

UNIVERSITY OF BIRMINGHAM

Research at Birmingham

Selective predation by benthivorous fish on stream macroinvertebrates – The role of prey traits and prey abundance

Worischka, Susanne; Schmidt, Susanne; Hellmann, Claudia; Winkelmann, Carola

DOI:

[10.1016/j.limno.2015.03.004](https://doi.org/10.1016/j.limno.2015.03.004)

License:

Other (please specify with Rights Statement)

Document Version

Peer reviewed version

Citation for published version (Harvard):

Worischka, S, Schmidt, S, Hellmann, C & Winkelmann, C 2015, 'Selective predation by benthivorous fish on stream macroinvertebrates – The role of prey traits and prey abundance', *Limnologica - Ecology and Management of Inland Waters*, vol. 52, pp. 41-50. <https://doi.org/10.1016/j.limno.2015.03.004>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

NOTICE: this is the author's version of a work that was accepted for publication. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published as Worischka, S., Schmidt, S.I., Hellmann, C., Winkelmann, C., Selective predation by benthivorous fish on stream macroinvertebrates and the role of prey traits and prey abundance, *Limnologica* (2015), <http://dx.doi.org/10.1016/j.limno.2015.03.004>

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Accepted Manuscript

Title: Selective predation by benthivorous fish on stream macroinvertebrates—the role of prey traits and prey abundance

Author: Susanne Worischka Susanne Isabel Schmidt Claudia Hellmann Carola Winkelmann



PII: S0075-9511(15)00034-1
DOI: <http://dx.doi.org/doi:10.1016/j.limno.2015.03.004>
Reference: LIMNO 25450

To appear in:

Received date: 15-10-2014
Revised date: 24-3-2015
Accepted date: 24-3-2015

Please cite this article as: Worischka, S., Schmidt, S.I., Hellmann, C., Winkelmann, C., Selective predation by benthivorous fish on stream macroinvertebrates—the role of prey traits and prey abundance, *Limnologia* (2015), <http://dx.doi.org/10.1016/j.limno.2015.03.004>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1 **Selective predation by benthivorous fish on stream macroinvertebrates – the role of prey**
2 **traits and prey abundance**

3
4 Susanne Worischka ^{1,2}, Susanne Isabel Schmidt ³, Claudia Hellmann ² and Carola
5 Winkelmann ²

6
7 ¹ Dresden University of Technology, Institute of Hydrobiology, 01062 Dresden, Germany

8 ² University of Koblenz-Landau, Department of Biology, Universitätsstr. 1, 56070 Koblenz

9 ³ University of Birmingham, College of Life and Environmental Sciences, Birmingham B15

10 2TT, U.K.

11
12 **Corresponding author:** Susanne Worischka

13 Address: Dresden University of Technology, Institute of Hydrobiology, 01062 Dresden,
14 Germany

15 Email: susanne.worischka@tu-dresden.de

16
17
18
19
20
21 **Short title:** Prey selection by benthivorous fish

22
23 **Key words:** *Barbatula barbatula*, feeding behaviour, non-visual foraging, *Gobio gobio*, size
24 selectivity, searching image

25

25 **Abstract**

26 The prey selectivity of fish depends largely on traits of prey and predator. Preferable prey
27 traits might be different for visual predators (such as drift-feeding salmonids) and rather non-
28 visual predators (such as benthic feeders). We evaluated the explanatory power of five prey
29 traits and prey long-term abundance for the prey selection of small benthivorous fish by
30 analysing the macroinvertebrate community and the diet of gudgeon (*Gobio gobio*) and stone
31 loach (*Barbatula barbatula*) in two small submontane streams. Fuzzy Principal Component
32 Analyses, as well as electivity indices, revealed that the fish fed selectively. Prey size and
33 feeding type were the most descriptive variables for the fish diet, followed by mean
34 abundance, whereas microhabitat preference, locomotion mode and current velocity
35 preference were less important. The fish preferred prey that was both small and consistently
36 abundant, grazers and sediment feeders. Larger prey and shredders were avoided. The
37 selection patterns of both fish species differed from those of visual fish predators but strongly
38 resembled each other. Supporting this, in gudgeon which feeds slightly more visually than the
39 strictly nocturnal stone loach, selectivity concerning prey traits as well as prey mean
40 abundance was slightly more pronounced. We analysed also selectivity for prey clusters based
41 on the three most important variables. The observed selectivity patterns concerning these
42 clusters were less pronounced but supported the other results. The maximum (neutral)
43 electivity index was that of gudgeon for small, abundant grazers or sediment feeders,
44 including chironomids.

45 We conclude that prey selection of benthivorous fish that forage mainly non-visually can
46 largely be explained by a small number of prey traits which probably work in combination.
47 The prey preferences of these predators seem to be closely connected to their active foraging
48 mode and to depend partly on the ability to detect prey visually.

49

49 **Introduction**

50 Selectivity in predation largely depends on the traits of both predator and prey
51 (O'Brien, 1979). Since selective predation is one of the strongest mechanisms structuring
52 communities (Sih et al., 1985), knowledge about the influence of prey traits on predator
53 selectivity is a prerequisite for the understanding of community processes. In stream
54 communities, fish often are the top predators. Traits of preferred prey have been analysed for
55 several predatory fish species, but mostly for visual predators. For instance, for drift-feeding
56 salmonids, particularly the drift behaviour and the body size of the prey are important (e.g. de
57 Crespin de Billy and Usseglio-Polatera, 2002; Rader, 1997; Syrjänen et al., 2011). The
58 omnivorous cyprinid *Rutilus arcasii* showed an opportunistic feeding behaviour but also a
59 positive size selectivity (Lobón-Cerviá and Rincón, 1994). To our knowledge, similar studies
60 for benthic, less visual (e.g. olfactory) fish predators are rare, despite the finding that benthic
61 fish may have a stronger predation impact on benthic communities than drift-feeders (Dahl,
62 1998). Because small-bodied benthivorous fish often feed nocturnally and thus non-visually
63 (Culp et al., 1991; Fischer, 2004; Huhta et al., 2000), they might select prey according to
64 other traits than drift-feeders do.

65 In a field experiment in Gauernitzbach and Tännichtgrundbach, two small submontane
66 streams in Central Europe, the benthic fish species gudgeon (*Gobio gobio* L.) and stone loach
67 (*Barbatula barbatula* [L.]) affected the structure of the macroinvertebrate community
68 (Winkelmann et al., 2011; Winkelmann et al., 2014). These two species differ slightly in their
69 habitat preferences and activity rhythms, gudgeon preferring pools with low current velocities
70 but foraging not as strictly nocturnally as stone loach, which in turn uses pools as well as
71 riffles for foraging (Fischer, 2004; Worischka et al., 2012; Zweimüller, 1995). In contrast to
72 gudgeon, stone loach feeds strictly non-visually and locates prey mainly by olfaction and
73 probably also via the lateral line system (Filek, 1960; Street and Hart, 1985). The numerically

74 dominant prey in the diet of both fish species in the above-mentioned streams were larval
75 chironomids, as reported also by other authors (e.g. Magalhaes, 1993; Michel and Oberdorff,
76 1995; Smyly, 1955). Chironomids were also the most abundant group in Gauernitzbach and
77 the second-most abundant (next to gammarids) in Tännichtgrundbach. This suggests a rather
78 opportunistic feeding behaviour of the fish predators. However, their actual predation impact
79 was not only mesohabitat-specific (Worischka et al., 2014; Worischka et al., 2012) but also
80 strongly prey species-specific (Winkelmann et al., 2011; Winkelmann et al., 2007). This
81 provokes the question whether also active prey selection by the fish predators was important
82 in the community-structuring process. For instance, chironomids might be preferred not just
83 due to their availability in high numbers but due to one or more 'preferable' traits. In the same
84 way as trait-based sensitivity against stressors is not independently distributed over
85 macroinvertebrate taxa (Schuwirth et al., 2015), also vulnerability against a certain predator
86 might be determined by correlated traits. Additionally, chironomids might not be the only
87 preferred prey item because they share such traits with other taxa. In order to separate the
88 effects of numerical prey availability and prey traits on predator selectivity, we evaluated the
89 importance of long-term prey abundance patterns as an additional factor during the analysis.
90 Long-term mean abundance – even though not a prey trait - is a variable influencing the
91 general encounter rate of a prey to a predator and thus can enhance the formation of a
92 searching image (Tinbergen, 1960). This is not restricted to visual predation (Atema et al.,
93 1980). The importance of abundance for prey selectivity can be seen in the switching
94 behaviour of predators: They often respond to changes in relative prey abundance by shifting
95 their preference to the most abundant prey and feeding disproportionately on it (Murdoch,
96 1969; Real, 1990). We assume that such short-term responses simply integrate over longer
97 time periods and, together with searching images, could lead to a general preference for
98 constantly abundant prey which goes beyond opportunistic feeding.

99 We investigated the prey selection by gudgeon and stone loach in Gauernitzbach and
100 Tännichtgrundbach over four years in a reach scale field predation experiment. We addressed
101 the following questions: (1) Do the two fish predators feed opportunistically or selectively,
102 and do they show similar prey preferences in spite of different spatial and temporal activity
103 patterns? (2) Can certain prey traits and/or long-term prey abundance explain feeding
104 selectivity of benthic fish? (3) Do the fish predators prefer any groups of prey being defined
105 by shared traits? For this purpose, we quantitatively analysed the macroinvertebrate
106 communities of the streams and the diet composition of the benthic fish, characterizing prey
107 taxa using five traits as well as their long-term mean abundance.

108

109 **Methods**

110 Study site and experimental design

111 Fish and benthic macroinvertebrates were sampled in Gauernitzbach (2nd order, 4.6 km long)
112 and Tännichtgrundbach (3rd order, 5.6 km long), which are tributaries of the River Elbe in
113 southeast Germany (51°06'46.63"N, 13°32'45.04"E; 51°05'12.43"N, 13°35'55.88"E).
114 Besides being located in close vicinity to each other, the streams have very similar physical
115 and chemical characteristics and benthic community compositions (Schmidt et al., 2009;
116 Winkelmann et al., 2003; Worischka et al., 2012). For a large-scale field experiment on top
117 down food web manipulation (Winkelmann et al., 2014; Worischka et al., 2014), an
118 experimental section of 400 m was separated in each stream, using 5 mm steel mesh. After
119 removing all fish (mainly trout stocked for angling) by backpack electrofishing (EGFI 650,
120 Bretschneider Spezialelektronik, Chemnitz, Germany), the experimental sections were
121 stocked with gudgeon and stone loach obtained from streams or small rivers from the same
122 region. Both species are small-bodied, benthivorous, and inhabit mainly streams and small
123 rivers of the Eurasian temperate zone, including the study streams. Fish density was

124 monitored at least four times a year by electrofishing. Losses due to winter mortality, bird
125 predation and occasional emigration during floods were compensated by restocking the fish
126 sections at least twice a year. Prey selection analysis was performed during two sampling
127 periods (2005-2006, 2009-2010) when fish were present in both streams with average
128 densities $\pm SD$ of 0.21 ± 0.19 ind m^{-2} (gudgeon) and 0.20 ± 0.17 ind m^{-2} (stone loach). These
129 densities exceeded those before the experiment (when trout as predators and competitors were
130 still present) but are in the same range as natural densities observed in comparable streams
131 (Erös et al., 2003; Santoul et al., 2005). The conditions of the predation experiment are
132 therefore well comparable to those of other, 'strictly natural' stream communities.

133

134 Sampling and processing of the samples

135 Six benthic macroinvertebrate samples from each stream, from three pool and three riffle
136 locations, were collected with a Surber sampler (0.12 m^2 , 500 μm mesh size) every four
137 weeks, throughout the entire study period. The samples were sorted under a dissecting
138 microscope. The invertebrates were identified to the lowest practicable taxonomic level,
139 enumerated and measured to the nearest 0.1 mm. For prey taxa including large individuals
140 (*Ancylus fluviatilis*, *Dugesia gonocephala*, Limnephilidae and *Tipula* sp.) not only length but
141 also thickness (the second-largest dimension) was measured in the benthos samples. The
142 individual dry body masses were calculated using length-mass regressions (Benke et al.,
143 1999; Burgherr and Meyer, 1997; Hellmann et al., 2013; Meyer, 1989). Gudgeon for diet
144 analysis were collected on 21 occasions and stone loach on 22 occasions in both streams,
145 between April and October of the four study years, but always with a time lag of at least 4
146 weeks after stocking. Each sampling was carried out shortly after sunrise when the fish had
147 full guts. Five to ten individuals of each species were caught by electrofishing and killed
148 immediately. After measuring total length to the nearest 1 mm and weighing to the nearest 0.1

149 g, their digestive tracts were removed, cooled between ice packs during transport to the
150 laboratory, and stored at -18°C . We aimed to synchronise benthos and fish sampling,
151 attempting to complete electrofishing the day after benthos sampling. When this was not
152 possible (i.e. the time lag exceeded 1 day), benthic macroinvertebrate densities were
153 interpolated to the respective fish sampling date by calculating the time-weighted average of
154 the benthic densities observed at the nearest sampling dates before and after the respective
155 fish sampling date. Diet analyses were based on the contents of the stomach (stone loach) or
156 anterior gut (gudgeon). Fish diet samples were processed individually, in the same way as the
157 benthos samples, and all individuals of a fish species and a date were pooled later for
158 calculations. The gape width (G) of the fish was estimated from total length (TL) using linear
159 regression equations. These were derived from previous TL and G measurements of
160 individuals from both streams (unpublished data). The equations are $G = 0.0643 TL - 0.147$
161 for gudgeon ($R^2 = 0.88$, $p < 0.0001$, $n = 382$) and $G = 0.035 TL + 0.889$ for stone loach ($R^2 =$
162 0.81 , $p < 0.0001$, $n = 153$). Gudgeon in our study had a total length of 100.0 ± 24.2 mm (mean
163 $\pm SD$) and an estimated gape width of 6.4 ± 1.7 mm. The mean total length of stone loach was
164 101.1 ± 30.0 mm with gape width 5.0 ± 0.5 mm.

165

166 Data analysis

167 Six variables describing the macroinvertebrate prey were used in this study (Table 1): five
168 traits which we assumed to be of importance for predator selectivity and, additionally, long-
169 term mean abundance. We chose this limited number of variables for two reasons. First, many
170 traits are inter-correlated in benthic macroinvertebrates (Poff et al., 2006) and we tried to
171 choose relatively independent traits *a priori*. Second, prey traits which are of any importance
172 for visual predators only (such as drift behaviour or crypsis), were excluded. Each of the
173 selected variables had 3 to 5 categories. Four of the traits (feeding type, locomotion mode,

174 microhabitat preference and current velocity preference) were taken from a trait compilation
175 by Tachet et al. (2002); the fifth trait (body size) was parameterized from own data. We
176 omitted some trait categories from the compilation of Tachet et al. (2002), which were not
177 relevant for our study streams, e.g. microhabitat ‘macrophytes’. The assignment of each taxon
178 to the categories was achieved using a fuzzy coding procedure (Chevenet et al., 1994). This
179 procedure includes the use of weightings expressing the affinity of a taxon to each of the
180 categories. Following Tachet et al. (2002), we used weightings between 0 and 3 for feeding
181 type and current velocity preference and weightings between 0 and 5 for locomotion mode
182 and microhabitat preference. These weightings were transformed into relative proportions
183 within each trait (between 0 and 1). For chironomids, we weighted their trait categories
184 according to the relative abundances of the three dominant subfamilies Orthoclaadiinae,
185 Tanypodinae and Chironominae (together forming 97.5% of the chironomids, based on
186 routine emergence trap samplings throughout the study period, C. Hellmann, unpublished
187 data) as recommended by Sheldon and Meffe (1993). Additionally, higher proportions for the
188 feeding type category ‘predator’ than proposed by Tachet et al. (2002) were employed for
189 *Gammarus* spp., *Hydropsyche* spp. and *Isoperla grammatica*, according to results of a
190 previous study from the same streams (Hellmann et al., 2013). The trait body size was based
191 on body mass data from our macroinvertebrate samples. It was also a convenient proxy for
192 energy content per individual because the energy contents per mg dry mass found in the
193 database collected by Brey et al. (2010) were similar for all prey taxa ($20.9 \pm 2.3 \text{ J mg}^{-1}$, mean
194 $\pm SD$, $n = 37$), except for molluscs with shells, which were rarely eaten by the fish. Five size
195 categories were defined *a priori* (Table 1). The assignment of a taxon to the size categories
196 was done as follows: We calculated the mean individual dry body mass (geometric mean) of
197 each taxon for each sampling date and stream separately. The obtained values were each
198 assigned to one of the five size categories, and their relative frequencies constituted the

199 weightings for each taxon in the fuzzy coding. Long-term mean abundance was also coded
200 like a trait: We assigned density values (ind m^{-2}) for each taxon at each sampling date and
201 stream to three abundance categories (Table 1) and used the relative frequencies of the
202 categories for each taxon as weightings.

203 In total, 42 benthic macroinvertebrate taxa identified in the streams, including the
204 dummy taxon ‘others’, were assigned to the six variables (i.e. five traits plus mean
205 abundance), forming a ‘taxa \times traits’ array (Table S1 in supporting information). For
206 convenience, we kept the commonly used denotation ‘traits’ instead of the more general term
207 ‘variables’. The taxon ‘others’ received average weightings for all categories. In order to
208 avoid a biased estimation of prey selection, we included only the actual edible prey size
209 spectrum for the fish in the calculations. This was based on a gape width of 4.5 mm, which
210 was estimated as the lower value of $\bar{G} - 1 SD$ of both fish species, (i.e. 4.7 mm for gudgeon
211 and 4.5 mm for stone loach). Thus, prey individuals thicker than 4.5 mm qualified as non-
212 edible for most of the fish; these were therefore excluded from the calculations. For
213 Oligochaeta (except *Eiseniella* sp.) in the benthos samples we used correction factors of 0.2
214 for abundance and 5 for body mass. The correction was necessary because individuals of the
215 dominant subfamily (Naidinae) tend to fragment into roughly five fragments per individual
216 during sampling (personal observations). This leads to abundance being easily overestimated
217 and body mass being underestimated. In the fish diet samples, no corrections were needed
218 because only a few whole individuals and no fragments were found. Terrestrial prey was
219 excluded from the calculations, contributing only $0.6\% \pm 1.6\%$ (mean $\pm SD$, all samples) to
220 the total numeric abundance in the fish diets.

221 A ‘benthos samples \times traits’ array and a ‘diet samples \times traits’ array were created for each
222 fish species. For the arrays, the fuzzy-coded categories of each of the six variables were
223 weighted with the relative abundances of the taxa in the respective samples, for each sampling

224 date and stream. The different foraging habitat preferences of gudgeon and stone loach
 225 (Worischka et al., 2012) were accounted for in the benthos samples. For gudgeon which used
 226 almost exclusively pool mesohabitats, macroinvertebrate abundances from pool samples were
 227 weighted higher than those from riffle samples (97 resp. 3 %) whereas for stone loach, both
 228 mesohabitats were weighted equally. This was done in order to reflect the actual mesohabitat-
 229 specific prey availability for each fish species and so to avoid a biased selectivity analysis.
 230 We performed a fuzzy principal component analysis (FPCA) on the ‘benthos samples × traits’
 231 and ‘diet samples × traits’ arrays (R-package *ade4* version 1.5-1; Dray and Dufour, 2007;
 232 Thioulouse et al., 1997) to assess the importance of the variables, i.e. traits, for the difference
 233 between the corresponding benthos and diet samples (hypothesis 1). FPCA is a robust
 234 modification of principal component analysis (Cundari et al., 2002) and was successfully
 235 applied to fish diet analysis before (Sanchez-Hernandez, 2014; Sanchez-Hernandez et al.,
 236 2011). In order to compare the available prey in the benthos directly to the consumed prey, we
 237 combined the two arrays to one joint dataset (one below the other, Legendre and Legendre,
 238 2012, p 702) for each fish species.
 239 Prey selection of the fish sampled on each date was calculated using the relativized electivity
 240 index E^* (Vanderploeg and Scavia, 1979), based on both prey traits and prey taxa:

$$241 \quad E_i^* = \frac{W_i - (1/n)}{W_i + (1/n)} \quad (1)$$

242 with

$$243 \quad W_i = \frac{r_i / p_i}{\sum_i r_i / p_i} \quad (2)$$

244 with r_i being the proportion of a prey item i in the diet and p_i its proportion in the
 245 environment, and n being the number of different prey items. E^* can have values between -1
 246 (complete avoidance) and, theoretically, 1 (complete preference), with $E^* = 0$ indicating
 247 neutral selection. Among the large number of available electivity indices, E^* was

248 recommended in the reviews by Lechowicz (1982) and, with minor reservations, by Lazzaro
249 (1987). We chose it for our study because it has the random value 0 (which we regard to be
250 most intuitive), is robust against variation of the number of prey types and amenable to (non-
251 parametrical) statistical testing. For the trait-based calculation of E^* we used the relative
252 abundance data for trait categories from the fuzzy-coded ‘benthos samples \times traits’ and ‘fish
253 diet samples \times traits’ arrays as r_i and p_i . A general challenge in electivity calculation is the
254 occurrence of a taxon in a diet sample but not in the corresponding benthos sample. This
255 happens occasionally with rare taxa and results in a seemingly infinite quotient between the
256 relative abundances in the diet and in the environment. We attempted to solve this problem
257 while maintaining a high taxonomic resolution by replacing the respective zero values (only
258 for taxa actually eaten by the fish in this sample) in the benthos samples by a value of ‘half of
259 the minimum detection level’ (0.5 individuals per benthos sample or 4.265 ind m⁻²). The
260 constrained habitat use of gudgeon was, like for the FPCA, incorporated by weighting the
261 macroinvertebrate abundances in the benthos from pools higher. In addition to analysing size
262 selection regarding whole prey taxa, we wanted to get an idea of selection for the same size
263 categories *within* one prey taxon. For this purpose we used the example of *Gammarus* spp.,
264 which was abundant in the benthos with a broad size spectrum and frequently eaten by the
265 fish, calculating E^* for each size category.

266 In order to see whether the fish show any preferences for prey taxa sharing certain
267 combinations of traits or variables, we grouped the prey taxa by the most meaningful
268 variables from the previous analyses. We intended to create a clearer and more realistic
269 classification by omitting those variables we already found to have less influence on the prey
270 selectivity of the fish. For this purpose, we reduced the ‘taxa \times traits’ array to those three
271 variables clearly identified as important in both the FPCA (highest loadings on the first two
272 axes) and the trait-based electivity indices (highest ranges). We performed a hierarchical

273 cluster analysis based directly on the reduced array. The number of clusters was determined
274 manually from the dendrogram by cutting at the height H with the largest difference to the
275 two 'neighbouring' solutions, i.e. at $H = 1.62$. For each of the obtained 8 clusters, E^* was
276 calculated. All statistical analyses and graphics were carried out using the software R (version
277 3.0.2, R Development Core Team, 2013).

278

279 **Results**

280 Multivariate analysis of selective vs. opportunistic feeding

281 Gudgeon and stone loach showed similar and pronounced prey selectivity patterns in
282 our study (for a detailed presentation of the diet composition see Table S2 in the supporting
283 information). In the FPCA plots of the combined datasets for benthos and gudgeon diet (Fig.
284 1), the first axis with an eigenvalue of 0.052 explained a major part (78%) of the total inertia
285 (0.067) whereas the second axis contained much less information (eigenvalue = 0.009 or
286 14%). In the FPCA plot of the combined datasets for benthos and stone loach diet (Fig. 2), the
287 eigenvalues of the first two axes (0.039 and 0.014) were slightly lower than for gudgeon but
288 still explained a major part (56% and 20%) of the total inertia (0.068). The plots showed
289 similar characteristics for gudgeon and stone loach, especially concerning the distribution of
290 the variables (Figs. 1d and 2d). Categories of size, feeding type and abundance were most
291 prominent whereas the other variables seemed to have a very low explanatory power. For
292 both fish species, the arrows of the samples largely follow two main directions, corresponding
293 to the categories 'small', 'abundant' and 'grazer' but are directed opposite the categories
294 'medium sized' and 'shredder'.

295 The differences between the corresponding diet and benthos samples (lengths of the
296 arrows) were mostly larger than the differences among samples, indicating selective predation
297 by both fish species. The stone loach diet samples were more widespread than those of

298 gudgeon, indicating a higher variability in food composition. Additionally, the arrows appear
299 mostly shorter than for the benthos-gudgeon comparison, indicating a slightly weaker
300 selectivity in stone loach. The FPCA plots for both fish species have further characteristic
301 patterns in common: The benthos samples showed a seasonal pattern along the first axis and a
302 separation between the two streams along the second axis. In summer and fall, the difference
303 between streams was greater than in spring. The seasonal differences seemed larger than those
304 between the streams. In the fish diet samples, however, these differences were much smaller,
305 indicating that both fish species showed true and similar preferences independent of stream or
306 season. In addition, the FPCA plots indicated no systematic differences between the two
307 sampling periods (2005-2006 and 2009-2010).

308

309 Electivity indices for single prey variables and prey groups

310 Gudgeon showed significant electivity indices, i.e. $E^* \neq 0$, for 18 of the 26 categories,
311 stone loach only for 6 categories (Fig. 3, Table 2, two-sided Wilcoxon tests with Holm
312 correction, $p < 0.05$, $n = 21$ for gudgeon and $n = 22$ for stone loach). However, only few
313 categories were preferred, most strongly 'very small', 'small' and 'sediment feeder' by
314 gudgeon, and 'sediment feeder' and 'microhabitat wood/roots' by stone loach. By far more
315 categories were avoided by the fish, most strongly 'very large', 'large' and 'shredder' by
316 gudgeon, and 'shredder', 'large' and 'medium-sized' by stone loach. Among all prey items
317 within the edible size spectrum, both fish predators generally preferred small prey taxa and
318 avoided large ones. In contrast, we observed an avoidance of the two smallest size classes
319 *within* the taxon *Gammarus* spp. (Fig. 4) and neutral selectivity for the larger ones. For
320 gudgeon, a preference of abundant prey over common and rare prey was visible although not
321 statistically significant (Fig. 3, Table 2). Stone loach, in general, showed a smaller total range
322 of electivity indices.

323 The variables with the highest ranges of electivity indices between the categories were
324 size, feeding type and mean abundance for both fish species (Table 2), and the categories
325 yielding the highest mean E^* values (independent of their significance) belonged mostly to
326 these three variables (Fig. 3). Because the same three variables were also prominent in the
327 FPCA, the division into prey groups by cluster analysis was based only on them. We found
328 eight distinct groups of prey taxa characterised by one or more categories of the three
329 variables (Fig. 5a): very large sediment feeders (group 1, only *Eiseniella tetraedra*), rare
330 small taxa (2, e.g. *Isoperla* sp.), rare shredders (3, e.g. *Capnia bifrons*), highly abundant
331 grazers and sediment feeders (4, e.g. Chironomidae), highly abundant shredders (5, e.g.
332 *Gammarus* spp.), filter feeders (6, e.g. *Hydropsyche* spp.), predators (7, e.g. *Dugesia*
333 *gonocephala*) and medium-sized grazers (8, e.g. *Rhithrogena semicolorata*). Again, we
334 observed very similar selectivity patterns for gudgeon and stone loach, i.e. a negative average
335 selectivity for most of these prey groups (Figs. 5b and 5c, two-sided Wilcoxon tests with
336 Holm correction, $p < 0.05$, $n = 21$ for gudgeon, $n = 22$ for stone loach). Group 4 was selected
337 neutrally by gudgeon (sole positive E^* value) and groups 1, 4, 6 and 8 by stone loach. The
338 electivity indices of the fish predators for each single taxon are given in Table S2 (supporting
339 information).

340

341 Discussion

342 Selective vs. opportunistic feeding

343 Combining two different approaches (multivariate analyses and electivity indices), we
344 evaluated the prey selection of gudgeon and stone loach as top predators in two small streams
345 and identified the most important of six prey-characterising variables. The results
346 concordantly suggest that the benthivorous fish foraged rather selectively than
347 opportunistically, selecting some trait categories over others. This selectivity was observed

348 during all seasons even with the fish diets showing a dependency of the predators on
349 seasonally changing prey availability. The trait-based approach seems therefore useful to
350 detect and describe prey selection not only for drift-feeding fish (e.g. Rader, 1997) but also of
351 benthic feeders in streams.

352

353 Importance of prey traits and mean abundance for selectivity

354 Two of the five analysed prey traits (size and feeding type), and long-term abundance
355 as additional characterising variable had a strong influence on predator selectivity in our
356 study. First and foremost, gudgeon and stone loach exhibited a strong size selectivity,
357 preferring very small and small prey species. This was not due to gape limitation because only
358 the edible size spectrum was included in the analyses. Such a feeding behaviour is in contrast
359 to that of mainly visually foraging fish, which under ideal conditions prefer large, i.e.
360 energetically favourable, prey individuals (Allan, 1981; Rincón and Lobón-Cerviá, 1995;
361 Turesson et al., 2002). Even some non-visually foraging fish such as nocturnal planktivores
362 showed a positive selection for larger prey, which was mediated mainly by size-dependent
363 encounter rate (Holzman and Genin, 2005). The apparently paradoxical size selection of
364 gudgeon and stone loach might be explained on the one hand by their preferred foraging
365 mode, i.e. actively searching the stream bottom (Filek, 1960; Worischka et al., 2012), which
366 makes size-dependent activity of the prey less important for encounter rate. On the other
367 hand, we may also take into account that small taxa are usually more abundant than large taxa
368 (Meehan, 2006). A selection of small prey therefore may indirectly select for abundant prey,
369 and *vice versa*. This was observed with gudgeon and stone loach, which showed a relative
370 preference not only for the categories ‘very small’, ‘small’ and ‘abundant’, but also for small-
371 bodied and abundant prey taxa (chironomids and simuliids, respectively, see Table S1 and
372 S2 in the supporting information). Small size classes of one abundant prey taxon, *Gammarus*

373 spp., were rather avoided by both fish species, but they were also less frequent in the benthos
374 than the medium and large size classes during the sampling periods. Therefore, we suspect
375 that the apparent size selectivity was in fact selectivity for abundant prey taxa. We assume
376 that this behaviour could be a number-maximizing feeding tactic, comparable to that found by
377 Rakocinski (1991) for small darter species. In Optimal Foraging Theory (Emlen, 1966;
378 MacArthur and Pianka, 1966), prey size determines energy content and handling time and
379 prey abundance determines the encounter rate. An increasing selectivity for larger (i.e.
380 energetically more profitable) prey with increasing absolute prey abundance (Werner and
381 Hall, 1974) is likely only as long as handling time is constant and prey is encountered
382 simultaneously, a typical situation for planktivorous fish. For small benthivorous fish species,
383 it is more realistic to assume that handling time is relatively long and increases with prey size,
384 prey is encountered sequentially, and satiation occurs sooner during feeding. Under these
385 conditions, an increasing preference for smaller prey would be the most efficient feeding
386 tactic (Gill, 2003; Hart and Ison, 1991).

387 Thus, the consideration of size and abundance in combination seems to be necessary in
388 prey selectivity analyses. Switching as a short-time response to fluctuations in relative prey
389 abundances seems to be common in fish predators (Hughes and Croy, 1993; Ringler, 1979;
390 Zhao et al., 2006) and probably also occurred in our study system. However, the fuzzy-coded
391 long-term mean abundance categories we used in our analysis represent more information
392 than just the momentary relative abundance, namely whether a prey is regularly encountered
393 by the predator with a high probability. Therefore, we assume that the general preference of
394 gudgeon and, to a lesser extent, also of stone loach for highly abundant prey can be explained
395 only with a combination of at least two mechanisms, a fast-acting one (switching) and a slow
396 one. The latter could be a certain 'inertia' of the searching image (Tinbergen, 1960), as
397 learning processes, for instance the acceptance of novel, rare prey types among known, highly

398 abundant prey types, are often associated with a time delay (Fraser et al., 2013). Another
399 learning process is the recognition of non-profitable patches in heterogeneous environments.
400 Here, predators seem to need much more time to identify such patches regarding prey
401 abundance than regarding prey body mass (Esposito et al., 2010). The search mode of
402 gudgeon and stone loach as benthic feeders is probably strongly patch-related. It is therefore
403 conceivable that the short-term preferences of gudgeon and stone loach have merged over
404 time into a general preference for abundant prey. Supporting this line of thought, Johnson et
405 al. (2007) as well as Uieda and Pinto (2011) indicate the highest electivity indices of fish
406 predators for the (overall) numerically dominant prey in the respective benthic community. In
407 more homogeneous pelagic predator-prey systems, where visual foraging is also more
408 important, prey ingestion more often seems to be proportional to relative prey abundances, or
409 the preferred prey is not the most abundant one (e.g. Storch et al., 2007; Verliin et al., 2011).

410 Macroinvertebrate feeding type was, next to size, the most important trait influencing
411 the prey selectivity of the fish; grazers and sediment feeders were generally preferred in our
412 study. In accordance with our findings, benthic grazers in stream enclosures were subject to a
413 strong top-down influence by benthivorous sculpins, which was partly explained by their
414 body size and partly by their feeding habit and resulting exposition (Rosenfeld, 2000). The
415 feeding modes grazing and sediment feeding are often closely associated in benthic
416 macroinvertebrates, i.e. many taxa use both (see Table S1 in the supporting information). In
417 contrast, the category 'shredder' was, although very common among the benthic
418 macroinvertebrates in the studied streams and also in the fish diet, negatively selected by the
419 fish. This was true even for highly abundant shredders as can be seen from the cluster-based
420 selectivity analysis, underlining the high relevance of prey feeding type for predator
421 selectivity. In a previous field experiment in Gauernitzbach (Winkelmann et al., 2007),
422 gudgeon had a much stronger predation effect on *Gammarus pulex* (an important shredder)

423 than on *Rhithrogena semicolorata* (an important grazer). A special characteristic of
424 macroinvertebrate shredders is that they are able to use their food source as refuge. The
425 effectiveness of this predator avoidance strategy has been shown by Szokoli et al. (in press).

426 The prey traits locomotion mode, microhabitat preference and current velocity
427 preference were of lower importance for prey selection in our study although all three may
428 theoretically influence the encounter rate from the prey side. For actively searching benthic
429 predators like gudgeon and stone loach, the locomotion mode of the prey might be less
430 important than for ambush predators or slow-moving active predators (Muotka et al., 2006;
431 Sih and Moore, 1990). Microhabitat preferences of benthic macroinvertebrates in streams
432 may influence predator encounter rate especially if they include the use of refuges such as
433 crevices (Fairchild and Holomuzki, 2005). This seems to have played a minor role in the
434 studied streams. The positive electivity indices for 'microhabitat wood' may result from a
435 temporary preference for simuliids and other abundant taxa with a high affinity to this
436 microhabitat type. Even though current velocity preferences of the fish were already
437 accounted for in the calculations, the electivity pattern of gudgeon concerning current velocity
438 preference as a prey trait was still stronger than that of stone loach, indicating that typical
439 riffle taxa were avoided by gudgeon also when they occurred in pools.

440

441 Selectivity for prey groups

442 Chironomids, numerically dominating the diet of both fish predators in the studied
443 streams, are small and highly abundant and, mostly, also grazers or sediment feeders. They
444 might share this 'preferable' combination of characteristics, which is equivalent to a trait
445 syndrome *sensu* Poff et al. (2006) with other prey taxa. Instead of prey selection based on
446 single prey variables or taxa, our third hypothesis therefore focussed on selection for prey
447 groups sharing combinations of variables. We found less distinct selectivity patterns than

448 Yamada et al. (2010), who could largely explain age-dependent diet composition of marine
449 seagrass-bed fishes with a model approach combining taxonomic and trait-based prey groups.
450 However, the patterns that we observed are in concordance with the other results of our study,
451 especially concerning selectivity for small and abundant taxa and the contrary influence of the
452 feeding types ‘grazer’/‘sediment feeder’ and ‘shredder’.

453

454 Consequences for predator coexistence

455 The prey selectivity differences found between the fish species correspond to
456 differences in their habitat use and foraging mode. For gudgeon, which partly detects prey
457 visually and has a greater affinity to pools (Worischka et al., 2012), we observed generally a
458 more distinct selectivity (positive and negative) than for stone loach. This concerned single
459 prey traits, for instance prey size or current velocity preference, but also prey groups sharing
460 trait combinations. A possible explanation for the lower degree of selectivity in stone loach
461 might be its strictly non-visual and benthic foraging mode (Filek, 1960; Worischka et al.,
462 2012). Compared to drift-feeding fish, much less is known about the preferred prey traits for
463 benthic feeders. The selectivity patterns we found for two benthic predators differed clearly
464 from those of drift-feeders and other visual predators (e.g. Rader, 1997) but resembled each
465 other remarkably, despite the above-mentioned differences. Gudgeon and stone loach even
466 seemed to select a similar spectrum of prey variables in both studied streams whereas the
467 benthic samples from the streams differed regarding these variables. The co-occurrence of
468 two top predators with such similar prey preferences suggests a strong food competition.
469 However, competition seems to be weakened by the different spatial and temporal activity
470 patterns (gudgeon being temporally flexible and stone loach spatially) which might have
471 facilitated resource partitioning (Worischka et al., 2012). Such competition-minimizing
472 mechanisms have been observed also in other studies (Copp, 1992; Greenberg, 1991;

473 Sanchez-Hernandez et al., 2011). But even without a strong resource partitioning, the shared
474 use of a highly abundant main food resource, i.e. chironomids, probably allows the two
475 predator species to coexist. Therefore, the observed prey selectivity patterns are most
476 probably advantageous for both fish predators.

477

478 **Acknowledgements**

479 This work was part of a long-term study funded by the German Research Foundation (Grant:
480 BE-1671-9/1-3). The project was designed and supervised by our dear mentor Jürgen
481 Benndorf who unexpectedly died in 2011. His great expertise, his inspiring way to impart
482 knowledge, and constant encouragement and support were invaluable to all of us. Susanne
483 Schmidt was funded by an FP 7 Marie Skłodowska Curie IEF grant (PIEF-GA-2009-235834).
484 We thank Gabriele Egerer, Anne Rother, Kristin Berg, Michael Schäffer, Michael Beilharz
485 and Christoph Köbsch for their help in the field and with sample analysis. Jean Thioulouse,
486 Sylvain Dolédec, Stéphane Dray, and René Sachse provided helpful comments on the data
487 analysis for this study. Andrew Sheldon and two anonymous referees gave valuable
488 comments and thus helped to improve earlier drafts of this manuscript. We also thank Jeremy
489 Wilkinson for linguistic advice.

490

491 **References**

492 Allan, J.D., 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain
493 stream. Can J Fish Aquat Sci 38, 184-192.

494 Atema, J., Holland, K., Ikehara, W., 1980. Olfactory responses of yellowfin tuna (*Thunnus*
495 *albacares*) to prey odors - chemical search image. J Chem Ecol 6, 457-465.

- 496 Benke, A.C., Huryn, A.D., Smock, L.A., Wallace, J.B., 1999. Length-mass relationships for
497 freshwater macroinvertebrates in North America with particular reference to the southeastern
498 United States. *J N Am Benthol Soc* 18, 308-343.
- 499 Brey, T., Müller-Wiegmann, C., Zittier, Z.M.C., Hagen, W., 2010. Body composition in
500 aquatic organisms - A global data bank of relationships between mass, elemental composition
501 and energy content. *J Sea Res* 64, 334-340.
- 502 Burgherr, P., Meyer, E.I., 1997. Regression analysis of linear body dimensions vs. dry mass
503 in stream macroinvertebrates. *Arch Hydrobiol* 139, 101-112.
- 504 Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of
505 long-term ecological data. *Freshwater Biol* 31, 295-309.
- 506 Copp, G.H., 1992. Comparative microhabitat use of cyprinid larvae and juveniles in a lotic
507 floodplain channel. *Environ Biol Fish* 33, 181-193.
- 508 Culp, J.M., Glozier, N.E., Scrimgeour, G.J., 1991. Reduction of predation risk under the cover
509 of darkness - avoidance responses of mayfly larvae to a benthic fish. *Oecologia* 86, 163-169.
- 510 Cundari, T.R., Sarbu, C., Pop, H.F., 2002. Robust fuzzy principal component analysis
511 (FPCA). A comparative study concerning interaction of carbon-hydrogen bonds with
512 molybdenum-oxo bonds. *J Chem Inf Comp Sci* 42, 1363-1369.
- 513 Dahl, J., 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream
514 assemblage. *Oecologia* 116, 426-432.
- 515 de Crespin de Billy, V., Usseglio-Polatera, P., 2002. Traits of brown trout prey in relation to
516 habitat characteristics and benthic invertebrate communities. *J Fish Biol* 60, 687-714.
- 517 Dray, S., Dufour, A.B., 2007. The ade4 package: Implementing the duality diagram for
518 ecologists. *J Stat Soft* 22, 1-20.
- 519 Emlen, J.M., 1966. The role of time and energy in food preference. *Am Nat* 100, 611-617.

- 520 Erös, T., Botta-Dukát, Z., Grossman, G.D., 2003. Assemblage structure and habitat use of
521 fishes in a Central European submontane stream: a patch-based approach. *Ecol Freshwater*
522 *Fish* 12, 141-150.
- 523 Esposito, S., Incerti, G., Giannino, F., Russo, D., Mazzoleni, S., 2010. Integrated modelling of
524 foraging behaviour, energy budget and memory properties. *Ecol Model* 221, 1283-1291.
- 525 Fairchild, M.P., Holomuzki, J.R., 2005. Multiple predator effects on microdistributions,
526 survival, and drift of stream hydropsychid caddisflies. *J N Am Benthol Soc* 24, 101-112.
- 527 Filek, W., 1960. Vergleichende Verhaltensstudien an Grundfischen - Beiträge zum Verhalten
528 von *Noemacheilus barbatula* L. *Zeitschrift für Tierpsychologie* 17, 420 -426.
- 529 Fischer, P., 2004. Nocturnal foraging in the stone loach (*Barbatula barbatula*): fixed or
530 environmentally induced behavior? *J Freshwater Ecol* 19, 77-85.
- 531 Fraser, B.A., Hughes, K.A., Tosh, D.N., Rodd, F.H., 2013. The role of learning by a predator,
532 *Rivulus hartii*, in the rare-morph survival advantage in guppies. *J Evolution Biol* 26, 2597-
533 2605.
- 534 Gill, A.B., 2003. The dynamics of prey choice in fish: the importance of prey size and
535 satiation. *J Fish Biol* 63, 105-116.
- 536 Greenberg, L.A., 1991. Habitat use and feeding behavior of thirteen species of benthic stream
537 fishes. *Environ Biol Fish* 31, 389-401.
- 538 Hart, P.J.B., Ison, S., 1991. The influence of prey size and abundance, and individual
539 phenotype on prey choice by the three-spined stickleback, *Gasterosteus aculeatus* L. *J Fish*
540 *Biol* 38, 359-372.
- 541 Hellmann, C., Wissel, B., Winkelmann, C., 2013. Omnivores as seasonally important
542 predators in a stream food web. *Freshwater Sci* 32, 548-562.
- 543 Holzman, R., Genin, A., 2005. Mechanisms of selectivity in a nocturnal fish: a lack of active
544 prey choice. *Oecologia* 146, 329-336.

- 545 Hughes, R.N., Croy, M.I., 1993. An experimental analysis of frequency-dependent predation
546 (switching) in the 15-spined stickleback, *Spinachia spinachia*. *J Anim Ecol* 62, 341-352.
- 547 Huhta, A., Muotka, T., Tikkanen, P., 2000. Nocturnal drift of mayfly nymphs as a post-
548 contact antipredator mechanism. *Freshwater Biol* 45, 33-42.
- 549 Johnson, R.L., Coghlan, S.M., Harmon, T., 2007. Spatial and temporal variation in prey
550 selection of brown trout in a cold Arkansas tailwater. *Ecol Freshwater Fish* 16, 373-384.
- 551 Lazzaro, X., 1987. A review of planktivorous fishes - their evolution, feeding behaviors,
552 selectivities, and impacts. *Hydrobiologia* 146, 97-167.
- 553 Lechowicz, M.L., 1982. The sampling characteristics of electivity indices. *Oecologia (Berl.)*
554 52, 22-30.
- 555 Legendre, P., Legendre, L., 2012. *Numerical ecology*, 3 ed. Elsevier, Amsterdam, Oxford.
- 556 Lobón-Cerviá, J., Rincón, P.A., 1994. Trophic ecology of red roach (*Rutilus arcasii*) in a
557 seasonal stream - an example of detritivory as a feeding tactic. *Freshwater Biol* 32, 123-132.
- 558 MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am Nat* 100,
559 603-609.
- 560 Magalhaes, M.F., 1993. Feeding of an Iberian stream cyprinid assemblage - seasonality of
561 resource use in a highly variable environment. *Oecologia* 96, 253-260.
- 562 Meehan, T.D., 2006. Energy use and animal abundance in litter and soil communities.
563 *Ecology* 87, 1650-1658.
- 564 Meyer, E.I., 1989. The relationship between body length parameters and dry mass in running
565 water invertebrates. *Arch Hydrobiol* 117, 191-103.
- 566 Michel, P., Oberdorff, T., 1995. Feeding habits of fourteen European freshwater fish species.
567 *Cybium* 19, 5-46.
- 568 Muotka, T., Juntunen, A., Meissner, K., 2006. Differential vulnerability determines the diet of
569 a slow-moving predatory stream insect. *Freshwater Biol* 51, 1486-1495.

- 570 Murdoch, W.W., 1969. Switching in general predators. Experiments on predator specificity
571 and stability of prey populations. *Ecol Monogr* 39, 335-&.
- 572 O'Brien, W.J., 1979. Predator-prey interactions of planktivorous fish and zooplankton. *Am.*
573 *Scientist* 67, 572-581.
- 574 Poff, N.L., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P., Kondratieff, B.C., 2006.
575 Functional trait niches of North American lotic insects: traits-based ecological applications in
576 light of phylogenetic relationships. *J N Am Benthol Soc* 25, 730-755.
- 577 R Development Core Team, 2013. R: A language and environment for statistical computing,
578 version 3.0.2. R Foundation for Statistical Computing, Vienna, Austria. [http://www.R-](http://www.R-project.org/)
579 [project.org/](http://www.R-project.org/).
- 580 Rader, R.B., 1997. A functional classification of the drift: traits that influence invertebrate
581 availability to salmonids. *Can J Fish Aquat Sci* 54, 1211-1234.
- 582 Rakocinski, C., 1991. Prey-size relationships and feeding tactics of primitive stream-dwelling
583 darters. *Can J Fish Aquat Sci* 48, 681-693.
- 584 Real, L.A., 1990. Predator switching and the interpretation of animal choice behavior: the
585 case for constrained optimization, in: Hughes, R.N. (Ed.), *Behavioural Mechanisms of Food*
586 *Selection*. Springer Verlag, Berlin Heidelberg, pp. 1-22.
- 587 Rincón, P.A., Lobón-Cerviá, J., 1995. Use of an encounter model to predict size-selective
588 predation by a stream-dwelling cyprinid. *Freshwater Biol* 33, 181-191.
- 589 Ringler, N.H., 1979. Selective predation by drift-feeding brown trout (*Salmo trutta*). *J Fish*
590 *Res Board Can* 36, 392-403.
- 591 Rosenfeld, J., 2000. Effects of fish predation in erosional and depositional habitats in a
592 temperate stream. *Can J Fish Aquat Sci* 57, 1369-1379.

- 593 Sanchez-Hernandez, J., 2014. Age-related differences in prey-handling efficiency and feeding
594 habitat utilization of *Squalius carolitertii* (Cyprinidae) according to prey trait analysis.
595 *Biologia* 69, 696-704.
- 596 Sanchez-Hernandez, J., Vieira-Lanero, R., Servia, M.J., Cobo, F., 2011. Feeding habits of
597 four sympatric fish species in the Iberian Peninsula: keys to understanding coexistence using
598 prey traits. *Hydrobiologia* 667, 119-132.
- 599 Santoul, F., Mengin, N., Céréghino, R., Figuerola, J., Mastrorillo, S., 2005. Environmental
600 factors influencing the regional distribution and local density of a small benthic fish: the
601 stone loach (*Barbatula barbatula*). *Hydrobiologia* 544, 347-355.
- 602 Schmidt, S.I., König-Rinke, M., Kornek, K., Winkelmann, C., Wetzel, M.A., Koop, J.H.E.,
603 Benndorf, J., 2009. Finding appropriate reference sites in large-scale aquatic field
604 experiments. *Aquat Ecol* 43, 169-179.
- 605 Schuwirth, N., Kattwinkel, M., Stamm, C., 2015. How stressor specific are trait-based
606 ecological indicators for river management? *Sci Total Environ* 505, 565-572.
- 607 Sheldon, A.L., Meffe, G.K., 1993. Multivariate analysis of feeding relationships of fishes in
608 blackwater streams. *Environ Biol Fish* 37, 161-171.
- 609 Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K., 1985. Predation, competition,
610 and prey communities - a review of field experiments. *Annu Rev Ecol Syst* 16, 269-311.
- 611 Sih, A., Moore, R.D., 1990. Interacting effects of predator and prey behaviour in determining
612 diets, in: Hughes, R.N. (Ed.), *Behavioural mechanisms of food selection*. Springer Verlag,
613 Berlin Heidelberg New York, pp. 771-796.
- 614 Smyly, W.J.P., 1955. On the biology of the stone-loach *Nemacheilus barbatula* (L.). *J Anim*
615 *Ecol* 24, 167-186.
- 616 Storch, A.J., Schulz, K.L., Cáceres, C.E., Smyntek, P.M., Dettmers, J.M., Teece, M.A., 2007.
617 Consumption of two exotic zooplankton by alewife (*Alosa pseudoharengus*) and rainbow

- 618 smelt (*Osmerus mordax*) in three Laurentian Great Lakes. Can J Fish Aquat Sci 64, 1314-
619 1328.
- 620 Street, N.E., Hart, P.J.B., 1985. Group size and patch location by the stone loach,
621 *Noemacheilus barbatulus*, a non-visually foraging predator. J Fish Biol 27, 785-792.
- 622 Syrjänen, J., Korsu, K., Louhi, P., Paavola, R., Muotka, T., 2011. Stream salmonids as
623 opportunistic foragers: the importance of terrestrial invertebrates along a stream-size gradient.
624 Can J Fish Aquat Sci 68, 2146-2156.
- 625 Szokoli, F., Winkelmann, C., Berendonk, T.U., Worischka, S., in press. The effects of fish
626 kairomones and food availability on the predator avoidance behaviour of *Gammarus pulex*.
627 Fund Appl Limnol.
- 628 Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2002. Invertebrés d'eau douce -
629 systématique, biologie, écologie. CNRS Editions, Paris, p. 587.
- 630 Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE-4: A multivariate analysis
631 and graphical display software. Stat. Comput. 7, 75-83.
- 632 Tinbergen, L., 1960. The natural control of insects in pinewoods. Archives Néerlandaises de
633 Zoologie 13, 265 – 343.
- 634 Turesson, H., Persson, A., Bronmark, C., 2002. Prey size selection in piscivorous pikeperch
635 (*Stizostedion lucioperca*) includes active prey choice. Ecol Freshwater Fish 11, 223-233.
- 636 Uieda, V.S., Pinto, T.L.F., 2011. Feeding selectivity of ichthyofauna in a tropical stream:
637 space-time variations in trophic plasticity. Community Ecology 12, 31-39.
- 638 Vanderploeg, H.A., Scavia, D., 1979. Two electivity indices for feeding with special
639 reference to zooplankton grazing. J Fish Res Board Can 36, 362-365.
- 640 Verliin, A., Kotta, J., Orav-Kotta, H., Saks, L., Vetemaa, M., 2011. Food selection of
641 *Coregonus lavaretus* in a brackish water ecosystem. J Fish Biol 78, 540-551.

- 642 Werner, E.E., Hall, D.J., 1974. Optimal foraging and the size selection of prey by the bluegill
643 sunfish (*Lepomis macrochirus*). *Ecology* 55, 1042-1052.
- 644 Winkelmann, C., Hellmann, C., Worischka, S., Petzoldt, T., Benndorf, J., 2011. Fish
645 predation affects the structure of a benthic community. *Freshwater Biol* 56, 1030-1046.
- 646 Winkelmann, C., Koop, J.H.E., Benndorf, J., 2003. Abiotic features and macroinvertebrate
647 colonization of the hyporheic zones of two tributaries of the River Elbe (Germany).
648 *Limnologica* 33, 112-121.
- 649 Winkelmann, C., Schneider, J., Mewes, D., Schmidt, S.I.S., Worischka, S., Hellmann, C.,
650 Benndorf, J., 2014. Top-down and bottom-up control of periphyton by benthivorous fish and
651 light supply in two streams. *Freshwater Biol* 59, 803-818.
- 652 Winkelmann, C., Worischka, S., Koop, J.H.E., Benndorf, J., 2007. Predation effects of
653 benthivorous fish on grazing and shredding macroinvertebrates in a detritus-based stream
654 food web. *Limnologica* 37, 121-128.
- 655 Worischka, S., Hellmann, C., Berendonk, T.U., Winkelmann, C., 2014. Fish predation can
656 induce mesohabitat-specific differences in food web structures in small stream ecosystems.
657 *Aquat Ecol* 48, 367-378.
- 658 Worischka, S., Koebsch, C., Hellmann, C., Winkelmann, C., 2012. Habitat overlap between
659 predatory benthic fish and their invertebrate prey in streams: the relative influence of spatial
660 and temporal factors on predation risk. *Freshwater Biol* 57, 2247-2261.
- 661 Yamada, K., Hori, M., Tanaka, Y., Hasegawa, N., Nakaoka, M., 2010. Contribution of
662 different functional groups to the diet of major predatory fishes at a seagrass meadow in
663 northeastern Japan. *Estuar Coast Shelf S* 86, 71-82.
- 664 Zhao, X.X., Fox, M.G., Lasenby, D.C., 2006. Effect of prey density, prey mobility and habitat
665 structure on size selection and consumption of amphipods by a benthic feeding fish. *Arch*
666 *Hydrobiol* 165, 269-288.

667 Zweimüller, I., 1995. Microhabitat use by two small benthic stream fish in a 2nd order stream.

668 *Hydrobiologia* 303, 125-137.

669

670

Accepted Manuscript

670 **Tables**671 **Table 1** Variables and their categories characterising prey, as used in calculations and plots.

| Trait abbr. | Trait (explanation) | Categories abbr. | Categories (explanation) |
|------------------------|---|-----------------------------|----------------------------------|
| abu | mean abundance (<i>log</i> 10 of mean abundance (ind m ⁻²)) | a1 | low (≤ 1) |
| | | a2 | medium (1 ... ≤ 2) |
| | | a3 | high (2 ... ≤ 4) |
| fty | feeding type | ff | filter feeder |
| | | fg | grazer |
| | | fp | predator |
| | | fse | sediment feeder |
| | | fsh | shredder |
| loc | locomotion mode | lc | crawling |
| | | ld | digging |
| | | lse | sessile |
| | | lsw | swimming |
| mha | microhabitat | ma | algae/macrophytes |
| | | mg | gravel/sand/silt |
| | | ml | leaf litter |
| | | mm | mud |
| | | ms | stones |
| | | mw | wood, roots |
| size | size (<i>log</i> 10 of body mass (mg dry)) | s1 | very small (≤ -2) |
| | | s2 | small ($-2 \dots \leq -1$) |
| | | s3 | medium ($-1 \dots \leq 0$) |
| | | s4 | large (0 ... ≤ 1) |
| | | s5 | very large (1 ... ≤ 2) |
| vel | current velocity preference | v1 | zero (0 ms ⁻¹) |
| | | v2 | low ($< 0.25\text{ms}^{-1}$) |
| | | v3 | high ($> 0.25 \text{ms}^{-1}$) |

672

672 **Table 2** Range of the electivity indices E^* of gudgeon and stone loach for the single
 673 categories within each variable (mean of all sampling dates and streams $\pm SD$) and results of
 674 Wilcoxon test with Holm correction, p_{adj} values < 0.05 (broad) indicate that E^* was
 675 significantly different from 0 (see also Fig. 3).

| Variable | Gudgeon | | | Stone loach | | | |
|-------------|----------|-----------------|-----|--------------|-----------------|-----|--------------|
| | Category | Range of E^* | V | p_{adj} | Range of E^* | V | p_{adj} |
| abu | | 0.57 \pm 0.32 | | | 0.39 \pm 0.25 | | |
| a1 | | | 36 | 0.043 | | 114 | 1.000 |
| a2 | | | 8 | 0.001 | | 8 | 0.001 |
| a3 | | | 189 | 0.072 | | 159 | 1.000 |
| fty | | 0.61 \pm 0.24 | | | 0.67 \pm 0.25 | | |
| ff | | | 167 | 0.456 | | 130 | 1.000 |
| fg | | | 167 | 0.456 | | 175 | 0.596 |
| fp | | | 58 | 0.322 | | 17 | 0.005 |
| fse | | | 207 | 0.011 | | 32 | 0.046 |
| fsh | | | 7 | 0.000 | | 19 | 0.007 |
| loc | | 0.35 \pm 0.18 | | | 0.38 \pm 0.23 | | |
| lc | | | 4 | 0.000 | | 48 | 0.316 |
| lc | | | 27 | 0.015 | | 80 | 1.000 |
| lse | | | 228 | 0.000 | | 162 | 1.000 |
| lsw | | | 38 | 0.050 | | 59 | 0.703 |
| mha | | 0.37 \pm 0.16 | | | 0.34 \pm 0.14 | | |
| ma | | | 68 | 0.456 | | 63 | 0.912 |
| ml | | | 15 | 0.003 | | 82 | 1.000 |
| mm | | | 80 | 0.687 | | 105 | 1.000 |
| msa | | | 101 | 0.711 | | 37 | 0.093 |
| mst | | | 210 | 0.007 | | 156 | 1.000 |
| mw | | | 209 | 0.008 | | 206 | 0.019 |
| size | | 1.03 \pm 0.44 | | | 0.85 \pm 0.34 | | |
| s1 | | | 201 | 0.020 | | 165 | 1.000 |
| s2 | | | 207 | 0.011 | | 176 | 0.596 |
| s3 | | | 17 | 0.004 | | 17 | 0.005 |
| s4 | | | 11 | 0.001 | | 31 | 0.045 |
| s5 | | | 12 | 0.006 | | 55 | 0.596 |
| vel | | 0.24 \pm 0.14 | | | 0.25 \pm 0.19 | | |
| v1 | | | 203 | 0.016 | | 109 | 1.000 |
| v2 | | | 88 | 0.711 | | 156 | 1.000 |
| v3 | | | 10 | 0.001 | | 80 | 1.000 |

676

677

678

678 **Figures and legends**

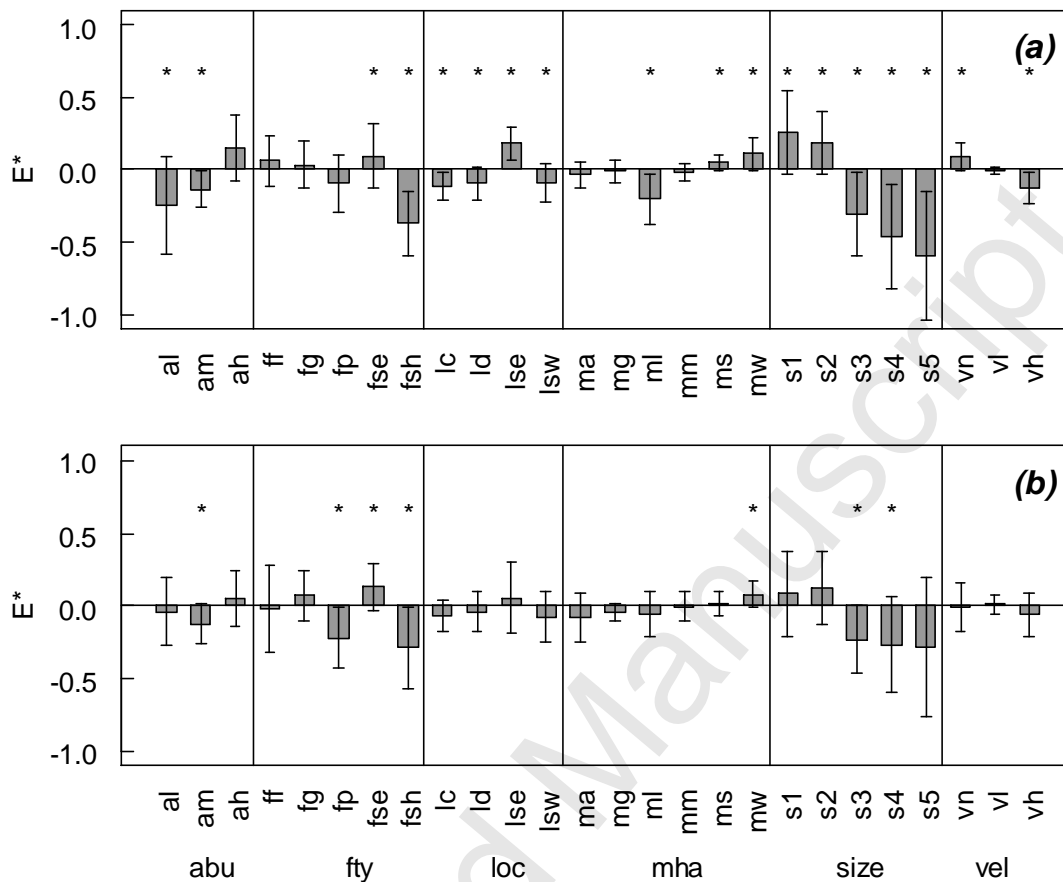
679

680 **Figure 1** FPCA of the samples of benthos and gudgeon diet. (a) – (c) Plots of the samples,
681 arrows connect the benthos sample (arrow origin) with the respective diet sample (arrow
682 head) for each date and stream. All three plots represent the same dataset, only grouped by (a)
683 stream with G = Gauernitzbach and T = Tännichtgrundbach, (b) season with 1 = spring, 2 =
684 summer, 3 = fall, and (c) year with 05 = 2005 etc. (d) Plot of the variables and the
685 eigenvalues of the axes for this FPCA. Bottom right: scaling of the axes for all four plots.
686 Trait abbreviations see Table 1.

687

688 **Figure 2** FPCA of the samples of benthos and stone loach diet. (a) – (c) Plots of the samples,
689 arrows connect the benthos sample (arrow origin) with the respective diet sample (arrow
690 head) for each date and stream. All three plots represent the same dataset, only grouped by (a)
691 stream with G = Gauernitzbach and T = Tännichtgrundbach, (b) season with 1 = spring, 2 =
692 summer, 3 = fall, and (c) year with 05 = 2005 etc. (d) Plot of the variables and the
693 eigenvalues of the axes for this FPCA. Bottom right: scaling of the axes for all four plots.
694 Trait abbreviations see Table 1.

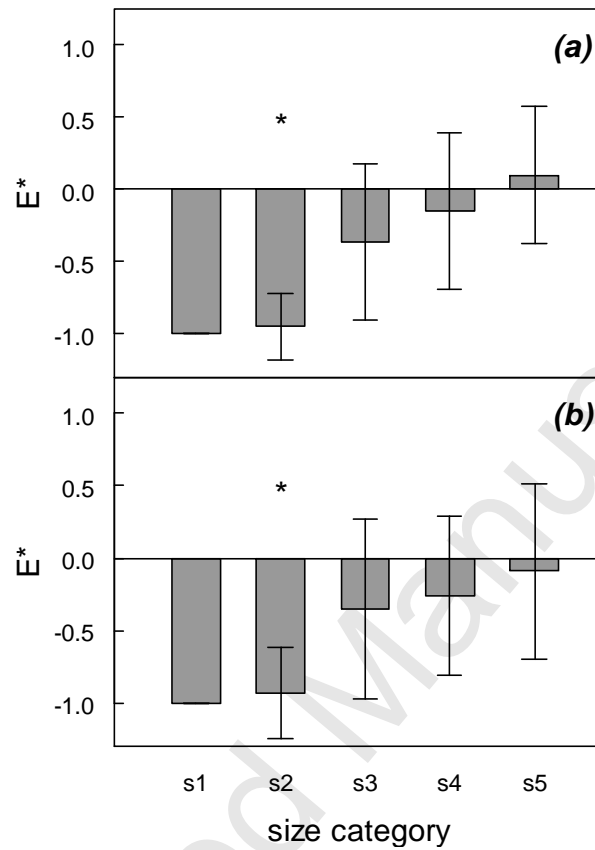
695



695

696 **Figure 3** Electivity indices E^* of gudgeon (a) and stone loach (b) for the categories of the
 697 variables mean abundance (abu), feeding type (fty), microhabitat preference (mha), loco-
 698 motion type (loc), size, and current velocity preference (vel). Black lines = median, black
 699 squares = mean, boxes = quartiles, whiskers = range. Trait and trait category abbreviations see
 700 Table 1. Asterisks indicate E^* values significantly different from 0 (p -values see Table 2).

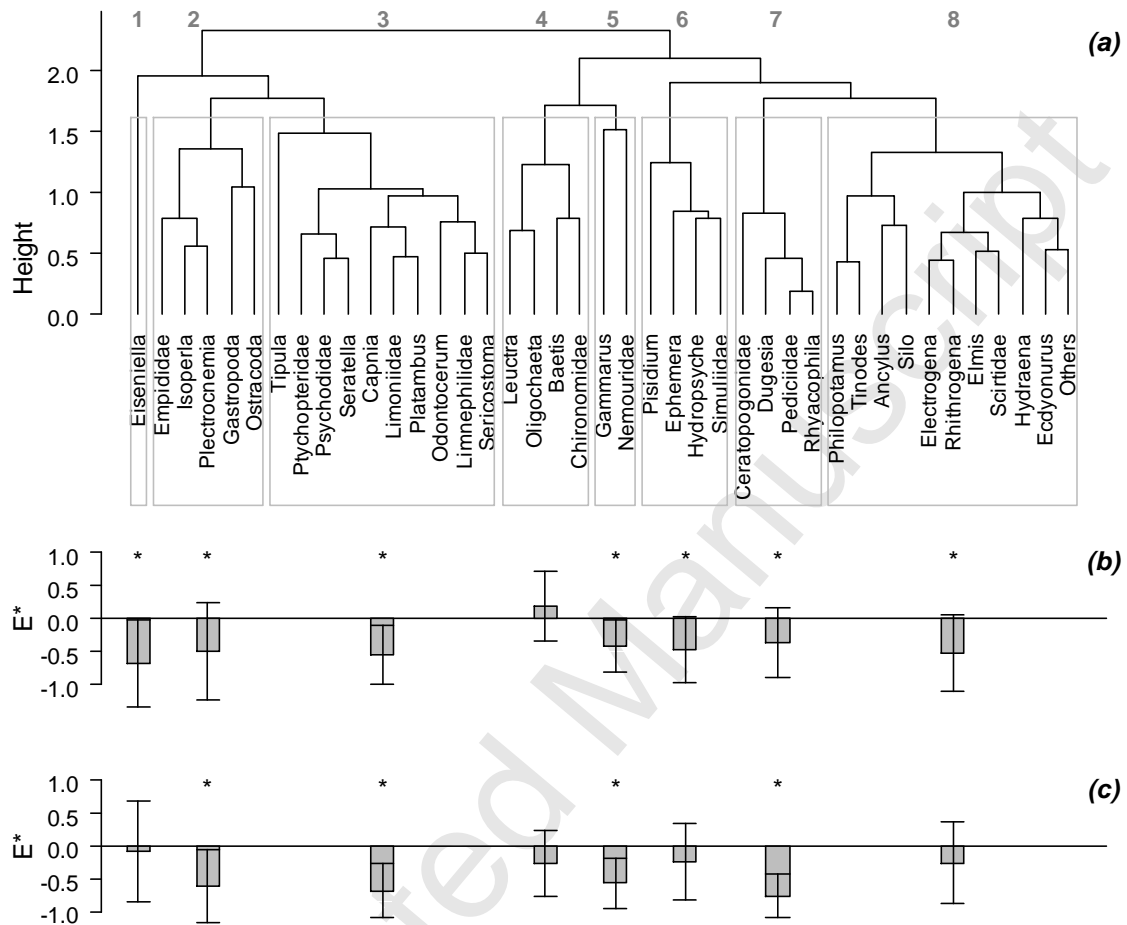
701



701

702 **Figure 4** Electivity indices E^* of (a) gudgeon and (b) stone loach for size classes of
 703 *Gammarus* spp. in the streams Gauernitzbach and Tännichtgrundbach (mean \pm SD of all
 704 sampling occasions). Size classes correspond to size categories in Table 1. Asterisks mark
 705 significant differences from 0 (s1 not tested).

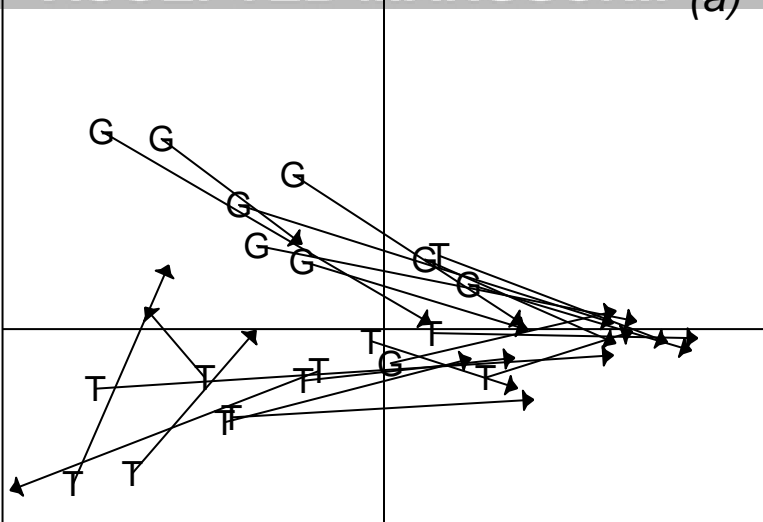
706



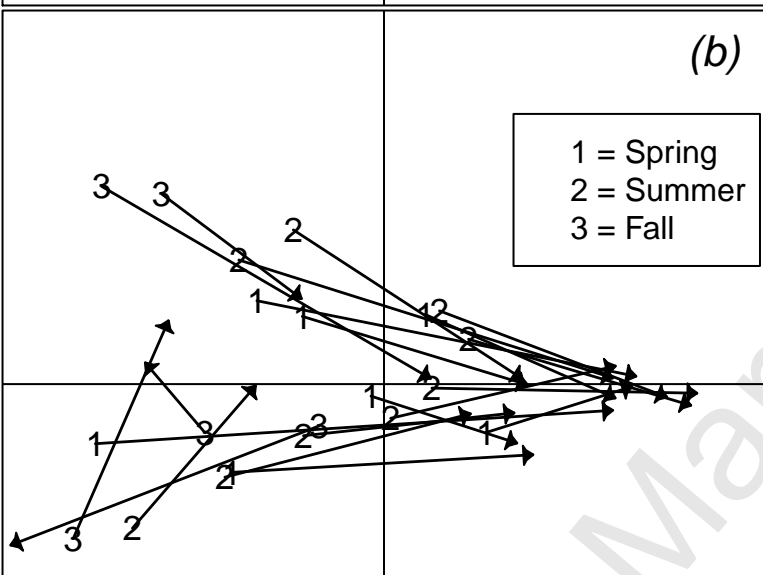
707

708 **Figure 5** Hierarchical cluster analysis (a) of the ‘taxa × traits’ array (grey numbers and
 709 rectangles mark the prey groups) and electivity indices E^* of gudgeon (b) and stone loach (c)
 710 for each prey group (mean ± SD of all sampling occasions, gudgeon $n = 21$, stone loach $n =$
 711 22). E^* values significantly different from 0 are marked with asterisks.

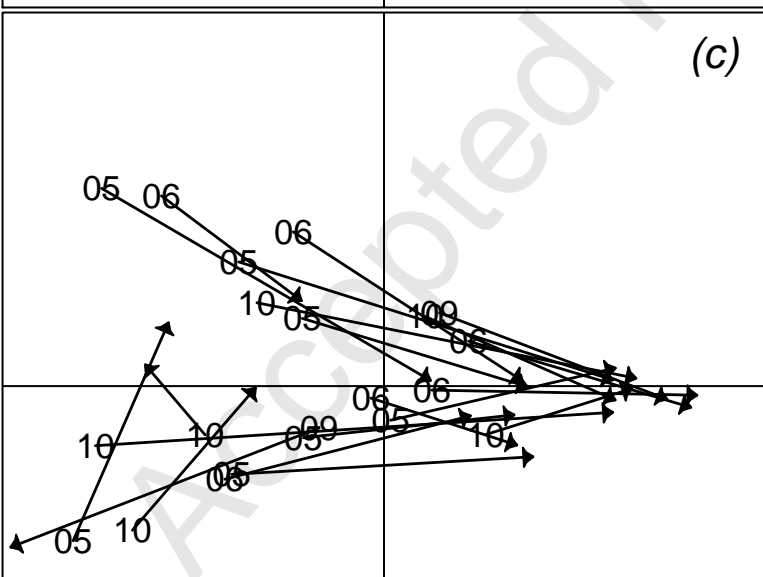
712



(b)



(c)



(d)

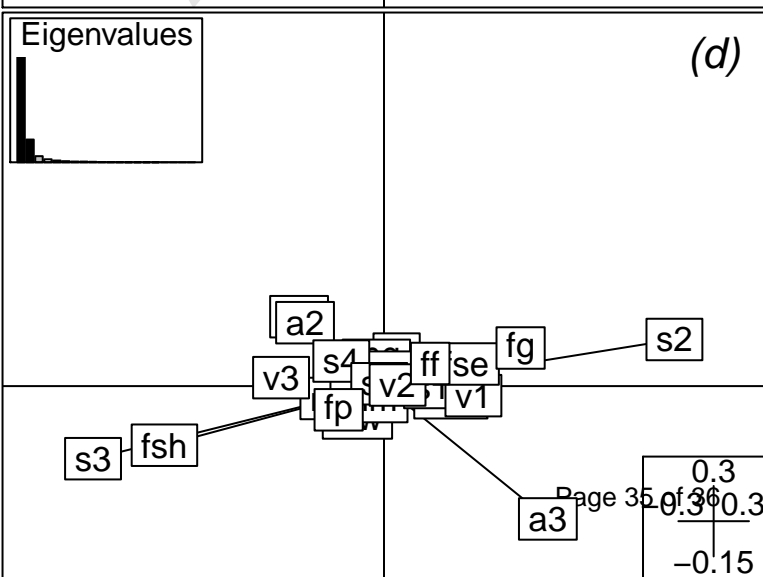


Figure 2

