TITLE:

Contribution of environmental and spatial factors to the structure of stream fish assemblages at different spatial scales

AUTHOR(S):

Nakagawa, Hikaru

CITATION:

Nakagawa, Hikaru. Contribution of environmental and spatial factors to the structure of stream fish assemblages at different spatial scales. *Ecology of Freshwater Fish* 2014, 23(2): 208-223

ISSUE DATE:

2014-04

URL:

<http://hdl.handle.net/2433/199856>

RIGHT:

This is the peer reviewed version of the following article: Nakagawa, H. (2014), Contribution of environmental and spatial factors to the structure of stream fish assemblages at different spatial scales. *Ecology of Freshwater Fish*, 23: 208–223, which has been published in final form at <http://dx.doi.org/10.1111/eff.12070>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.; This is not the published version. Please cite only the published version.; この論文は出版社版ではありません。引用の際には出版社版をご確認ください。

1 **Title:** Contribution of environmental and spatial factors to the structure of stream fish assemblages
2 at different spatial scales

3 **Author:** Hikaru Nakagawa

4 **Email-address:** nakagawa@terra.zool.kyoto-u.ac.jp

5 **Telephone:** 075-753-4077

6 **Fax:** 075-753-4100

7 **Address:** Graduate School of Science, Kyoto University, Kitashirakawa-Oiwake-cho, Sakyo-ku,
8 Kyoto-city, Kyoto 606-8502, Japan

9 **Short title:** Scale-dependent contribution of environmental and spatial factors in fish assemblages

10 **Key words:** hierarchical river structures, habitat selection, dispersal process, scale dependency,
11 source–sink dynamics

12

13

14 **Abstract**

15 To compare the contributions of environmental and spatial factors in structuring assemblages of
16 temperate stream fish on different spatial scales, I evaluated the distance decay of fish assemblage
17 similarity and correlations among species compositions, environmental factors and geographical
18 locations at medium (inter-reach scale, spatial extent 40 km) and fine (inter-microhabitat scale,
19 spatial extent <200 m) scales. Partial redundancy analysis and variation partitioning indicated that
20 the ordinal rank of the relative importance of environmental and spatial factors differed among
21 scales. At the medium scale, the distance decay of similarity of species composition was steep at
22 approximately >10-km scale, and the assemblage structure was simply explained by the distance
23 between sites and several environmental factors (e.g. elevation and current velocity). In contrast,
24 the distance between microhabitats explained only a small portion of the variance in species
25 composition at the fine scale, and fish assemblages were affected by several spatial patterns of
26 habitat (or some environmental features associated with those spatial patterns). Environmental
27 factors at the fine scale (e.g. substratum characteristics and presence/absence of cover) correlated
28 with each other and were spatially structured, and their contribution to species variance was
29 smaller than that at the medium scale. These results provide evidence for scale-dependent
30 alternation of the rank of the relative importance of environmental and spatial factors in structuring
31 assemblages of stream fishes via the turnover of crucially contributing factors from medium to fine

32 spatial scales.

33

34 **Introduction**

35 The contribution of ‘environmental factors’ and ‘spatial factors’ in determining community

36 structure is currently an important topic in community ecology. This dichotomy was recently

37 synthesised in a metacommunity theory (Leibold et al. 2004; Cottenie 2005). Leibold et al. (2004)

38 categorised metacommunity theories into 4 paradigms (neutral model, patch dynamics, mass

39 effects and species sorting), questioning whether the structuring of local communities is affected

40 by dispersal limitation, interspecific interactions and habitat heterogeneities. In a river, various

41 biotic and abiotic environments exhibit characteristic spatial structures across multiple scales (e.g.

42 channel networks at the river system scale, directional 1-dimensional structure at the segment scale

43 and environmental patches at the reach and microhabitat scales; Frissell et al. 1986; Montgomery

44 & Buffington 1997) and hierarchical structures are expected to affect both environmental and

45 spatial processes at each scale. Therefore, to evaluate the contributions of environmental and

46 spatial factors in the determination of a riverine community structure, consideration of scale

47 dependency is essential (Holyoak et al. 2005; Heino 2011).

48 Several studies have examined the contributions of environmental and spatial factors in

49 assemblages of fishes in streams and demonstrated taxonomic or functional group dependency

50 (Hoeinghaus et al. 2007), the effect of non-native species (Sály et al. 2011), temporal variability
51 (Erős et al. 2012), region dependency (Kautza & Sullivan 2012) and spatial scale dependency.
52 Spatial scale dependency is considered to be the most important factor and has been repeatedly
53 examined (Magalhães et al. 2002; Mykrä et al. 2007; Heino 2011; Sály et al. 2011). However,
54 many previous studies have considered the changes in contribution from large to medium spatial
55 scales (i.e. variation among regions, water systems, segments and reaches) and not from medium
56 to fine scales (i.e. variation among microhabitats).

57 As with the change from large to medium scales, the contribution of environmental and
58 spatial factors in stream assemblages is also likely to change from medium to fine scales. Previous
59 studies have demonstrated that environmental factors decrease their contribution and spatial
60 factors display the opposite pattern in structuring stream assemblages, with a decrease in spatial
61 scale from large to medium (Magalhães et al. 2002; Mykrä et al. 2007). This trend is a
62 consequence of the large contribution of source–sink effects (mass effects or rescue effects;
63 Amarasekare 2003) at the medium scale and the small (but significant) contribution of
64 biogeographical backgrounds at the large scale (Magalhães et al. 2002). When scaling down from
65 medium to finer scales, the contribution of environmental factors is predicted to be large across all
66 spatial scales via the turnover of corresponding environmental factors, because many previous
67 studies have documented associations between various environmental factors and fish species

68 composition across inter-regional to inter-microhabitat scales (Matthews 1998; Wang et al. 2003;
69 Durance et al. 2006; Heino 2011). In contrast, the contribution of spatial factors is predicted to
70 decline at finer spatial scales because the spatial processes that determine stream assemblage
71 structures strongly associate with the dispersal of individuals that are less constrained by distance
72 at fine scales [e.g. neutral processes at river system scales (Muneepeerakul et al. 2008) and mass
73 effects at reach or segment scales (Falke & Fausch 2010)]. For these reasons, I predicted that the
74 contribution of environmental factors is larger and that of spatial factors is smaller when the
75 spatial scale is decreased (i.e. the reverse pattern of the scale dependency from large to medium
76 scales). However, previous studies on the contributions of environmental and spatial factors in
77 stream assemblages were based on presence/absence data or total individual numbers in reaches or
78 larger sampling units (Magalhães et al. 2002; Mykrä et al. 2007; but see Sály et al. 2011 who
79 compared the presence/absence and relative abundance data at medium and large scales) the scale
80 dependency from medium to fine scale has not yet been examined.

81 Therefore, I conducted a quantitative and detailed investigation of fish distribution and
82 environmental factors at medium and fine scales by direct underwater observations. I predicted
83 that environmental factors would be significant in assemblage structuring at both scales by
84 alternating the responsible factors between the 2 scales. In contrast, spatial factors would be
85 significant only at the medium scale because dispersal constraints among habitat patches would

86 decrease at the fine scale. Based on the above predictions, the contribution of the environment
87 would therefore increase and the contribution of space would decrease with a reduction in spatial
88 scale. The contributions of individual factors, for both environmental and spatial factors, in
89 assemblage structuring using partial redundancy analysis (partial RDA) were examined. The
90 effects of dispersal processes were also examined by evaluating the distance decay of both species
91 composition and habitat similarity. The contributions of environmental and spatial factors were
92 evaluated using variation partitioning (VP). Based on these results, I demonstrate scale
93 dependency of the contributions of environmental and spatial factors in describing the variance of
94 assemblages of fishes in stream from medium to fine spatial scales and discuss the key processes
95 contributing to assemblage structuring.

96

97

98 **Materials and methods**

99 *Research area*

100 The study was conducted along the main stem of the Yura River, from the headwater to about 40
101 km downstream in the lower reaches, in the northern part of Kyoto Prefecture, western Japan (Fig.
102 1a, b and c). The research area is separated from the lower part of the river by a large dam. The
103 Yura River flows from the Sugio Ridge (750 m a.s.l.), located on the border between Kyoto and

104 Fukui prefectures, and the river course has a length of about 146 km and a catchment area of about
105 1880 km². The regional climate is warm-temperate with monsoon effects. At the location of the
106 upper quarter of the research area (35°18'N, 135°43'E, 356 m a.s.l.), the annual mean temperature
107 is 11.9°C, annual precipitation is 2298 mm and snow depth in winter is approximately 1 m. The
108 catchment area in the upper part of the research area (0–15 km from the headwater) is covered by
109 conifer plantations of *Cryptomeria japonica* and deciduous broad-leaved forests dominated by
110 *Fagus crenata* and *Quercus crispula* (data from Ashiu Forest Research Station, Field Science
111 Education and Research Center, Kyoto University, <http://www.fserc.kais.kyoto-u.ac.jp/asiu/>).
112 Residential and agricultural use in the catchment area in the lower part of the research area (15–40
113 km from the headwater) is less than 5% (data from Nantan City, Kyoto, Japan), and I therefore
114 considered that the effects of these uses on fish species composition were negligible. Artificial
115 protective structures on riverbanks are relatively rare, and most areas of the riverbanks are
116 bordered by forests. Some sediment control dams exist in the middle part of the research area, but
117 all dams have a fishway, and the species composition of fish did not show sudden changes at any
118 dam in a preliminary analysis (see also Results). Thus, I considered that artificial or natural
119 structures restricting dispersal of fishes probably do not exist in the main stream from the
120 headwater to the dam 40 km below.

121

122 *Hierarchical river habitat structure and spatial scales*

123 The spatial patterns of fish assemblages at medium (inter-reach scale, spatial extent 40 km) and
124 fine (inter-microhabitat scale, spatial extent <200 m) scales were examined. In my research area,
125 the medium and fine scales reflect the inter-reach (intra-segment or intra-river longitudinal) scale
126 and the inter-microhabitat (intra-reach) scale, respectively, in the hierarchical river structure
127 (Frissell et al. 1986; Allan & Castillo 2007). A reach is defined as a repeating sequence of channel
128 units (such as a riffle–pool–run sequence; Frissell et al. 1986; Allan & Castillo 2007). In the Yura
129 River, the length of 1 reach (riffle–pool–run sequence) is approximately 50 m at the upper sites in
130 the research area and 200 m at the lower sites on average.

131 A microhabitat is recognised as decimetre-scale environmental sets that are patchily
132 distributed within a reach, such as deep locations, boulders, crevices in the bedrock or cover in the
133 riverbank (Frissell et al. 1986).

134

135 *Sampling sites and observation plots*

136 Twenty-one sampling sites that represented all the river structures contained within the research
137 area were established: sites 1 (uppermost) to 21 (lowest) (Fig. 1c). No sampling sites were
138 established in the river between 4 to 10 km from the headwater because of access difficulties. The
139 Yura River originates from a spring in the forest floor. The uppermost site of the research area was

140 1.5 km downstream from the origin. The lowest sampling site was located just upstream of the
141 dam reservoir.

142 Ten line transects were set perpendicular to water flow along the channel at each sampling
143 site (Fig. 1d). The interval between transects was adjusted according to river size: 5-m intervals at
144 the upper 4 sites (sites 1–4); 20-m intervals at sites 14, 20 and 21 and 10-m intervals at all other
145 sites. Each sampling site included at least 1 reach (1–3 reaches). Plots were established along each
146 transect at regular intervals (4–8 plots per transect; Fig. 1d). Plots were the minimum unit of
147 observation and measurement. The number of observation plots along the transects was adjusted
148 according to channel width: 4 plots at the upper 4 sites (sites 1–4; mean wet width <5 m), 8 plots
149 at sites 14, 20 and 21 (mean wet width >20 m) and 6 plots at the other sites (mean wet width 5–20
150 m). A red-coloured sounding lead was placed at the centre of each observation plot as a landmark
151 for fish observation and environmental measurements.

152

153 *Fish observations*

154 Fish observations were conducted in the summer from 20 August to 27 September 2009. During
155 this season, the water temperature of the river is at its annual maximum, and all fish species are
156 active (Nakagawa, unpublished data). Observations were conducted by snorkelling during the day
157 (10:00–15:00) and night (22:00–3:00), because some fish species are active at night. Water

158 temperature was measured at the start time of each observation. Snorkelling observations were
159 conducted by the line-transect method using the following procedure: First, I dived into the right
160 or left side of a stream channel and moved to 1 m downstream of a transect. Five minutes later, the
161 fish showed normal behaviour, I quietly moved along the transect and observed the fish. When an
162 individual fish was found, I recorded its species and the nearest landmark lead. All observations
163 were conducted by the same person (HN). The observation time was approximately 20 min
164 (including waiting time) per transect. A waterproof hand light and headlight were used for night
165 observations. Because diet and habitat shifts during larval and juvenile periods occur in some
166 target species (Nakamura 1969), data for larval fish were excluded from the analysis.

167 The number of individuals of each species observed at a plot at each sampling site (4 plots at
168 sites 1–4, 6 plots at sites 5–13 and 15–19 and 8 plots at sites 14, 20 and 21) was used to determine
169 fish distribution data at the fine scale. In the research area, 27 fish species were observed in total
170 (Nakagawa, unpublished data). Although the bluegill sunfish, *Lepomis macrochirus*, was
171 introduced from North America, this species was included in the analysed data set because it
172 became established in this river at least 14 years prior to the study (National Census on River
173 Environments of Japan 1993); hence, its distribution is not likely to be restricted by its initial
174 location of introduction. The largemouth bass, *Micropterus salmoides*, was also introduced from
175 North America, but I did not observe this species in the research area, probably because it is

176 primarily lentic and restricted to dam reservoirs. *Anguilla japonica*, *Plecoglossus altivelis* and
177 *Oncorhynchus masou* were excluded from the analysed data set as they are introduced annually by
178 a local fishery cooperative, and I could not determine the innate distribution of these species.
179 Among the material species in this study, *Zacco platypus*, *Cyprinus carpio*, *Carassius auratus* and
180 *L. macrochirus* occupy the dam reservoir (National Census on River Environments of Japan
181 1993); however, *Z. platypus* mainly occupies stream habitats (Nakamura 1969), and the other
182 species are rare in the upper to middle reaches of the Yura River (see Results). Therefore, the
183 effect of the dam reservoir seems to be small in this research. The total number of individuals of
184 each species at each sampling site was used for fish distribution data at the medium scale. Day and
185 night data were pooled.

186

187 *Environmental data*

188 Environmental factors were categorised into medium- and fine-scale descriptors on the basis of
189 previous studies that referred to the spatial scales critical for habitat selection by fish (Table 1). For
190 example, in general, water temperature gradually increases from upper to lower reaches at the
191 kilometre scale, and therefore the distribution of a fish species determined by temperature
192 tolerance would be responsive at this scale (Fausch et al. 1994). Water temperature was therefore
193 categorised as a medium-scale factor. Pinpoint habitat patches such as cover and boulders are used

194 as short-term habitats for refuge or foraging sites (Sechnick et al. 1986; Fuselier & Edds 1995;
195 Nakagawa et al. 2012); thus, these were considered fine-scale factors.

196 Fine-scale data (i.e. water depth, current velocity, substratum characteristics and
197 presence/absence of cover) were measured at the point of each landmark lead (i.e. each
198 observation plot) after fish observations. Water depth was measured with accuracy of 1 cm using a
199 metre stick. Current velocity was measured at 60% water column depth using a portable
200 tachometer (Model 3651 Pocket Tachometer, Cosmo-Riken, Osaka, Japan). To measure substrate
201 characteristics, a 50 × 50-cm quadrat with 10 × 10-cm cells (total of 25 cells) was placed on a
202 landmark. Furthermore, the major substrate type was recorded, which was characterised by
203 sediment particle size, in each cell based on the Wentworth–Udden particle scale (<2 mm, sand;
204 2–4 mm, granules; 5–64 mm, pebbles; 65–256 mm, cobbles; >256 mm, boulders; bedrock;
205 Wentworth 1922). Cover was defined as over-hanging branches and leaves of terrestrial plants that
206 were more than 50 cm long.

207 A portion of the medium-scale data was calculated as the mean of measurements for all
208 observation plots or transects included in each sampling site. This method was applied for water
209 depth, current velocity, substrate characteristics, presence/absence of cover and channel width. The
210 other portion of medium-scale data (the gradient of the river bed at each sampling site) was
211 obtained from a 1:25,000 map published by the Geospatial Information Authority of Japan. The

212 gradient of the river bed was represented as the mean of 30 gradient measurements for 100-m
213 intervals within ± 1.5 km of the upper and lower reaches around the sampling site. Water
214 temperatures measured at each observation were averaged. Flow rate was calculated as the product
215 of the means of water depth, current velocity and channel width at each sampling site.

216

217 *Spatial data*

218 Spatial variables at each spatial scale were constructed using Moran's eigenvector mapping
219 (MEM) technique. MEM describes the spatial structures of species composition by the eigenvalues
220 and eigenvectors that represent the spatial relationships between sampling points across various
221 spatial scales (Dray et al. 2006). The MEM approach offers advantages over direct geographical
222 coordinate or trend-surface (i.e. polynomial) approaches in that MEM ensures independence
223 between spatial variables and detects wider-range spatial structures. These methods have been
224 reviewed in detail by Okuda et al. (2010) (see also Borcard & Legendre 2002; Borcard et al. 2004;
225 Dray et al. 2006).

226 Spatial patterns of the observed assemblages were analysed separately for the medium and
227 fine spatial scales. For the medium scales, the 21 sampling sites on the main stream were
228 approximated by points on a 1-dimensional line, such that the order and interval of the points
229 reflected the location of the sampling sites (see upper figure in Appendix 1). For the fine scale,

230 disposition of the observation plots was approximated in each sampling site by 10×4 grids with a
231 10:1 aspect ratio at the upper 4 sites (sites 1–4); 10×8 grids with a 10:1 aspect ratio at sites 14, 20
232 and 21; and 10×6 grids with a 10:1 aspect ratio at the other sites (see the lower figures in
233 Appendix 1). A spatial weighting matrix (SWM) was constructed for the medium-scale data and
234 21 SWMs for the fine-scale data from the distances of neighbouring sampling sites and then from
235 the distances from each of the neighbouring observation plots within a sampling site, respectively
236 (Dray 2010). Moran's eigenvectors (MEVs) were calculated from an SWM and used as the spatial
237 variables. An MEV exhibited a wave-like spatial pattern when plotted on the location of the
238 sampling sites or observation plots (see Results) and represented the autocorrelation patterns of
239 these sites and plots (Dray 2010).

240

241 *Tests of distance decay in fish assemblages and environmental similarities*

242 The similarity indices of species composition and habitat characteristics were calculated between
243 sampling sites at the medium scale and between observation plots at the fine scale to analyse the
244 decay of these similarities with distance. The distance was defined as the straight-line distance
245 between pairs of observation plots at the fine scale and as the distance along the river between
246 pairs of sampling sites at the medium scale. At the fine scale, similarities between <5 m and >50 m
247 distant plots were eliminated from the analysis because they did not exist in common at all

248 sampling sites. The Bray–Curtis similarity index (1– the Bray–Curtis dissimilarity), based on the
249 number of individuals of each species at sampling sites or observation plots, was used to express
250 the similarity of species composition. The correlation between the similarity of species
251 composition and distance was examined using Mantel tests at each scale. The environmental
252 characteristics measured at the medium and fine scales (Table 1) were used to calculate the habitat
253 similarity at each scale. For evaluating habitat similarity, principal components analysis was
254 conducted on the basis of the environmental characteristics for each spatial scale and obtained
255 principal component (PC) scores of observation plots for PC 1–4 at the medium scale and PC 1–5
256 at the fine scale; these explained >80% of the total variance in environmental characteristics for
257 each spatial scale. Subsequently, the multidimensional Euclidian distance (D) of the PC scores was
258 used to calculate the index of habitat similarity. By using the transformation $1-D/(1+D)$, D has
259 been converted into a similarity index ranging from 0 to 1. The correlation between habitat
260 similarity and distance was examined using Mantel tests at each spatial scale.

261

262 *Multivariate analysis*

263 In the multivariate analyses of VP procedure, the Hellinger transformation (rows of the data set are
264 standardised by their row sum and then a square root transformation, Legendre & Gallagher 2001)
265 was applied to data for species composition in each plot or each site to adjust the difference in the

size of observation units and avoid the horseshoe bias (Peres-Neto et al. 2006). VP analysis was conducted to evaluate the contributions of environmental and spatial factors in determining spatial patterns of assemblages at different spatial scales. The total variation contained in the distribution data for fishes was segregated into unique environmental and spatial components using redundancy analysis (RDA) based on a VP approach (Borcard et al. 1992). RDA is a constrained ordination technique and serves as a multivariate extension of linear regression analysis (Legendre & Legendre 1998; Beisner et al. 2006; Okuda et al. 2010). The environmental variables were log-transformed (Stewart-Koaster et al. 2007; Erős et al. 2009). A forward selection technique was conducted according to Blanchet et al. (2008) before RDA for the environment and spatial variables to find the statistically relevant variables. VP was calculated from 3 RDAs as follows. The first RDA uses sets of both environmental and spatial variables and obtains the total variation of a distribution data for fishes explained by environmental and spatial variables, expressed as [E + S]. The second RDA calculates the fraction [E] that is explained by environmental variation, involving co-effects of spatial variables. The third RDA calculates the fraction [S] explained by the spatial variation, including co-effects of environmental variables. [E + S], [E] and [S] were adjusted for a multiple coefficient of determination ($R^2_{adj.}$) according to Peres-Neto et al. (2006). Note that, in some cases (e.g. small sample size, large number of explanatory variables), negative values can be obtained. The other fractions can be obtained as follows: the fraction of variation

284 explained by environmental factors independent of spatial factors is $[EP] = [E + S] - [S]$, the
285 fraction of variation explained by spatial factors independent of environmental factors is $[SP] = [E$
286 $+ S] - [E]$, the fraction of variation explained by correlations between environmental and spatial
287 factors is $[ES] = [E] + [S] - [E + S]$, and the residual fraction of variation is $[R] = 1 - [E + S]$.
288 $[EP]$ and $[SP]$ indicate the independent effects of observed environmental conditions (associated
289 with niche explanations) and spatial arrangement (representing local dispersal processes or an
290 environmental factor associated with that spatial pattern), respectively, in determining the spatial
291 variation in species composition. $[ES]$ represents the fraction explained by variables that cannot be
292 statistically divided into environmental and spatial factors (Peres-Neto et al. 2006). $[R]$ is the
293 unexplained spatial variation in species composition and includes the effects of unmeasured
294 environmental factors and stochastic mechanisms. The VP approach has the potential risk of
295 underestimating the relative contributions of environmental factors when important environmental
296 factors are not included in the data set (Gilbert & Bennett 2010; Smith & Londholm 2010). For
297 example, river-bank characteristics were not included as environmental factors because of their
298 explicit correlations with the spatial arrangements of observation plots. Therefore, possible
299 spurious correlation of a spatial factor must be considered when interpreting the results of VP
300 (Gilbert & Bennett 2010; Smith & Londholm 2010). However, despite this problem, the VP
301 approach is a good tool in the first step of partitioning out environmental and spatial components

302 from the total variation in species composition using appropriate adjustments [e.g. the unimodal
303 distribution of species (Peres-Neto et al. 2006; Legendre & Gallagher 2001), the inflation of
304 variance (Blanchet et al. 2008) and sampling density (Peres-Neto et al. 2006)].

305 The significance of the testable variance fractions (i.e. [EP], [SP] and [ES]) was tested using
306 permutation tests with 9999 randomisations of the correspondence between the spatial patterns of
307 species composition and each set of environmental and spatial predictors according to the tutorial
308 of the statistical software CANOCO (Borcard et al. 1992; Leps & Smilauer 2003). For each spatial
309 and environmental predictor at the fine scale, significance was also tested for each sampling site
310 because the selected predictors differed among sites. *P*-values were adjusted by the number of
311 variables in each VP or partial RDA using the Bonferroni method.

312 Forward selection of variables, VP, permutation tests, partial RDA and MEM were
313 performed using the statistical software R (R Development Core Team 2010) with the add-on
314 packages ‘vegan’ (Oksanen et al. 2008), ‘spacemakerR’ (Dray 2010) and ‘packfor’ (Blanchet et al.
315 2008).

316

317 **Results**

318 *Fish species composition and its distance decay*

319 A total of 9520 individuals of 27 fish species were observed, and data for 9402 individuals of 24

species were used for analyses (Appendix 2). Uneven distribution patterns biased towards the upper, upper-middle, lower-middle or lower reaches at the medium scale were observed in some fish species; thus, species composition changed along the river course (Fig. 2). Several fish species exhibited bell-curve-like patterns of distribution, having a centre of distribution with high population density at a certain position in the river course and a skirt of distribution with low population density (Fig. 2).

Similarity in species composition was significantly correlated with the distance at the medium scale (Mantel test, $r = 0.772$, $P = 0.001$, Fig. 3a) but not at the fine scale ($r = 0.014$, $P = 0.424$, Fig. 3b). The decay of species similarity was particularly clear at 10 km or larger scales (Fig. 3a).

Habitat environments and their distance decay

In general, at the medium scale, water temperature, gradient of the river bed, flow rate and mean width of the river channel simply decreased or increased from upper to lower reaches. In contrast, other factors (e.g. mean water depth and mean current velocity) did not demonstrate such simple patterns along the upper–lower locations of the river (Appendix 3). Distance decay in similarity of habitat environment was detected at both the medium scale (Mantel test, $r = 0.629$, $P = 0.001$; Fig. 3c) and the fine scale (Mantel test, $r = 0.075$, $P = 0.040$; Fig. 3d), but the effect was much weaker

338 for the latter. In contrast to the distance decay patterns in species composition similarity, habitat
339 similarity was nearly constant around the 10–20-km spatial scale.

340

341 *Partitioning of environmental and spatial factors and significance of individual factors*

342 I obtained data sets for species composition at the fine scale, environmental variables and spatial
343 variables at 1063 observation plots, excluding plots where no fish were observed. According to the
344 VP analysis, the predictor variables explained 85.98% of the total variation in species composition
345 at the medium scale and the mean variation of 36.5% at the fine scale (Tables 2 and 3).

346 At the medium scale, 3 environmental variables (elevation, water temperature and mean
347 current velocity) and 6 spatial variables (MEV 1–6) were selected (Table 2). At the fine scale, the
348 number of selected environmental variables was 2 at site 18, 1 at sites 2, 3, 6, 7, 9, 11–15 and 21
349 and none at the others (Table 3). The number of selected spatial variables varied from 1 to 13
350 among sites (Table 3).

351 The fractions of variation explained by pure environmental predictors [EP], pure spatial
352 predictors [SP] and by both environmental and spatial predictors [ES] changed with the spatial
353 scale (Tables 2 and 3). The results of permutation tests indicate the significance of [ES] at both
354 scales, but [ES] explained a larger fraction (68.2%) at the medium scale compared with the mean
355 value of the fine scale (4.2%). In each site examination at the fine scale, [ES] was significant at 10

356 of the 21 sites. [SP] explained the largest portion (31.5% of the mean) at the fine scale and the
357 second largest portion (12.6%) at the medium scale and was significant at both scales. At all
358 sampling sites, with the exception of site 14, [SP] significantly explained the variation in species
359 composition at the fine scale. [EP] explained a relatively small portion of the variation at both
360 scales (5.2% and 1.0% of the mean at the medium and at the fine scales, respectively) and was
361 significant only at the medium scale. [EP] was significant at 3 of 21 and 7 of 21 sites with and
362 without Bonferroni adjustment.

363 The results of partial RDA excluding the effect of spatial variables indicated a significant
364 effect of elevation and mean current velocity at the medium scale (Table 2). At the fine scale, the
365 significance of individual variables (water depth, current speed, several substrate characteristics or
366 presence/absence of cover) was indicated at 6 of 21 sites, but a consistent pattern among sites was
367 not detected (Table 3). The elevation and mean current velocity at the medium scale, water depth,
368 current speed, several substrate characteristics and the presence/absence of cover at the fine scale
369 were significantly correlated with the number of individuals of several fish species in sampling
370 sites or observation plots (general linear model, $P < 0.05$; see also Appendix 4).

371 The results of partial RDA excluding the effect of environmental variables indicated
372 significant effects of MEVs 1, 2 and 3 at the medium scale (Table 2). MEVs 1, 2 and 3 exhibited
373 fluctuating patterns, with wavelengths ranging from approximately 10 to 20 km (Fig. 4). Their

374 peak positions and fluctuating patterns corresponded well with the distribution of some fish
375 species (e.g. MEV 1 was significantly correlated with the distributions of *Zacco temminckii*,
376 *Pungtungia herzi* and *Squalidus gracilis*; $r^2 = 0.58, 0.55$ and 0.51 , respectively; all $P < 0.001$; Figs
377 2c and 4).

378 At the fine scale, the number of significant spatial variables ranged from 0 to 2 and 0 to 6
379 with and without Bonferroni correction, respectively, in the partial RDA (Table 3). Three spatial
380 variables commonly explained a large proportion of the variation in species composition across
381 several sites (MEV 2 at sites 6, 8, 10, 12 and 19; MEV 4 at sites 12 and 16–19 and MEV 45 at
382 sites 5–8, 10, 13, 17 and 18). These spatial variables exhibited characteristic spatial patterns, i.e.
383 horizontal patterns relative to a river channel for MEVs 2 and 4 or patch-like patterns for MEV 45
384 (Fig. 5).

385

386 Discussion

387 *Scale dependency of the contribution of environmental and spatial factors across medium to fine*
388 *scales*

389 Contrary to my original prediction, the results of VP analysis indicated the contribution of spatial
390 factors associated with the distance between sites or an arrangement of local habitats in the
391 determination of fish species composition at both the medium and fine spatial scales in the middle

392 to upper Yura River. Results at the medium spatial scale were consistent with those of previous
393 studies in which dispersal processes such as dispersal limitation, mass effects and patch dynamics
394 played key roles in determining the distribution of several species of stream organisms (Cottenie
395 2005) and fish communities in a river (Magalhães et al. 2002; Falke & Fausch 2010; Winemiller et
396 al. 2010). However, in the present study, the distance decay of the similarity of species
397 composition was steeper at the medium scale (especially ≥ 10 km) than that at the fine scale. These
398 results indicate that the dispersal of fish individuals was strongly determined by the distance
399 between local habitat patches at the medium scale. The differing patterns observed for the distance
400 decay of species composition and that of habitat characteristics at the medium scale also support
401 dispersal processes rather than habitat selection of fishes. The distance decay of species
402 composition at medium spatial scales (spatial extent about 4–50 km) has also been reported in
403 several stream fish assemblages (Magalhães et al. 2002; McGarvey & Ward 2008). In contrast, the
404 practically negligible distance decay at the fine scale indicates that distance between microhabitats
405 explained only a portion of the contribution of spatial predictors in structuring assemblages.
406 Several fine-scale spatial predictors showed 2-dimensional patterns (i.e. horizontal patterns
407 relative to a river channel and patch-like patterns) that were significantly associated with the
408 variation in species composition at several sampling sites. This result may be related to the home
409 ranges of fish as discussed in the next section.

410 The contributions of environmental predictors in explaining fish assemblages were
411 significant at medium spatial scales when the effect of correlations with spatial predictors was
412 removed. This finding supports classical niche theories, such as habitat template theory
413 (Southwood 1977; Townsend & Hildrew 1994) and species sorting theory (MacArthur 1958;
414 Pianka 1966), in which interspecific variation in habitat niches is considered a key factor in
415 structuring communities at medium scales. In contrast, the variation of assemblage structures
416 explained by environmental factors was small at the fine scale, and the largest part of that could
417 not be divided into environmental and spatial factors. Subsequently, in the forward selection of
418 environmental variables, only 1 variable was selected at most sampling sites. These patterns
419 indicate that environmental gradients of microhabitats in a reach were strongly spatially structured
420 and correlated with each other. Therefore, in contrast to the medium scale, pure environmental
421 processes may explain only a limited part of the assemblage structure of stream fishes at the fine
422 scale. The scale dependency of the contribution of environmental factors in the determination of
423 fish distribution has been reported for individual species across various spatial scales (Fausch et al.
424 1994; Inoue et al. 1997; Perkin & Gido 2011), but for fish assemblages, only large to medium
425 scales have been considered and not medium to fine scales (Wang et al. 2003; Durance et al.
426 2006).

427

428 *Processes determining species composition at each spatial scale*

429 1. *Medium scale*

430 At the medium scale, the spatial variation in species composition was largely explained by
431 distance, reflecting the distance decay of species composition and bell-curve-like distribution
432 along the river course for some fish species. These patterns are typically caused by dispersal
433 constraints of individuals by distance or an environmental factor that is strongly structured
434 spatially (Peres-Neto et al. 2006). Although the further concern about the effect of unmeasured and
435 spatially structured factors is needed, these results might support previous findings indicating the
436 importance of source–sink effects not only in the population dynamics of individual species but
437 also in the assemblage determination of stream fishes (Falke & Fausch 2010). Source–sink
438 dynamics are an aspect of metacommunity dynamics, in which dispersal from a large source
439 population of component species maintains small sink populations in neighbouring local
440 communities that cannot be maintained by self-reproduction and would become extinct without
441 immigration from other local communities (Amarasekare 2003). Dispersal of individuals from a
442 source population maintains a sink population of a species, which helps to increase the local
443 richness and diversity of species (Amarasekare 2003; Holyoak et al. 2005). In the present study
444 area, no artificial structures were present that strongly restricted fish dispersal. However, if any
445 artificial barriers, such as a sediment control dam without a fishway, are constructed and restrict

446 the free movement of fish, sink populations may become extinct (Jager et al. 2001), and the
447 richness and diversity of local fish assemblages may decrease (Stewart et al. 2001). My results
448 re-emphasize the importance of river connectivity in maintaining the species diversity of fishes,
449 which is a crucial issue for stream fish conservation (Nilsson et al. 2005).

450 Independently and along with the spatial predictors, the environmental predictors of
451 elevation and mean current velocity significantly explained the variation in species composition at
452 the medium scale. In addition, the local density of several fish species was significantly correlated
453 with mean current velocity within a reach. This variable changed within a spatial extent of <10 km.
454 Within this spatial range, the distance decay in species composition was not steep. Previous studies
455 on single fish species showed that fish select a reach with a favourite current velocity within a
456 scale for which the migration of individuals is not prevented (Table 1). The effect of habitat
457 selection along environmental gradients on assemblage structuring may be strong at the <10-km
458 scale; thus, a shifting point of the rank of the relative importance of environmental and spatial
459 factors may exist within the medium scale (400–40,000 m).

460

461 2. *Fine scale*

462 At the fine spatial scale, contrary to my prediction, the variation in species composition was
463 significantly associated with spatial predictors at all sampling sites, with the exception of site 14

464 but was not simply explained by the distance. In contrast, environmental predictors explained a
465 relatively small portion of the total variation in species composition, although the environmental
466 factors significantly affected species composition at several sites at the fine scale.

467 In the situation where an environmental factor at medium or large spatial scales strongly
468 constrains the ecological traits of stream fishes, the contribution of environmental factors may be
469 small because of decreased interspecific variation in habitat selectivity (Grossman et al. 2010). In
470 general, environmental harshness seems to be stronger in the upper reaches than in the lower
471 reaches (Grossman et al. 2010), so it is predictable that the contribution of environmental factors
472 will be small in the upper reaches and large in the lower reaches. However, the fraction explained
473 by environmental variables was not large in the lower reaches, but it was large at 2 sites in the
474 upper reaches (Table 3). In addition, a previous study reported the interspecific variation in habitat
475 use of the dominant fish species in the upper middle reaches of the research area (Nakagawa et al.
476 2012). Therefore, the effect of an environmental factor probably does not explain the small
477 contribution of environmental factors in the assemblage structuring of stream fishes at the fine
478 scale.

479 To simultaneously explain both the large contribution of spatial factors and weak habitat
480 selectivity, a dispersal process at the fine spatial scale may need to be considered. This process
481 may be associated with the home range of individuals. Several significant environmental features

482 (deep pool, cobbles, crevice of bedrock and cover) usually function as a refuge or rest site (Table
483 1) and may be used as a core site within the home range of individual fish (usually smaller than a
484 few hundred metres for fish of <50 cm standard length; Minns 1995), as shown in studies of
485 stream and marine fishes (Miller & Geibel 1973; Lowe et al. 2003; Jorgensen et al. 2006;
486 Watanabe 2008). When fish use a particular environmental patch as a core site within their home
487 range, some environmental factors will exhibit relationships with the distribution of that fish
488 species. On the other hand, in situations where fish limit their movement within a fixed area
489 independently of environmental gradients around a core site, some spatial factors would also
490 exhibit relationships with the distribution of that fish species. This situation would also affect
491 species composition because of spatial autocorrelation in individual species density that relates to
492 the core site distribution. Horizontal and patch-like patterns of spatial predictors that are
493 significantly related to fish distribution may corroborate the importance of the home range and
494 associated core sites in structuring fish assemblages.

495

496 *Concluding remarks*

497 The present study successfully demonstrated that the ordinal rank of the relative importance of
498 environmental and spatial factors changes between 2 spatial scales via alterations of multiple,
499 scale-dependent factors. However, large portions of the variation in species composition could not

500 be statistically attributed to either environmental or spatial factors. Furthermore, potentially
501 important environmental factors that were not included in the analysis may have resulted in
502 spurious correlations between species composition and spatial factors, such as primary production
503 (Vannote et al. 1980) or interspecific interactions (Hutchinson 1959; MacArthur & Levins 1967;
504 Amarasekare 2003). In future studies, I hope to strictly evaluate the effect of significant factors
505 using multi-site comparisons (Didham et al. 1998; Brown and Swan 2010) or environmental
506 control experiments (Eggleson and Lipcius 1992; Everett and Ruiz 1993). If the large
507 contributions of spatial factors and distance decay are caused by source–sink dynamics in a river
508 that is fragmented at a scale smaller than 10 km by natural or artificial structures, the contribution
509 of spatial factors will be smaller than that in a non-fragmented river, and the distance decay of
510 assemblage similarity will be steep at a smaller scale. Furthermore, if the home range of individual
511 fish affects assemblage structuring, the distribution of fishes will be explained by the distance
512 from the home-range core. This prediction may be testable with experiments using artificial
513 removal/placement of microhabitats functioning as home-range cores (e.g. cover or boulders).

514 The implication that fine-scale assemblage structure may be determined by factors that
515 change at a medium or larger spatial scale has an important meaning for the conservation of
516 species diversity in stream ecosystems. When conducting environmental assessments, if a
517 prediction concerning a certain effect is based on data that were only sampled within a planned

518 construction area (i.e. data that do not include factors changing at a larger spatial scale), the
519 assessment risks bias or misinterpretation (Roth et al. 1996). In the future, knowledge of current
520 community ecology that considers multiple-scale processes will be increasingly essential for
521 management decisions regarding modification or maintenance of stream environments.
522

523 **Acknowledgements**

524 I thank Katsutoshi Watanabe of Laboratory of Animal Ecology, Graduate School of Science,
525 Kyoto University, Takehiro Okuda of Fisheries Research Agency, National Research Institute of
526 Fisheries Science, Japan, and Mikio Inoue, Graduate School of Science and Engineering, Ehime
527 University, Takuya Sato, Field Science Education and Research Center, Kyoto University, for
528 numerous useful suggestions. I thank Koji Tominaga for helping field survey, and Michio Hori,
529 Teiji Sota and other members of Laboratory of Animal Ecology, Graduate School of Science,
530 Kyoto University for many helpful comments. I thank the staffs of Ashiu Forest Research Station,
531 Field Science Education and Research Center of Kyoto University, and the staff of Miyama
532 Gyokyo (Fisheries Cooperative of Miyama, Yura River), Kyoto, Japan. This study was supported
533 by Global COE Program A06 ‘Formation of a Strategic Base for Biodiversity and Evolutionary
534 Research: from Genome to Ecosystem’ from the Ministry of Education, Culture, Sports and
535 Technology, Japan.

536

537 **Literature cited**

538 Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis.
539 Ecology Letters 6: 1109–1122.

540 Beisner, B. E., Peres, P. R., Lindström, E. S., Barnett, A. & Longhi, M. L. 2006. The role of

- 541 environmental and spatial processes in structuring lake communities from bacteria to fish.
- 542 Ecology 87: 2985-2991.
- 543 Blanchet, F. G., Legendre, P. & Borcard, D. 2008. Forward selection of explanatory variables.
- 544 Ecology 89: 2623–2632.
- 545 Borcard, D., Legendre, P. & Drepeau, P. 1992. Partialling out the spatial component of ecological
- 546 variation. Ecology 73: 1045–1055.
- 547 Borcard, D. & Legendre, P. 2002. All-scale spatial analysis of ecological data by means of
- 548 principal coordinates of neighbor matrices. Ecological Modelling 153: 51–68.
- 549 Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. 2004. Dissecting the spatial structure
- 550 of ecological data at multiple scales. Ecology 85: 1826–1832.
- 551 Brown, B. L. & Swan, C. M. 2010. Dendritic network structure constrains metacommunity
- 552 properties in riverine ecosystems. Journal of Animal Ecology 79: 571–580.
- 553 Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community
- 554 dynamics. Ecology Letters 8: 1175–1182.
- 555 Didham, R. K., Hammond, P. M, Lawton, J. H., Eggleton, P. & Stork, N. E. 1998. Beetle species
- 556 responses to tropical forest fragmentation. Ecological Monograph 68: 295–323.
- 557 Dray, S., Legendre, P. & Peres-Neto P. R. 2006. Spatial modeling: a comprehensive framework for
- 558 principal coordinate analysis of neighbor matrices (PCNM). Ecological Modeling 196:

- 559 483–493.
- 560 Dray, S. 2010. Moran’s eigenvectors of spatial weighting matrices in R. In: S. Dray, Legendre, P.
- 561 & Peres-Neto, P. R. 2006. appendix of spatial modeling: a comprehensive framework for
- 562 principal coordinate analysis of neighbor matrices (PCNM). *Ecological Modeling* 196:
- 563 483–493.
- 564 Durance, I. Lepichon, C. & Ormerod, S. J. 2006. Recognizing the importance of scale in the
- 565 ecology and management of riverine fish. *River Research and Applications* 22: 1143–1152.
- 566 Eggleston, D. B. & Lipcius, R. N. 1992. Shelter selection by spiny lobster under variable predation
- 567 risk, social conditions, and shelter size. *Ecology* 73: 992–1011.
- 568 Elliott, J. M. 1981. Some aspects of thermal stress of freshwater teleosts. In: Pickering, A. D., ed.
- 569 *Stress and Fish*. London: Academic Press, pp. 209–245.
- 570 Erős, T., Heino, J., Schmera, D. & Rask, M. 2009. Characterising functional trait diversity and
- 571 trait–environment relationships in fish assemblages of boreal lakes. *Freshwater Biology*
- 572 54:1788–1803.
- 573 Erős, T., Sály, P., Takács, P., Specziar, A. & Bíró, P. 2012. Temporal variability in the spatial and
- 574 environmental determinants of functional metacommunity organization – stream fish in a
- 575 human modified landscape. *Freshwater Biology* 57:1914–1928.
- 576 Everett, R. A. & Ruiz, G. M. 1993. Coarse woody debris as a refuge from predation in aquatic

- 577 communities. *Oecologia* 93: 475–486.
- 578 Falke, J. A. & Fausch, K. D. 2010. From metapopulations to metacommunities: linking theory
579 with empirical observations of the spatial population dynamics of stream fishes. In: Gido, K.
580 B. & Jackson, D. A., eds. *Community ecology of stream fishes: concepts, approaches, and*
581 *techniques*. Bethesda: American Fisheries Society, pp. 207–235.
- 582 Fausch, K. D., Hawkes, C. L. & Persons, M. G. 1988. Models that predict standing crop of stream
583 fish from habitat variables: 1985–85. United States of Agriculture Forest Service Pacific
584 Northwest Research Station General Technical Report PNW-GTR-213.
- 585 Fausch, K. D., Nakano, S. & Ishigaki, K. 1994. Distribution of Two congeneric charrs in streams
586 of Hokkaido Island, Japan: considering multiple factors across scales. *Acta Oecologia* 100:
587 1–12.
- 588 Fausch, K. D., Nakano, S. & Kitano, S. 1997. Experimentally induced foraging mode shift by
589 sympatric charrs in a Japanese mountain stream. *Behavioral Ecology* 8: 414–420.
- 590 Frissell, C. A., Liss, W. L., Warren, C. E. & Hurley, M. D. 1986. A hierarchical framework for
591 stream habitat classification: viewing streams in a watershed context. *Environmental*
592 *Management* 10: 199–214.
- 593 Fuselier, L., & Edds, D. 1995. An artificial riffle as restored habitat for threatened Noesho madtom.
594 *North American Journal of Fish Management* 15: 499–503.

- 595 Gilbert, B. & Bennett, J. R. 2010. Partitioning variation in ecological communities: do the
596 numbers add up? *Journal of Applied Ecology* 47: 1071–1082.
- 597 Grossmann, G. D., Ratajczak Jr, R. E., Farr, M. D., Wagner, C. M. & Petty, J. T. 2010. Why there
598 are fewer fish upstream. In: Gido, K. B. & Jackson, D. A., eds. *Community ecology of*
599 *stream fishes: concepts, approaches, and techniques*. Bethesda: American Fisheries Society,
600 pp. 63–81.
- 601 Heino, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm.
602 *Freshwater Biology* 56: 1703–1722.
- 603 Hill, J. & Grossman, G. D. 1993. An energetic model of microhabitat use for rainbow trout and
604 brookside dace. *Ecology* 74: 685–698.
- 605 Hill, W. R., Mulholland, P. J. & Marzolf, E. R. 2001. Stream ecosystem responses to forest leaf
606 emergence in spring. *Ecology* 82: 2306–2319.
- 607 Hoeinghaus, D.J., Winemiller, K.O. & Birnbaum, J.S. 2007. Local and regional determinants of
608 stream fish assemblage structure: inferences based on taxonomic vs. functional groups.
609 *Journal of Biogeography* 34:324–338.
- 610 Holyoak, M., Leibold, M. A. Monquet, N. M., Holt, R. D. & Hoops, M. S. 2005.
611 *Metacommunities: a framework for medium scale community ecology*. In: Holyoak, M.,
612 Leibold, M. A. & Holt, R. D., eds. *Metacommunities: spatial dynamics and ecological*

- 613 communities. Chicago: The University of Chicago Press, pp. 1–31.
- 614 Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kind of animals.
- 615 American Naturalist 93: 145–159.
- 616 Inoue, M., Nakano, N. & Nakayama, F. 1997. Juvenile masu salmon (*Oncorhynchus masou*)
- 617 abundance and stream habitat relationships in northern Japan. Canadian Journal of Fisheries
- 618 and Aquatic Sciences 54: 1331–1341.
- 619 Jager, H. I., Chandler, J. A., Lepla, K. B. & Winkle W. V. 2001. A theoretical study of river
- 620 fragmentation by dams and its effects on white sturgeon populations. Environmental
- 621 Biology of Fishes 60: 347–361.
- 622 Jorgensen, S. J., Kaplan, D. M., Klimley, A. P., Morgan, S. G., O’Farrell, M. R. & Botsford, L. W.
- 623 2006. Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home
- 624 range. Marine Ecology Progress Series 327: 157–170.
- 625 Karst, J., Gilbert, B. & Lechowicz, M. J. 2005. Fern community assembly: the roles of chance and
- 626 the environment at local and intermediate scales. Ecology 86: 2473–2486.
- 627 Kautza, A. & Sullivan, M.P. 2012. Relative effects of local-and landscape-scale environmental
- 628 factors on stream fish assemblages: evidence from Idaho and Ohio, USA. Fundamental and
- 629 Applied Limnology 180: 259–270.
- 630 Lammens, E. H. R. R. & Hoogenboezem, W. 1991. Diet and feeding behavior. In: Winfield, I. J. &

- 631 Nelson, J. S., eds. Cyprinid fishes: systematics, biology and exploitation. London: Chapman
632 & Hall, pp. 353–377.
- 633 Legendre, P. & Legendre, L. F. J. 1998. Numerical ecology, second English edition. Elsevier,
634 Amsterdam, pp. 853.
- 635 Legendre, P. & Gallagher, E. D. 2001. Ecological meaningful transformation for ordination of
636 species data. *Acta Oecologia* 129: 271–280.
- 637 Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R.
638 D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. 2004. The
639 metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*
640 7: 601–613.
- 641 Leps, J., & Smilauer, P. 2003. Multivariate analysis of ecological data using CANOCO. New York:
642 Cambridge University Press, 267 pp.
- 643 Lowe, C. G., Topping, D. T., Cartamil, D. P., Papastamatiou, Y. P. 2003. Movement patterns, home
644 range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take
645 marine reserve. *Marine Ecology Progress Series* 256: 205–216.
- 646 MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests.
647 *Ecology* 39: 599–619.
- 648 MacArthur, R. H. & Levins, R. 1967. The limiting similarity, convergence, and divergence of

- 649 coexisting species. *American Naturalist* 101: 377–385.
- 650 Magalhães, M.F., Batalha, D.C., Collares-Pereira, M.J. 2002. Gradients in stream fish assemblages
651 across a Mediterranean landscape: contributions of environmental factors and spatial
652 structure. *Freshwater Biology* 47:1015–1031.
- 653 Matthews, W. J. 1998. Patterns in freshwater fish ecology. Norwell: Kluwer Academic Publishers,
654 756 pp.
- 655 McGarvey, D. J. & Ward, G. M. 2008. Scale dependence in the species-discharge relationship for
656 fishes of the southeastern U.S.A.. *Freshwater Biology* 53: 2206–2219.
- 657 Miller, D. J. & Geibel, J. J. 1973. Summary of blue rockfish and lingcod life histories, a reef
658 ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay,
659 California. California: State of California, Resources Agency, Department of Fish and Game,
660 137 pp.
- 661 Mills, C. A. 1991. Reproduction and life history. In: Winfield, I. J. & Nelson, J. S., eds. *Cyprinid*
662 *fishes: systematics, biology and exploitation*. London: Chapman & Hall, pp. 483–508.
- 663 Minns, C. K. 1995. Allometry of home range size in lake and river fishes. *Canadian Journal of*
664 *Fisheries and Aquatic Science* 52: 1499–1508.
- 665 Montgomery, D. R. & Buffington, J. M. 1997. Channel reach morphology in mountain drainage
666 basis. *Geological Society of America Bulletin* 109: 596–611.

- 667 Muneeppeerakul, R., Bertuzzo, E., Lynch, H. J., Fagan, W. F., Rinaldo, A. & Rodriguez-Iturbe, L.
668 2008. Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri
669 basin. *Nature* 453: 220–223.
- 670 Mykrä, H., Heino, J. & Muotka, T. 2007. Scale-related patterns in the spatial and environmental
671 components of stream macroinvertebrate assemblage variation. *Global Ecology and*
672 *Biogeography* 16: 149–159.
- 673 Nakagawa, H., Yamane, H., Yasugi, M., Fujita, T., Yokoi, K., Ashiwa, H., Kitada, N., Takano, H.,
674 Suzuki, N., Kishimoto, J., Maeda, H., Yamano, H., Ito, T., Maruyama, H., Tominaga, K.,
675 Hatakeyama, E., Goto, M. & Takahashi, D. 2012. Diel changes in resource use and diet
676 overlap in temperate stream fishes. *Ecological Research* 27: 417–426.
- 677 Nakamura, M. 1969. Cyprinidae in Japan (in Japanese). Tokyo: Research Institute for Natural
678 Resources, 455 pp.
- 679 Nakano, S. 1995. Individual differences in resource use, growth and emigration under the
680 influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat.
681 *Journal of Animal Ecology* 64: 75–84.
- 682 National Census on River Environments of Japan (in Japanese). 1993. Tokyo: Ministry of Land,
683 Infrastructure, Transport and Tourism.
- 684 Natsumeda, T. 2001. Space use by the Japanese fluvial sculpin, *Cottus pollux*, related to

- 685 spatio-temporal limitations in nest resources. *Environmental Biology of Fishes* 62: 393–400.
- 686 Nilsson, C., Reidy C. A., Dynesius, M. & Revenga, C. 2005. Fragmentation and flow regulation of
- 687 the world's large river systems. *Science* 308: 405–408.
- 688 Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L. & Stevens, M. H. H. 2008. vegan:
- 689 community ecology package, version 1.17-6. <http://cran.r-project.org/>.
- 690 Okuda, T., Noda, T, Yamamoto, T., Hori, M. & Nakaoka, M. Contribution of environmental and
- 691 spatial processes to rocky intertidal metacommunity structure. *Acta Oecologia* 36: 413–422.
- 692 Peres-Neto, P. R., Legendre, P., Dray, S. & Borcard, D. 2006. Variation partitioning of species data
- 693 matrices: estimation and comparison of fractions. *Ecology* 87: 2614–2625.
- 694 Perkin, J. S. & Gido, K. B. 2011. Stream fragmentation thresholds for a reproductive guild of great
- 695 plains fishes. *Fisheries* 36: 371–383.
- 696 Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American*
- 697 *Naturalist* 100: 33–46.
- 698 Power, M.E. 1984. Depth distributions of armored catfish: predator induced resource avoidance?
- 699 *Ecology* 65: 523–528.
- 700 Quist, M. C., Hubert, W. A. & Isaak, D. J. 2004. Fish assemblage structure and relations with
- 701 environmental conditions in a Rocky Mountain watershed. *Canadian Journal of Zoology* 82:
- 702 1554–1565.

- 703 R-Development-Core-Team. 2008. R: a language and environment for statistical computing, Ver.
- 704 2.11.1. R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/>.
- 705 Roth, N. E., Allan, J. D. & Erickson, D. L. 1996. Landscape influence on stream biotic integrity
- 706 assessed at multiple spatial scales. *Landscape Ecology* 11: 141–156.
- 707 Sály, P., Takács, P., Kiss, I., Bíró, P. & Erős, T. 2011. The relative influence of spatial context and
- 708 catchment- and site-scale environmental factors on stream fish assemblages in a human
- 709 modified landscape. *Ecology of Freshwater Fish* 20: 251–262.
- 710 Sechnick, C. W., Carline, R. F., Stein, R. A. & Rankin, E. T. 1986. Habitat selection by smallmouth
- 711 bass in response to physical characteristics of a simulated stream. *Transaction of American*
- 712 *Fisheries Society* 115: 314–321.
- 713 Shirvell, C. S. 1990. Role of instream rootwads as juvenile coho salmon (*Onchorhynchus Kisutch*)
- 714 and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. *Canadian Journal*
- 715 *of Fisheries and Aquatic Science* 47: 852–861.
- 716 Smith, T. W. & Lundholm, J. T. 2010. Variation partitioning as a tool to distinguish between niche
- 717 and neutral processes. *Ecography* 33: 648–655.
- 718 Southwood, T. R. E. 1977. Habitat templet for ecological strategies? *Journal of Animal Ecology*
- 719 46: 337–365.
- 720 Stewart, J. S., Wang, L. Lyons, J., Horwath, J. A. & Bannerman, R. 2001. Influences of

- 721 watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in agricultural
- 722 watersheds. *Journal of the American water resources association* 37: 1475–1487.
- 723 Stewart-Koster, B., Kennard, M.J., Harch, B.D., Sheldon, F., Arthington, A.H., Bradley J. Pusey,
- 724 B.J. 2007. Partitioning the variation in stream fish assemblages within a spatio-temporal
- 725 hierarchy. *Marine and Freshwater Research* 58: 675–686.
- 726 Tamada, K. 2010. River bed features affect the riverine distribution of two amphidromous
- 727 *Rhinogobius* species. *Ecology of Freshwater Fish* 20: 23–32.
- 728 Townsend, C. R. & Hildrew, A. G. 1994. Species traits in relation to a habitat templet for river
- 729 systems. *Freshwater Biology* 31: 265–275.
- 730 Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushing, C. E. 1980. The river
- 731 continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- 732 Wang, L., Lyons, J., Rasmussen, P., Seelbach, P., Simon, T., Wiley, M., Kanehl, P., Baker, E.,
- 733 Niemela, S., Stewart, P.M. 2003. Watershed, reach, and riparian influences on stream fish
- 734 assemblages in the Northern Lakes and Forest Ecoregion, U.S.A. *Canadian Journal of*
- 735 *Fisheries and Aquatic Sciences* 60:491–505.
- 736 Watanabe, K. 1994. A note on the reproductive ecology of the torrent catfish, *Liobagrus reini*
- 737 (Siluriformes: Amblycipitidae). *Japan. Journal of Ichthyology* 41:219–221.
- 738 Watanabe, K. 2008. Diel activity and reproductive territory of the Japanese bagrid catfish,

- 739 *Pseudobagrus ichikawai*. Environmental Biology of Fishes 81: 77–86.
- 740 Wentworth, C. K. 1922. A Scale of Grade & Class Terms for Clastic Sediments. The Journal of
- 741 Geology 30: 377–392.
- 742 Winemiller, K.O., Flecker, A. S. & Hoeinghaus, D. J. 2010. Patch dynamics and environmental
- 743 heterogeneity in lotic ecosystems. Journal of American Benthological Society 29: 84-99
- 744 Yamane, H., Yokoyama, T., Nagata, H. & Yamada, T. 2004. Reproductive ecology and life history
- 745 of the bagrid catfish, *Pseudobagrus nudiceps* (in Japanese). Japanese Journal of
- 746 Ichthyology 51: 135–147.
- 747

748 Table 1. Environmental factors measured along the Yura River study site and associated
749 mechanisms that determine community structure

750

Measured environmental factor	Ecological importance	Spatial scale
Water temperature	Thermal tolerance (e.g. Elliott 1981, Fausch et al. 1994)	Medium scale
Gradient of riverbed	A determinant factor of river morphology (e.g. Montgomery and Buffington 1997, Quist et al. 2004)	Medium scale
Flow rate	A determinant factor of river morphology (e.g. Buffington et al. 2003)	Medium scale
Mean width of river channel	An indicator of the canopy cover which affects primary production in a river (e.g. Hill et al. 2001)	Medium scale
Mean water depth of a research site	An indicator of the frequency of refuges for predators (e.g. Power 1984)	Medium scale
Mean current velocity of a research site	An indicator of the frequency of a lentic habitat (such as pools) which are used for foraging or resting (review in Fausch et al. 1988; e.g. Quist et al. 2004) A determinant factor of density of reproductive nests (e.g. Natsumeda 2001)	Medium scale
Mean frequency of each substrate type in a research site	An indicator of the frequency of habitat patches for feeding or spawning (review in Fausch et al. 1988, Mills 1991, Wootton 1998, e.g. Inoue et al. 1997, Quist et al. 2004) A determinant factor of the density of feeding site or reproductive substrate for some Japanese fishes [e.g. sand for <i>Zacco platypus</i> , <i>Pseudogobio esocinus</i> and <i>Hemibarbus labeo</i> (Nakamura 1969); gravel for <i>Tribolodon hakonensis</i> (Nakamura 1969); cobbles for <i>Rhinogobius</i> spp., <i>Tridentiger kuroiwae</i> and <i>Chaenogobius urotaenia</i> (Kawanabe and Mizuno 1989, Tamada 2010); boulders for <i>Pseudobagrus nudiceps</i> , <i>Liobagrus reinii</i> and <i>Cottus pollux</i> (Yamane 2004, Watanabe 1994, Natsumeda 2001, Nakagawa et al. 2012)]	Medium scale
Mean cover frequency of a research site	A determinant factor of the density of feeding sites, shelter and reproductive substrate (e.g. Shirvell 1990, Inoue et al. 1997) Reproductive substrate for some Japanese Cyprinids; <i>Squalidus gracilis</i> , <i>Carassius auratus</i> (Nakamura 1969)	Medium scale
Water depth at a plot	Refuge of predators (e.g. Power 1984)	Fine scale
Current velocity at a plot	A factor affecting foraging efficiency (e.g. Hill and Grossman 1993, Nakano 1995)	Fine scale
Frequency of each substrate type at a plot	Feeding site for some benthic feeders (review in Lamments and Hoogenboezem 1991) Shelter from predator or high current speed (e.g. Fuselier and Edds 1995; review in Matthews 1998) Feeding site or shelter for some Japanese fishes [e.g. sand for <i>Pseudogobio esocinus</i> , <i>Squalidus gracilis</i> and <i>Hemibarbus longirostris</i> (Nakamura 1969); Boulders for <i>Pangtungia herzi</i> , <i>Niwaella delicata</i> , <i>Pseudobagrus nudiceps</i> , <i>Liobagrus reinii</i> and <i>Cottus pollux</i> (Nakamura 1969, Kawanabe and Mizuno 1989, Nakagawa et al. 2012)]	Fine scale
Cover present/absent at a plot	Shelter from predator or high current speed (e.g. Sechnick et al. 1986, Shirvell 1990)	Fine scale

751 Table 2. Portion of variation ($R^2_{adj.}$) explained by pure environmental variables [EP], pure spatial
752 variables [SP], both environmental and spatial variables [ES], the total of environmental and
753 spatial variables [T] and the residual fraction of variation [R] estimated by variation partitioning
754 (VP), and that explained by each pure environmental variable and pure spatial variable (Moran's
755 eigenvector, MEV) obtained from partial redundancy analysis (partial RDA) at the medium scale.

	$R^2_{adj.}$	P-Value
EP	0.052	< 0.001
SP	0.126	< 0.001
ES	0.682	< 0.001
T	0.860	
R	0.140	
Environmental factors		
Elevation	0.025	0.009
Water temperature	0.011	0.208
Mean current velocity	0.020	0.024
Spatial factors		
MEV1	0.042	0.034
MEV2	0.056	0.004
MEV3	0.056	0.003
MEV4	0.015	0.517
MEV5	-0.007	1.000
MEV6	-0.002	0.565

757 Table 3. Portion of variation ($R^2_{\text{adj.}}$) explained by pure environmental variables [EP], pure spatial
758 variables [SP], both environmental and spatial variables [ES], the total of environmental and
759 spatial variables [T] and the residual fraction of variation [R] estimated by variation partitioning
760 (VP), and that explained by each pure environmental variable and pure spatial variable (Moran's
761 eigenvector, MEV) obtained from partial redundancy analysis (partial RDA) at the fine scale.
762 Mean $\pm$ SD in the left column shows the average and standard deviation of [EP], [SP], [ES], [T]
763 and [R] among all sampling sites. Dashes (–) represent unselected variables by forward selection.
764 MEVs that were not selected at any sampling sites were omitted. Bold values represent significant
765 effects ($P < 0.05$) with (**) and without (*) Bonferroni adjustment for species composition by a
766 permutation test.

768 **Figure legends**

769 Fig. 1. Locations of (a) the Yura River, (b) research area and (c) sampling sites. (d) Arrangement of
770 transects and plots.

771
772 Fig. 2. Longitudinal distribution pattern of fishes. (a) Fishes mainly distributed in the upper area.
773 (b) Fishes mainly distributed in the upper-middle area. (c) Fishes mainly distributed in the
774 lower-middle area. (d) Fishes mainly distributed in the lower area. Some rare species are omitted
775 for simplicity. The number of observed individuals was adjusted to a maximum of 1 by dividing
776 the maximum number of observed individuals among the sampling sites for each fish species.

777
778 Fig. 3. Distance–similarity relationships in species composition and habitat environment at the
779 medium and fine spatial scales. In each figure, values represent the similarity of a given pair of
780 sites (medium scale) or plots (fine scale). The displayed curve is a running median with a sampling
781 proportion of 0.5. At the fine scale, similarities between <5 m and >50 m distant plots were
782 eliminated from the analysis because they did not exist in common at all sampling sites.

783
784 Fig. 4. Ordinations of Moran’s eigenvectors (MEVs) 1, 2 and 3 along the river course that were
785 significantly correlated with the distribution pattern of fishes at the medium scale, obtained for a

786 spatial weighting matrix calculated using the approximate spatial structure of the arrangement of
787 sampling sites.

788

789 Fig. 5. Mappings of Moran's eigenvectors (MEVs) 2, 4 and 45 along the river course that were
790 significantly correlated with the distribution pattern of fishes at the fine scale, obtained for a
791 spatial weighting matrix calculated using the approximate spatial structure of the arrangement of
792 sampling plots at sites 5–13 and 15–19.

793

Figure 1 (Nakagawa, H)

Figure 2 (Nakagawa, H)

795

Figure 3 (Nakagawa, H)

Figure 4 (Nakagawa, H)

797

Figure 5 (Nakagawa, H)

798

799

800 **Appendix 1**

801

802 Appendix 1. Approximated spatial structure of the community and arrangement of sampling sites

803 and plots. (a) The spatial structure at the medium scale that approximated a 1-dimensional

804 structure. (b) The spatial structure at the fine scale that approximated a grid structure (see

805 Materials and methods for details).

806 Appendix 2

807 Appendix 2. Observed number of individuals of each fish species at each sampling site.

Species \ Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	day	night	Total
<i>Oncorhynchus masou</i> ^{*1}	2	2	4	1	3	0	0	1	9	0	2	0	0	0	0	0	0	0	0	0	0	12	12	24
<i>Cottus pollux</i>	8	3	5	7	0	9	5	2	4	0	0	0	3	0	4	0	3	0	0	0	0	1	52	53
<i>Phoxinus oxycephalus</i>	157	36	177	106	13	34	12	13	41	1	0	0	1	4	0	0	0	1	0	0	0	336	260	596
<i>Liobagrus reinii</i>	0	0	0	0	32	16	9	9	29	22	17	8	31	0	1	13	22	0	0	0	0	5	204	209
<i>Niwaella delicata</i>	0	0	0	0	25	72	37	67	31	124	51	1	12	0	2	0	19	9	0	0	0	359	91	450
<i>Tribolodon hakonensis</i>	0	0	0	0	39	40	118	41	82	36	48	12	51	36	18	47	54	60	4	10	17	592	121	713
<i>Zacco temminckii</i>	0	0	0	0	11	10	62	20	5	56	33	128	154	78	172	122	135	94	63	61	34	564	674	1238
<i>Rhinogobius flumineus</i>	0	0	0	0	40	178	189	193	161	147	161	405	297	183	170	263	118	285	263	100	40	3017	176	3193
<i>Odontobutis obscura</i>	0	0	0	0	0	1	1	0	0	0	0	4	0	3	2	0	0	0	0	0	0	3	8	11
<i>Plecoglossus altivelis</i> ^{*1}	0	0	0	0	1	0	1	0	4	9	16	3	3	8	5	23	10	7	0	1	1	77	15	92
<i>Pangtungia herzi</i>	0	0	0	0	1	1	2	0	0	7	8	14	21	29	33	68	14	61	24	3	5	151	140	291
<i>Hemibarbus longirostris</i>	0	0	0	0	0	0	0	0	0	1	0	0	4	7	4	17	4	24	2	0	0	13	50	63
<i>Squalidus gracilis</i>	0	0	0	0	0	0	0	0	0	1	1	5	4	25	30	36	29	13	0	3	0	86	61	147
<i>Pseudogobio esocinus</i>	0	0	0	0	0	0	1	0	0	12	7	29	26	80	20	50	23	30	22	24	29	48	305	353
<i>Zacco platypus</i>	0	0	0	0	0	0	2	3	0	2	5	11	119	56	48	179	85	392	177	347	355	1207	574	1781
<i>Coreoperca kawamebai</i>	0	0	0	0	0	0	0	0	0	0	0	8	10	25	10	8	8	0	7	0	2	53	25	78
<i>Cobitis bilwae</i>	0	0	0	0	0	0	0	0	0	1	0	4	5	38	15	3	8	1	0	0	13	43	45	88
<i>Pseudobagrus nudiceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	4	3	2	4	9	13	4	43	47
<i>Hemibarbus labeo</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	27	14	37	5	42
<i>Lepomis macrochirus</i> ^{*2}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2
<i>Squalidus chankaensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	18	6	13	19
<i>Tridentiger kuroiwae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	10	11	2	13
<i>Chaenogobius urotaeni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	6	6
<i>Rhinogobius</i> sp. OR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	1	6	1	7
<i>Anguilla japonica</i> ^{*1}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	2
<i>Cyprinus carpio</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1
<i>Carassius carassius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
Total	167	41	186	114	165	361	439	349	366	419	349	632	741	575	545	833	535	985	568	593	557	6635	2885	9520

808

809 *1 Artificially introduced by local fisheries.

810 *2 Invasive species from North America.

811

812 Appendix 3

813 Appendix 3. Mean $\pm$ SD of environmental factors at each sampling site.

Sampling site	Elevation (m)	Water temperature (°C)	Gradient of riverbed (%)	Flow rate (m³/s)	River width (m)	Water depth (cm)	Current velocity (cm/s)	Frequency of each substrate type (%)					Presence/absence of covers (0 or 1)
								Sand	Gravel	Cobble	Boulder	Bed rock	
1	650	14.8	0.03	0.05	3.0 $\pm$ 1.4	17.4 $\pm$ 16.4	10.5 $\pm$ 12.2	0.06 $\pm$ 0.21	0.61 $\pm$ 0.31	0.20 $\pm$ 0.18	0.01 $\pm$ 0.03	0.13 $\pm$ 0.32	0.03 $\pm$ 0.16
2	640	15.0	0.02	0.12	4.0 $\pm$ 1.5	11.5 $\pm$ 6.9	25.2 $\pm$ 23.2	0.04 $\pm$ 0.08	0.58 $\pm$ 0.24	0.22 $\pm$ 0.16	0.13 $\pm$ 0.15	0.03 $\pm$ 0.13	0.03 $\pm$ 0.16
3	630	15.0	0.02	0.19	4.8 $\pm$ 1.7	19.3 $\pm$ 17.4	25.4 $\pm$ 56.9	0.23 $\pm$ 0.38	0.41 $\pm$ 0.34	0.15 $\pm$ 0.20	0.01 $\pm$ 0.03	0.20 $\pm$ 0.29	0.00 $\pm$ 0.00
4	620	15.0	0.02	0.15	5.4 $\pm$ 1.0	27.5 $\pm$ 19.0	10.5 $\pm$ 15.8	0.04 $\pm$ 0.08	0.52 $\pm$ 0.31	0.19 $\pm$ 0.17	0.03 $\pm$ 0.08	0.23 $\pm$ 0.35	0.03 $\pm$ 0.16
5	400	19.2	0.02	1.14	5.8 $\pm$ 1.1	57.4 $\pm$ 32.5	38.8 $\pm$ 32.3	0.01 $\pm$ 0.04	0.37 $\pm$ 0.34	0.15 $\pm$ 0.18	0.17 $\pm$ 0.20	0.30 $\pm$ 0.37	0.00 $\pm$ 0.00
6	370	19.8	0.01	0.88	11.6 $\pm$ 3.7	32.3 $\pm$ 31.8	25.3 $\pm$ 26.7	0.06 $\pm$ 0.18	0.51 $\pm$ 0.35	0.24 $\pm$ 0.23	0.04 $\pm$ 0.09	0.16 $\pm$ 0.35	0.03 $\pm$ 0.18
7	370	19.9	0.01	1.09	11.0 $\pm$ 3.3	32.6 $\pm$ 24.6	35.1 $\pm$ 42.9	0.04 $\pm$ 0.12	0.50 $\pm$ 0.33	0.26 $\pm$ 0.24	0.14 $\pm$ 0.22	0.06 $\pm$ 0.19	0.03 $\pm$ 0.17
8	350	20.4	0.01	0.91	9.6 $\pm$ 2.9	49.9 $\pm$ 42.5	20.5 $\pm$ 27.1	0.06 $\pm$ 0.15	0.63 $\pm$ 0.33	0.18 $\pm$ 0.19	0.00 $\pm$ 0.02	0.13 $\pm$ 0.31	0.00 $\pm$ 0.00
9	320	20.6	0.02	0.83	9.4 $\pm$ 2.1	27.6 $\pm$ 17.0	34.8 $\pm$ 31.9	0.02 $\pm$ 0.08	0.44 $\pm$ 0.24	0.41 $\pm$ 0.20	0.12 $\pm$ 0.15	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
10	300	19.4	0.01	1.83	12.6 $\pm$ 4.6	53.3 $\pm$ 44.4	29.7 $\pm$ 32.1	0.03 $\pm$ 0.13	0.71 $\pm$ 0.30	0.17 $\pm$ 0.18	0.01 $\pm$ 0.03	0.08 $\pm$ 0.26	0.00 $\pm$ 0.00
11	290	19.2	0.01	1.84	11.6 $\pm$ 3.4	33.3 $\pm$ 29.6	50.6 $\pm$ 40.8	0.03 $\pm$ 0.12	0.64 $\pm$ 0.31	0.23 $\pm$ 0.22	0.02 $\pm$ 0.09	0.08 $\pm$ 0.25	0.00 $\pm$ 0.00
12	280	19.0	0.00	0.87	15.5 $\pm$ 2.0	25.1 $\pm$ 16.2	24.8 $\pm$ 22.4	0.08 $\pm$ 0.17	0.66 $\pm$ 0.27	0.20 $\pm$ 0.20	0.02 $\pm$ 0.07	0.03 $\pm$ 0.15	0.00 $\pm$ 0.00
13	280	18.3	0.01	1.19	13.1 $\pm$ 3.0	28.5 $\pm$ 18.4	33.6 $\pm$ 22.8	0.08 $\pm$ 0.16	0.49 $\pm$ 0.25	0.31 $\pm$ 0.21	0.06 $\pm$ 0.11	0.06 $\pm$ 0.21	0.00 $\pm$ 0.00
14	260	20.5	0.01	2.27	35.8 $\pm$ 12.6	62.8 $\pm$ 39.4	11.9 $\pm$ 7.3	0.18 $\pm$ 0.34	0.69 $\pm$ 0.39	0.05 $\pm$ 0.09	0.00 $\pm$ 0.02	0.08 $\pm$ 0.26	0.08 $\pm$ 0.27
15	250	19.2	0.01	2.02	12.3 $\pm$ 3.8	71.0 $\pm$ 36.4	27.8 $\pm$ 18.2	0.18 $\pm$ 0.29	0.53 $\pm$ 0.36	0.11 $\pm$ 0.14	0.03 $\pm$ 0.12	0.16 $\pm$ 0.31	0.27 $\pm$ 0.45
16	220	19.9	0.01	1.68	19.8 $\pm$ 2.5	42.9 $\pm$ 31.7	21.5 $\pm$ 22.2	0.16 $\pm$ 0.26	0.34 $\pm$ 0.26	0.31 $\pm$ 0.22	0.10 $\pm$ 0.14	0.08 $\pm$ 0.20	0.03 $\pm$ 0.18
17	200	20.0	0.01	3.62	13.9 $\pm$ 3.0	67.4 $\pm$ 42.4	44.0 $\pm$ 37.1	0.06 $\pm$ 0.19	0.34 $\pm$ 0.31	0.26 $\pm$ 0.26	0.06 $\pm$ 0.14	0.27 $\pm$ 0.35	0.05 $\pm$ 0.22
18	190	20.7	0.01	1.91	17.4 $\pm$ 3.2	35.7 $\pm$ 16.6	34.1 $\pm$ 27.6	0.02 $\pm$ 0.08	0.26 $\pm$ 0.27	0.34 $\pm$ 0.27	0.11 $\pm$ 0.19	0.27 $\pm$ 0.38	0.00 $\pm$ 0.00
19	170	20.8	0.01	2.22	19.2 $\pm$ 2.3	38.6 $\pm$ 33.2	31.8 $\pm$ 28.1	0.04 $\pm$ 0.17	0.71 $\pm$ 0.34	0.12 $\pm$ 0.15	0.02 $\pm$ 0.06	0.12 $\pm$ 0.29	0.00 $\pm$ 0.00
20	160	20.7	0.00	3.50	25.9 $\pm$ 3.8	44.9 $\pm$ 27.8	33.2 $\pm$ 31.2	0.07 $\pm$ 0.19	0.43 $\pm$ 0.29	0.35 $\pm$ 0.25	0.06 $\pm$ 0.11	0.09 $\pm$ 0.23	0.00 $\pm$ 0.00
21	160	19.5	0.01	3.53	24.1 $\pm$ 3.5	90.9 $\pm$ 60.3	18.3 $\pm$ 20.0	0.11 $\pm$ 0.26	0.46 $\pm$ 0.39	0.21 $\pm$ 0.28	0.07 $\pm$ 0.16	0.15 $\pm$ 0.32	0.00 $\pm$ 0.00

814

815

816 Appendix 4

818 Appendix 4. Relationships between environmental factors and the number of observed individuals
819 at medium (a), (b) and fine (c)–(i) scales. Fish species for which the total number of observed
820 individuals was <20 are omitted. In (a)–(h), lines show significant regression lines with and without
821 Bonferroni adjustment between environmental factors and the observed number of individuals of
822 each species. Line types show the significance of correlation by linear regression: thin lines indicate
823 $P < 0.05$ and bold lines indicate $P < 0.05$ with Bonferroni adjustment. In (i), circles show means and
824 bars denote the SDs for each species. Black and grey circles indicate the existence of a significant
825 difference with $P < 0.05$ with and without Bonferroni adjustment, respectively, by ANOVA testing.
826