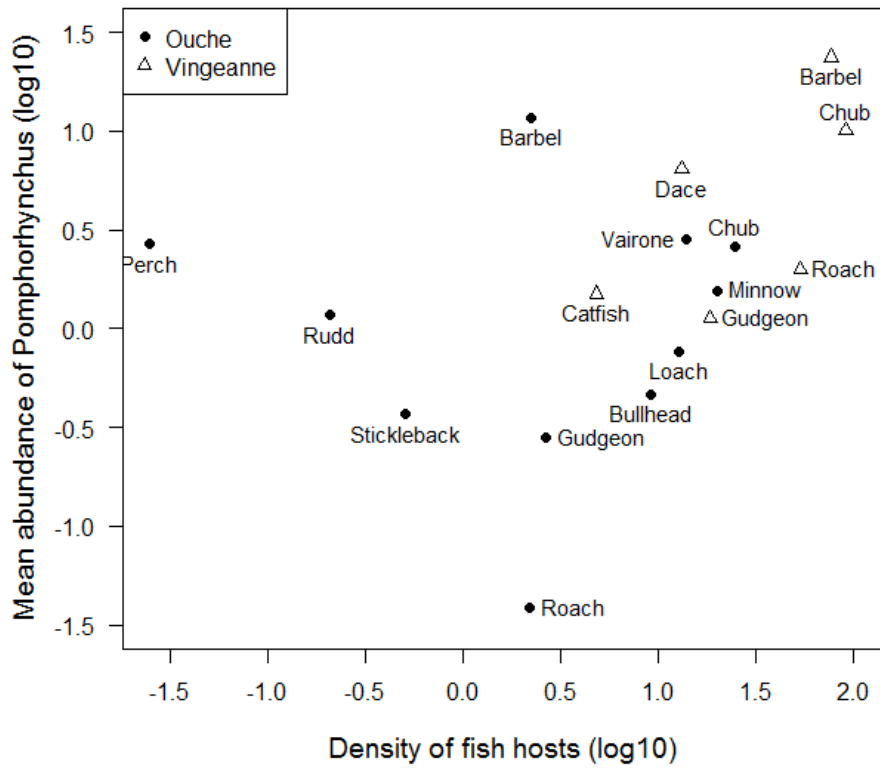


Fig. S4. Relationship between fish density (nb.m⁻²) and mean abundance of intestinal *Pomphorhynchus laevis s.l.* after log-transformation, across nine fish species from the Ouche River.

Supplementary figure S5

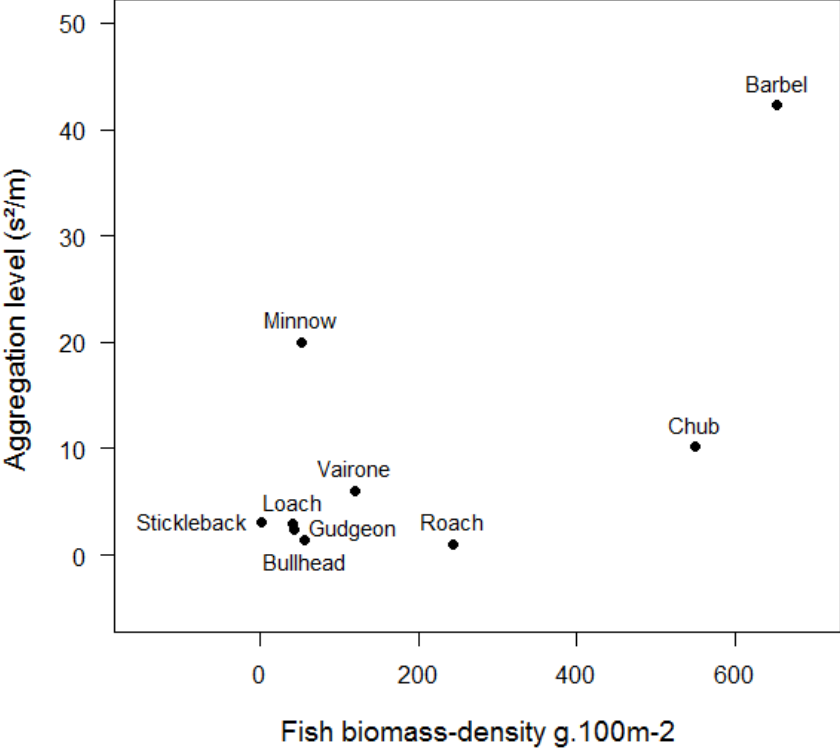


Fig. S5. Relationship between parasite aggregation level (estimated using the variance-to-mean ratio of abundance) and fish biomass-density, among nine fish species from the Ouche River.

Supplementary figure S6

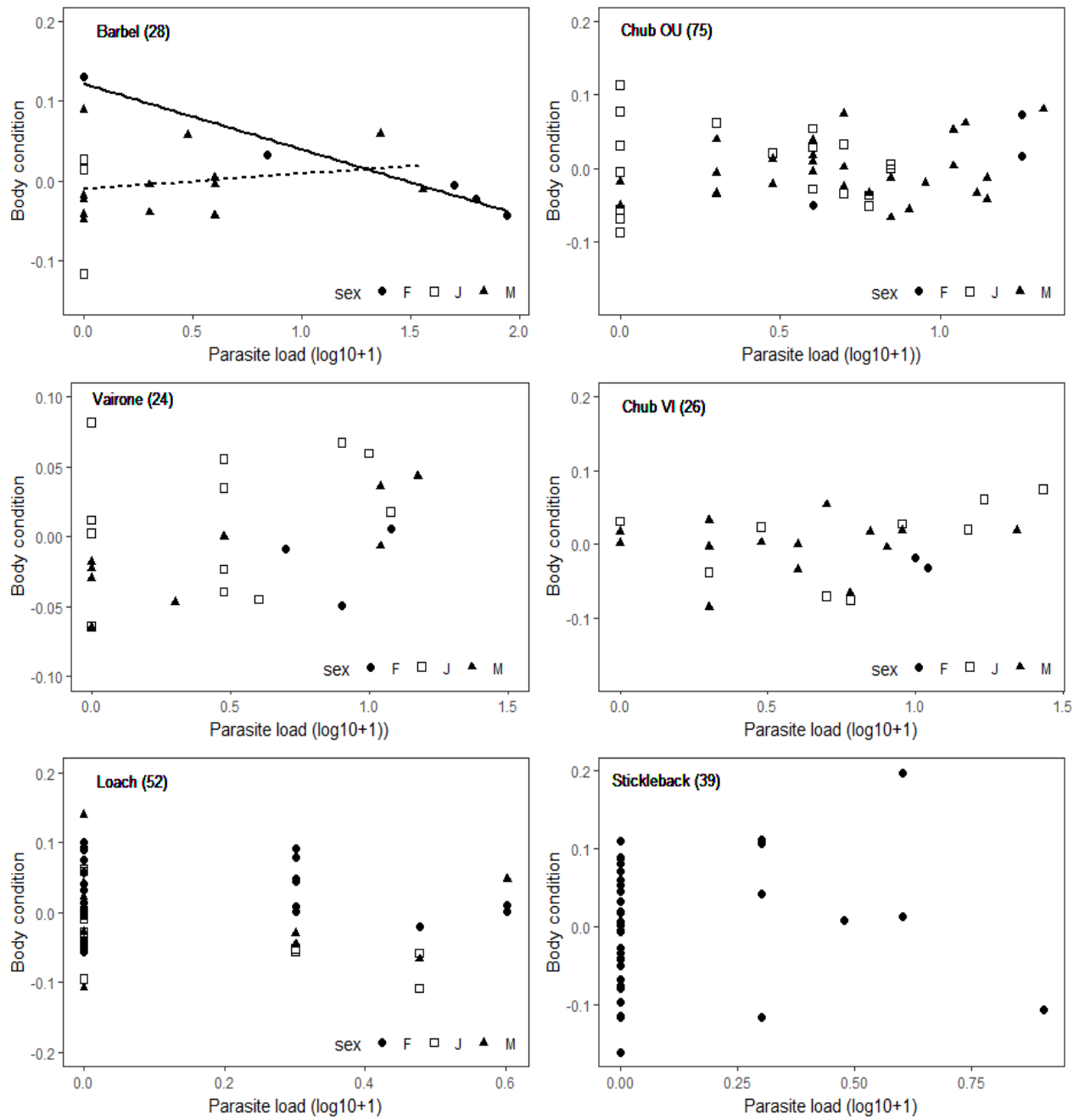


Fig. S6. Relationship between body condition of individual fish and *Pomphorhynchus laevis s.l.* abundance, according to fish host sex and species. Body condition is measured as the residuals of the regression of whole body weight on body size (log₁₀-transformed). Significant relationships are represented by a regression line. Numbers in bracket are sample sizes.

Supplementary figure S7

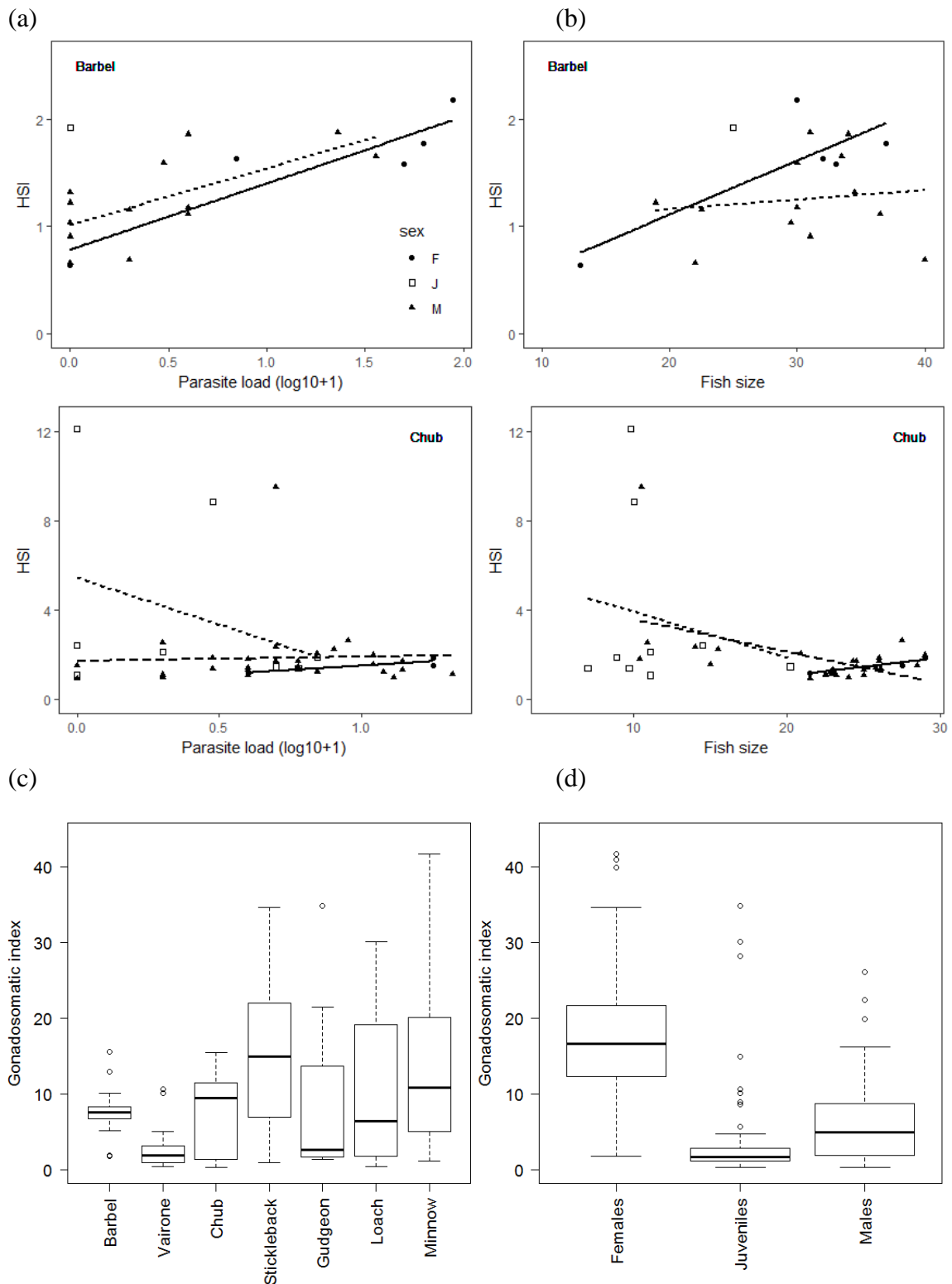


Fig. S6. Individual hepatosomatic index (HSI) in relation to (a) parasite load and (b) individual fish size, according to sex (female: plain line), for barbel and chub; and gonadosomatic index according to fish species (c) and sex (d) in the Ouche locality.

