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9   **Within-lake distribution patterns of fish assemblages: the relative role of spatial,**

10   **temporal and random environmental factors in assessing fish assemblages with**

11   **gillnetting in a large and shallow temperate lake**

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25   Running headline: WITHIN-LAKE DISTRIBUTION PATTERNS OF FISH

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26   **Abstract**

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28   Identifying components of variability in fish assemblage samples is important for

29   understanding the organization of assemblages, perform ecosystem health assessment and

30   design sampling strategy for monitoring programs. In this study, the relative role of spatio-

31   temporal factors and associated environmental variables (water transparency and temperature)

32   was quantified in gillnet samples in a large and shallow lake (Lake Balaton, Hungary). The

33   majority of the variance (56.1%) in the relative abundance data (%) was related to the vertical

34   segregation of fish. This gradient substantially affected the number-per-unit-effort (NPUE) of

35   the dominant species, the surface-oriented bleak *Alburnus alburnus* and the benthic common

36   bream *Abramis brama*, total NPUE, mean fish mass and species richness and diversity as

37   well. At the lake level, horizontal habitat heterogeneity (i.e. littoral vs. offshore) accounted for

38   only 8.3% of the total variance in relative abundance data, but was important in structuring

39   the NPUE of the ruffe *Gymnocephalus cernua* and the pikeperch *Sander lucioperca*. The

40   longitudinal environmental gradient (i.e. lake basin), year and season of the sampling, water

41   transparency and temperature proved to have significant effect on relative abundance only at

42   the habitat level, but were important component of variability of the NPUE in some species at

43   lake level too. Since sampling schemes should consider the main gradients in fish assemblage

44   distributions the use of surface and pelagic gillnets should be more intensively incorporated in

45   the study and monitoring of fish assemblages in shallow lakes and lake habitats.

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47   Key words: catch-per-unit-effort; gillnet sampling; relative abundance; spatio-temporal

48   heterogeneity; variance partitioning; vertical habitat gradient.

INTRODUCTION

Knowledge of spatial and temporal patterns of fish assemblage structure and their associated environmental factors is a fundamental requirement for understanding aquatic ecosystem functioning and evaluating ecosystem health for environmental management. Over large geographical and habitat scales, environmental filtering (the survival or elimination of species in the community in response to environmental constraints), connectivity/isolation and human impacts are generally the most important determinants of assemblage variability (Holmgren & Appelberg, 2000; Jackson *et al.*, 2001; Blanck *et al.*, 2007; Prchalová *et al.*, 2008; Erős *et al.*, 2009; Sharma *et al.*, 2011). However, at smaller scales (e.g. within a particular stream or lake), time of the sampling, microhabitat use of fish, biotic interactions and sampling gear related bias may also strongly affect sample composition and variability (Hansson & Rudstam, 1995; Jackson *et al.*, 2001; Winfield, 2004; Lund *et al.*, 2010; Specziár *et al.*, 2012).

In general, within lake factors can be classified into space- and time related gradients/cycles and random processes. Space related gradients are comprised of horizontally (i.e. littoral vs. offshore) and vertically (i.e. benthic vs. pelagic) structured habitat heterogeneity, and other environmental gradients involving variances of concentrations of nutrients and contaminants, as well as human activities. Time related gradients can be decomposed to diel and seasonal cycles and to between year components. Random components include a series of uncontrollable phenomenon, such for example small-scale patchiness of fish distribution and changes of weather, some of which may also affect sampling efficiency (Hansson & Rudstam, 1995; Linløkken & Haugen, 2006; György *et al.*, 2012). Therefore, within lake organization of fish assemblages is a consequence of complicated processes driven by the environmental heterogeneity (both in time and space)

76 and the differences in ecological features of fish species and their size groups (Jackson *et al.*,

77 2001; Winfield, 2004; Lund *et al.*, 2010). Each fish species has specific habitat and food

78 preference, environmental and competitive tolerance, behaviour, and their preferences and

79 activity may vary by size and in time (Holmgren & Appelberg, 2000; Jackson *et al.*, 2001;

80 Blanck *et al.*, 2007). These factors, together with the intra- and inter-specific interactions

81 (Fisher, 2000; Jackson *et al.*, 2001; Hölker *et al.*, 2002) result non-random, within lake

82 patterns of fish assemblages. However, fish distribution generally is also affected by at least

83 one random component arising from the formation of fish shoals and their movements within

84 and among resource patches (Hensor *et al.*, 2005). Further, since most fishing gears are

85 selective, estimation of fish assemblage structure and its response to environmental changes

86 generally is effected by limitations of the sampling method applied.

87

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89   One of the most popular sampling methods in still waters is the gillnetting. Gillnetting is a

90 passive fishing method, which catching efficiency varies among fish species and size groups,

91 depends on stock density, the environmental circumstances (e.g. weather, water temperature

92 and transparency, habitat structure, feeding conditions) and the sampling conditions (e.g. net

93 construction, time of the day, soak time) (review: Hamley, 1975; and more recently:

94 Linløkken & Haugen, 2006; Olin *et al.*, 2004; Pierce *et al.*, 2010; Prchalová *et al.*, 2011;

95 György *et al.*, 2012). Standardized sampling protocols control large part of the gear related

96 variance in the samples, but generally not those being linked to random variations in sampling

97 conditions. For example, water transparency and temperature are factors that can significantly

98 influence gillnet catches, and may vary across sampling sites and days, especially in shallow,

99 wind exposed waters (Hansson & Rudstam, 1995; Linløkken & Haugen, 2006; György *et al.*,

100 2012). Although it is widely investigated how these factors affect fish assemblage or fish

101 assemblage sample variability, it is still largely unknown what are their relative importance in

102 structuring gillnet samples at the lake level.

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105   Goal of this study was to partition the variance characterizing gillnet samples along the

106   main dimensions of regulatory factors under a standardized sampling protocol in a large and

107   shallow lake (Lake Balaton, Hungary). Specifically, it was examined to what extent

108   variability of sample composition, species richness and diversity, mean fish body mass and

109   fish abundance (measured as catch-per-unit-effort; CPUE) can be related to spatial, temporal

110   and random environmental factors at the lake level. It was hypothesized that segregation of

111   fish assemblages among the main habitat types (i.e. littoral vs. offshore) and water layers (i.e.

112   benthic vs. non-benthic) will be the basic force of gillnet sample variability at the whole lake

113   level. Although Lake Balaton is a very shallow lake with a mean depth of 3.2 m, previous

114   studies indicated rather strong vertical patterns in the distribution of fish assemblages

115   (Specziár *et al.*, 2009; Specziár, 2010). It was also examined to what extent variability of

116   different assemblage attributes could be related to spatial, temporal and random

117   environmental factors in the benthic and surface water layers in the offshore area of Lake

118   Balaton. Since variations of the water temperature and the water transparency are hardly

119   controllable in large lake monitoring requiring multiple sampling days for a complete survey,

120   it is particularly important to assess the rate of the bias they may cause in fish assemblage

121   assessments.

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124   **MATERIALS AND METHODS**

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127   STUDY AREA

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130   Lake Balaton is the largest shallow lake (surface area: 593 km^2; mean depth: 3.2 m) in

131   Central Europe, situated at 46° 42' - 47° 04' N, 17° 15' - 18° 10' E and 104.8 m above sea

132   level. The lake is meso-eutrophic with mean annual chlorophyll-a concentrations of 3.6-18.7

133   mg m^{-3} (Istvánovics *et al.*, 2007). Forty-seven percent of the lakeshore is covered by reed

134   grass, but submerged macrophytes occur sparsely in the littoral zone. The lake is slightly

135   alkaline, it contains about 400 mg l^{-1} of Ca^{2+} and Mg^{2+}(HCO$_3^-$)$_2$, its pH varies between 8.2

136   and 9.1, and has a conductivity of 550-671 µs cm^{-1}. In general the lake is turbid with a Secchi

137   depth varying between 0.2 m and 0.8 m, although in exceptional cases (e.g. under ice cover)

138   water transparency may reach 1.5-1.8 m. Oxygen deficiency has never been registered in the

139   lake, and concentrations of pollutants are low or insignificant. Detailed information on the

140   limnology and fish fauna of the lake can be found in reviews by Herodek *et al.* (1988), Bíró

141   (1997) and Istvánovics *et al.* (2007).

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143

144   SAMPLING

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147   This study is based on methodically fully compatible gillnet surveys conducted between

148   July 2005 and October 2010. For samplings, multi-mesh gillnets compatible with the

149   European standard EN 14 757 (CEN, 2005) and made by Nippon Verkko oy (Finland) were

150   used. In order to assess characteristic depth strata of the lake, the following gear set up was

151   used. The standard benthic gillnet (BG) composed of 12 conventional mesh-sizes between 5

152   and 55 mm (43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35 and 29 mm; knot to knot)

153   supplemented with 65 and 80 mm mesh-sizes, being 1.5 m high and in total 35 m long (length

154   of each mesh panel is 2.5 m) was the basic gear of sampling and was used at each sampling

155   occasion (i.e. site × date) in triplicate. Weighting of the BG (linear density of the buoyancy

156   line in water: 7 g m^{-1}; linear density of the lead line in air: 22 g m^{-1}) was set to ensure dipping

157   of the lead line to the bottom. At sites with ≥2 m water depth, the surface-set version of the

158   standard gillnet (SG) was also used in triplicate. Weighting of the SG (linear density of the

159   buoyancy line in water: 31 g m^{-1}; linear density of the lead line in air: 22 g m^{-1}) was set to

160   ensure floating of the buoyancy line on the water surface.

161

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163   Fish assemblages were sampled at 16 sites distributed across the four basins of the lake

164   (Fig. 1). Gillnets were set in the morning (after sunrise). Nets were positioned linearly with

165   one net length gap between them adjusted with a rope to ensure that the nets do not influence

166   each other's performance. In order to avoid the saturation of nets by fish and the related biases

167   (Olin *et al.*, 2004; Prchalová *et al.*, 2011), soak time must be kept short in Lake Balaton

168   (Specziár *et al.*, 2009). Therefore, sampling intervals of 1 to 4 hours were applied based on

169   our experience on expected CPUE values by sampling sites and seasons. Altogether, 96

170   sampling occasions yielded catch data from 468 net sets.

171

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173   Catch of each net was processed separately. Captured fish were identified, counted by

174   species, measured to the nearest millimetre standard lengths and gram wet mass. Gillnet

175   catches were expressed in both NPUE (number of fish captured per one hour per net) and

176   BPUE (mass of fish captured per one hour per net). Note, that for brevity only the results

177   based on NPUE are presented here. Altogether, 35,606 specimens of 18 fish species and three

178   hybrids [roach *Rutilus rutilus* (L. 1758) × common bream *Abramis brama* (L. 1758), bleak

179   *Alburnus alburnus* (L. 1758) × *A. brama* and silver carp *Hypophthalmichthys molitrix*

180   (Valenciennes 1844) × bighead carp *H. nobilis* (Richardson 1845)] comprised the samples

181   (Table I).

182

183

184   Water depth and Secchi depth to the nearest 1 cm and water temperature to the nearest 0.1

185   ^{o}C were also measured at each sampling. Water depth, Secchi depth and temperature ranges

186   covered by this study were 1.30-4.80 m, 0.19-1.12 m and 12.4-26.2 ^{o}C, respectively.

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189   STATISTICAL ANALYSIS

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192   Data evaluation was performed at both the assemblage (i.e. relative abundance, species

193   richness and diversity data) and the species levels (i.e. NPUE by species), and for all samples

194   and the offshore BG and SG samples only.

195

196

197   For statistical analyses, the three parallel samples by gillnet types (i.e. for BG and SG)

198   were merged (averaged for density related indices and pooled for species richness data) for

199   each sampling occasion (i.e. site × date). The main reason of merging these parallel samples

200   by sampling occasions was to eliminate the high within sample variability in catch

201   composition that would substantially increase the error term in analyses, and to enable a

202   robust multivariate analysis (see also Lek *et al.*, 2011). High within sample variability could

203   be a joint effect of small-scale patchiness of fish distribution (i.e. fish form shoals by species

204   and size class) and the relatively short soak time.

205

206

207   Rare species (i.e. <0.1% representation in the whole data set) were excluded from relative

208   abundance analyses, but were considered in analyses exploring patterns of the total NPUE,

209   mean fish mass, and species richness and diversity. Hybrids were excluded from species

210   richness and diversity estimates, but included to calculations of the total NPUE and mean fish

211   mass. Species diversity was expressed by the Shannon-Wiener index.

212

213

214   Explanatory variables considered in the analyses were: 1) lake basin (four lake basins

215   representing a trophic gradient; Istvánovics *et al.,* 2007), 2) horizontally structured habitat

216   type (offshore, littoral north and littoral south), 3) sampled water layer (BG, SG), 4) year of

217   the sampling (2005-2010), 5) season of the sampling (spring, summer and autumn), 6) water

218   depth, 7) Secchi depth and 8) water temperature. Explanatory variables were classified to

219   three main variable groups as follows: 1) space (lake basin, habitat and water layer), 2) time

220   (year and season), and 3) environment (water depth, Secchi depth and water temperature).

221

222

223   At the lake level, variations of relative abundance data and their relationships with the

224   spatial, temporal and environmental factors were investigated with redundancy analysis

225   (RDA) using CANOCO version 4.5 (ter Braak & Šmilauer, 2002). The method of RDA was

226   chosen, because a preliminary detrended correspondence analysis (DCA) indicated a

227   relatively short gradient length ($\leq$2.10 in standard deviation units, see Lepš & Šmilauer 2003).

228   Response variables (i.e. relative abundance data) were $\arcsin(x^{0.5})$ transformed prior to

229   analyses. Of explanatory variables, lake basin, habitat, water layer, sampling year and season

230   were treated as categorical factors and re-coded into binary dummy variables (Lepš &

231   Šmilauer, 2003); whereas water depth, Secchi depth and water temperature were treated as

232   quantitative variables and were $\log_{10}(x+1)$ transformed. Since water depth strongly correlated

233   with lake basin and habitat, it was excluded from the model building.

234

235

236   Firstly, a preliminary overall RDA model was built, which included all potential

237   explanatory variables (Lepš & Šmilauer, 2003). The relative contribution of each variable to

238   the model was assessed by using the forward stepwise selection procedure, and their

239   significance was tested with Monte-Carlo permutation test with 9,999 permutations under the

240   full model. Based on this selection procedure, only significant explanatory variables ($P <$

241   0.05) were retained in the final RDA model. Similarly, statistical significance of ordination

242   axes and the whole model (i.e. including all axes) were tested using the Monte Carlo

243   permutation test with 9,999 permutations. Next, a series of RDA and partial RDAs were

244   conducted to partition the effects of spatial, temporal and random environmental factors on

245   gillnet sample composition (Cushman & McGarigal, 2002).

246

247

248   To assess how much of the variances of NPUE data of the dominant fish species and of

249   total NPUE, as well as of species richness, Shannon-Wiener diversity and mean fish body

250   mass was explained by the investigated spatial, temporal and environmental variables,

251   variance component analysis (VCA) was performed using Statistica 8.0 software (StatSoft,

252   Inc.). For the analyses, the restricted maximum likelihood method (all factors are random-

253   effects factors) was chosen because of the unbalanced distribution of data (Robindson, 1987).

254   This method iteratively optimizes parameter estimates for the effects in the model (Searle *et*

255   *al.*, 1992). Since the VCA requires categorical explanatory variables, values of the Secchi

256   depth and the water temperature were categorized into four evenly distributed ranges of ≤40

257   cm, 41-60 cm, 61-80 cm and >80 cm, and ≤15.0 $^{\circ}$C, 15.1-20.0 $^{\circ}$C, 20.1-25.0 $^{\circ}$C and >25.0 $^{\circ}$C,

258   respectively. Due to its close relatedness to lake basin and habitat type, water depth was

259   excluded from VCA analyses.

260

261

262 All analyses (i.e. RDA and VCA) were conducted also for offshore samples only, and

263 separately for BG and SG samples.

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265

266   **RESULTS**

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269 ASSEMBLAGE COMPOSITION

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272 At the lake level, the vertical segregation of fish assemblages in the water column was the

273 most important factor structuring the gillnet catches (Fig. 2). This gradient associated with the

274 first RDA axis that explained 62.6% of the total variance in the relative abundance data. The

275 benthic layer of the water column was dominated by the *A. brama*, and the upper layer by the

276 *A. alburnus*. All other fish species positioned left from the origin of the plot suggesting their

277 closer link to the benthic layer than the surface layer. The second RDA axis (4.7% of the total

278 variance) represented the littoral-offshore habitat gradient. Specifically, the ordination showed

279 the predominance of razor fish *Pelecus cultratus* (L. 1758) and *A. brama* in the offshore

280 catches, and the higher share of the *R. rutilus* and the white bream *Blicca bjoerkna* (L. 1758)

281 in the littoral samples. Overall, 69.3% of the total variance of relative abundance data was

282 described by the RDA model (Table II). Variation partitioning procedure showed that time

283 (i.e. year and season) and environmental factors (i.e. temperature and water transparency) had

284 little influence on relative abundance data. Most of the variance was associated with spatial

285 factors, where the water layer sampled was the most important variable. Pure water layer

286 effect accounted for 81.0% of the total explained variance (Fig. 3).

287

288

289   Significant RDA models were obtained for both the offshore BG (total explained

290   variance: 33.1%) and the offshore SG samples (total explained variance: 36.6%). Redundancy

291   analysis identified both seasonal and space related gradients in the percentage composition of

292   the BG catches [Fig. (4a)]. Autumn samples were characterized by a higher proportion of the

293   *A. brama*, while the opposite end of the gradient (i.e. spring) was associated with the *A.*

294   *alburnus*. The second RDA axis characterized changes along the longitudinal gradient of the

295   lake, with higher abundance of the *B. bjoerkna* in the shallowest and most productive Basin I.

296   However, a substantial part of the variance remained unexplained (66.9%) [Fig. (5a); Table

297   II]. Composition of SG samples varied mainly among lake basins and sampling years (RDA

298   axis 1). This variability was associated with the relative importance of *A. alburnus*, *P.*

299   *cultratus* and *A. brama* [Fig. (4b)]. The second RDA axis explained only 3.8% of the total

300   variance and reflected a weak association of higher shares of the *P. cultratus* with lower

301   temperatures and higher shares of the *A. brama* with higher temperatures in the samples,

302   respectively. However, a substantial part of the variance remained unexplained (63.4%) [Fig.

303   (5b); Table II].

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306   SPECIES RICHNESS, DIVERSITY, AND MEAN FISH MASS

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309   At the lake level, most of the variance in the species richness and the diversity, as well as

310   in the mean fish mass was associated with the water layer (Fig. 6). For offshore assemblages,

311   the contribution of the explanatory variables to the variability of these fish metrics varied by

312   water layers. In SG samples, most of the variance in the species richness occurred among lake

313   basins, and most of the variance in the species diversity occurred among sampling years.

314   Whereas, mean fish mass varied among basins and with water transparency [Fig. (7a)]. In BG

315   samples, most of the explained variance in these assemblage metrics was related to among

316   basin differences, but the majority of the variance remained unexplained [Fig. (7b)].

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319   CATCH-PER-UNIT-EFFORT

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322   Variance component analysis showed that lake level total NPUE, NPUE values of the

323   dominant *A. brama* and *A. alburnus* most importantly depended upon the water layer

324   sampled. However, other species responded differently; littoral versus offshore habitat

325   gradient was important component of variability in the NPUE of the ruffe *Gymnocephalus*

326   *cernua* (L. 1758) and the pikeperch *Sander lucioperca* (L. 1758), NPUE values of the asp

327   *Aspius aspius* (L. 1758) and the common carp *Cyprinus carpio* L. 1758 varied chiefly among

328   lake basins, among year variance was high in the *R. rutilus* and the monkey goby *Neogobius*

329   *fluviatilis* (Pallas 1814), NPUE values of the *R. rutilus* and the gibel *Carassius gibelio* (Bloch

330   1782) varied substantially among seasons, Secchi depth proved to be important in the *B.*

331   *bjoerkna* and the *C. gibelio*, and temperature affected NPUE values of the Volga pikeperch *S.*

332   *volgensis* (Gmelin 1789) and the *N. fluviatilis*. Explained proportion of variance of the NPUE

333   was high and varied by fish species between 47.3-97.6% (mean ± S.D., 86.2 ± 15.4) (Fig. 6).

334

335

336   Although some among basin, season and temperature related variations could be identified

337   in the benthic layer samples of the offshore area, most of the variance of the NPUE data, with

338   the exception of the *B. bjoerkna* and the *A. brama*, remained unexplained [Fig. (7a)]. In the

339   surface water layer of the offshore habitat, the water transparency had a predominant

340   influence on the NPUE both at the species level and for all fish [Fig. (7b)].

341

342

DISCUSSION

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345

346   In this study, the relative contribution of spatio-temporal heterogeneity and environmental

347   factors to the variability of gillnet samples was investigated in the large and shallow Lake

348   Balaton. As hypothesized, the majority of the variance was associated with habitat gradients.

349   However, contrary to the generally accepted dominance of the littoral versus offshore gradient

350   in shallow habitats (Romare *et al.*, 2003; Winfield, 2004), it was found that the vertical

351   segregation of fish was the most important factor shaping fish assemblage attributes. Lake

352   basin, temporal and random environmental factors were important factors only at the habitat

353   level, but not at the lake level.

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355

356   Vertical segregation of fish species within the water column and its effect on gillnet

357   sample composition is well known in deep lakes and reservoirs (Hansson, 1988; CEN, 2005;

358   Prchalová *et al.*, 2008; Vašek *et al.*, 2009), but it is much less investigated in shallow waters

359   (but see Deceliere-Vergés & Guillard, 2008; Lauridsen *et al.*, 2008; Lund *et al.*, 2010).

360   Moreover, in shallow lakes (i.e. <10 m water depth; CEN, 2005), fish monitoring programs

361   generally focus on benthic fish assemblages, and largely neglect the sampling of the upper

362   water layers. However, majority of the variance observed in gillnet samples was associated

363   with the vertical heterogeneity of fish distribution in Lake Balaton. Characteristic vertical

364   trends were found in the NPUE of the two dominant species, total NPUE, mean fish mass,

365   species richness and diversity and percent composition of samples. The benthic water layer of

366   Lake Balaton could be characterized with an *A. brama* predominated species rich fish

367   assemblage, while the surface water layer with an *A. alburnus* dominated species poor

368   assemblage (see also Specziár *et al.*, 2009; György *et al.*, 2012).

369

370

371   It is a common phenomenon in most lakes with well-oxygenated bottom region, that fish

372   diversity is higher in the benthic than in the upper water layers (Deceliere-Vergés & Guillard,

373   2008; Deceliere-Vergés *et al.*, 2009). However, total fish abundance and biomass not

374   necessarily follows the same trend. For example, in Lake Balaton, the total density of fish in

375   the surface water layer is as high as in the benthic water layer (Specziár *et al.*, 2009; Specziár,

376   2010). Similarly, Prchalová *et al.* (2008) and Vašek *et al.* (2009) found that most fishes

377   occurred in the upper water layers in the Želivka and Římov Reservoirs, respectively. The few

378   other studies which dealt with vertical patterns of fish assemblages in shallow lakes or

379   shallow lake habitats also pointed out that surface-oriented species may reach high densities,

380   which are comparable to that of benthic fish (Mous *et al.*, 2004; Olin & Malinen, 2003; Olin

381   *et al.*, 2009). Therefore, surface-oriented fish assemblages can be important components of

382   lake food webs and ecosystem productivity, and thus should be more intensively included in

383   shallow lake monitoring.

384

385

386   At the lake level, horizontal habitat heterogeneity played a secondary role explaining only

387   8.3% of the total variability in the percentage composition of catches. This factor explained

388   however most of the variance in the NPUE of the *S. lucioperca*, which species is more

389   abundant in the offshore area. Further variables, like lake basin, temporal and random

390   environmental factors proved to be important components of sample variability mainly at

391   species level. However, the total share of these factors in the observed variance was well

392   below 10% for most assemblage attributes. Therefore, one of the lessons of this study is that

393   the evaluation of long-term changes of the fish fauna should be primarily done at the habitat

394   level (i.e. littoral/offshore × water layer). Lake level conclusions may be then refined based

395   on the knowledge of habitat level processes.

396

397

398   When samples were controlled for the habitat effect and offshore samples were analysed

399   separately by water layers, relative roles of lake basin, time of sampling and random

400   environmental factors increased. However, their importance depended on assemblage

401   attribute, fish species, and water layer examined. The low consistency in the observed patterns

402   indicates the variable sensitivity of particular fish species and assemblage attribute estimates

403   to different environmental factors and seasonality. In addition, the share of the explained

404   variance generally was much lower than at the lake level.

405

406

407   In Lake Balaton, there are characteristic gradients of trophic state (Istvánovits *et al.*,

408   2007), food resource density and composition (Specziár & Vörös, 2001; Istvánovits *et al.*,

409   2007), and water depth (Herodek *et al.*, 1988) from basin I towards basin IV, which were

410   found significantly affect fish assemblage composition and stock density in most of previous

411   studies (Bíró, 1997; Tátrai *et al.*, 2008; Specziár, 2010) as well as in this one. However,

412   present results show that this component on average explains less than 20% of the total

413   variance in gillnet samples, except the lake level variability in the NPUE of the *A. aspius* and

414   the *C. carpio*. In contrast, such factors may be more important in waters exhibiting more

415   marked gradients. For example, in long canyon-shaped reservoirs significant trophic, depth,

416   temperature and oxygen concentration gradients may exist from the tributary towards the

417   dam, which basically influence fish assemblage composition and density as well as the

418   vertical distribution pattern of fish within the water column (Prchalová *et al.*, 2008; Vašek *et*

419   *al.*, 2009). Further, the role of temporal (both seasonal and among years) components of

420   sample variability proved to be moderate or low, which was in agreement with other studies

421   (Holmgren, 1999; Prchalová *et al.*, 2008). This indicates the stability of fish assemblages and

422   the sampling efficiency over these time scales both at the lake level and in the offshore area.

423   In contrast, in the littoral zone, a significant seasonal trend was documented in the CPUE,

424   characterized by a higher fish density during the spring and early summer (Specziár, 2001),

425   which corresponds well with the small-scale reproductive migration of fish in this season

426   (Winfield, 2004).

427

428

429   An increasing number of examples shows that gillnet CPUE is a poor indicator of fish

430   abundance, and that several environmental factors can basically affect the efficiency of

431   gillnetting (Hansson & Rudstam, 1995; Peltonen *et al.*, 1999; Mehner & Schulz, 2002;

432   Linløkken & Haugen, 2006; Dennerline *et al.*, 2012). Water temperature is undoubtedly one

433   of the most important factors, which influences the activity and behaviour of fish, and thereby

434   the performance of passive fishing gears. Fish activity and swimming speed supposedly

435   increase with water temperature, and accordingly the efficiency of gillnetting is expected to

436   increase as well (Linløkken & Haugen, 2006). In contrary to the above hypothesis, but in

437   accordance with the observations of Hansson & Rudstam (1995), here no significant

438   temperature effect was identified in gillnet catches neither in assemblage level indexes nor in

439   the NPUE of most fish species. Linløkken & Haugen (2006) showed that the effect of

440   temperature is most decisive at extreme ranges (e.g. below 5 $^{\circ}$C or above 20 $^{\circ}$C in perch and

441   roach). However, extreme temperature ranges were not investigated here.

442

443

444   Similarly, transparency of the water can affect gillnetting efficiency at least via two ways.

445   Firstly, in turbid water the probability that a fish observes the net before being entangled is

446   lower than in transparent water. Secondly, activity of most fishes is influenced by light

447   intensity, being highest at low light but not in complete darkness (Gjelland *et al.*, 2004 and

448   references therein). Since a wind over 1 to 4 m s^{-1} can disturb the sediment of the shallow

449   Lake Balaton, even day-to-day or site-to-site variations in the water transparency can be

450   considerable in this lake (Herodek *et al.*, 1988). However, a significant effect of water

451   transparency existed only in SG samples of the offshore area, where it influenced the NPUE

452   of the dominant species (*A. alburnus* and *P. cultratus*) and all fish, as well as the mean fish

453   size (see also György *et al.*, 2012), and at lake level in the NPUEs of the *B. bjoerkna* and the

454   *C. gibelio*. Hansson & Rudstam (1995) also found correlation between the water transparency

455   and gillnet CPUE in the Baltic Sea herring *Clupea harengus* L. 1758 and the sprat *Sprattus*

456   *sprattus* (L. 1758). In addition, Mous *et al.* (2004) showed that the water transparency affects

457   the vertical distribution pattern of the light-sensitive European smelt *Osmerus eperlanus* (L.

458   1758) in the shallow Lake IJssel. Considering the high light attenuation within the water

459   column of Lake Balaton, where more than 90% of the light attenuates within the upper 1 to 3

460   m water layer (Herodek *et al.*, 1988; V.-Balogh *et al.*, 2009), it is not surprising that water

461   transparency proved to be important in the uppermost water layer, but not in the deeper

462   layers. Recently, Prchalová *et al.* (2010) established some justifications and standards for

463   comparable gillnet sampling among different lowland European fish species and waterbodies

464   under variable turbidity.

465

466

467   The high proportion of the unexplained variance, especially in the habitat level analyses,

468   cautions that the monitoring of the effects of specific environmental gradients on the fish

469   fauna might require multiple sampling surveys to equalize (control) the effect of

470   uncontrollable (random) factors influencing sampling efficiency. However, when discussing

471   gillnet sample variability, the effect of two other factors, the time of the day when the

472   sampling is done and the saturation of the nets with fish should not be surpassed. Due to

473   cycles of fish activity and light condition, gillnet samples generally show marked diurnal

474   variability regarding both their composition and CPUE (Olin & Malinen, 2003; Vašek *et al.*,

475   2009). This effect was controlled in the present study by choosing a short and standard

476   sampling interval. However, controlling or adjusting the effect of the gillnet saturation is

477   much more problematic (Prchalová *et al.*, 2011), and generally, this issue is still largely

478   neglected by monitoring protocols. Although relatively short sampling intervals were applied

479   in this study, and, in addition, they were adjusted to habitat specific capture rates (see also

480   Olin *et al.*, 2004, 2009), this factor likely to contribute to the unexplained variance in samples.

481

482

483   To conclude, our study proves that the vertical habitat gradient may have significance

484   over both the horizontal habitat gradient and temporal variations in structuring gillnet samples

485   in shallow lakes. However, the high proportion of unexplained variance reflects the

486   importance of random and generally uncontrollable factors in gillnet monitoring. These

487   results demonstrate that sampling schemes should be planed carefully when considering the

488   main factors organizing the distribution of fish in the particular system. Since sampling

489   protocols should consider the main gradients in fish assemblage distributions the use of

490   surface and pelagic gillnets should be more intensively incorporated in the study and

491   monitoring of fish assemblages in shallow lakes and lake habitats.

492

493

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503   **References**

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663 TABLE I. List of species and hybrids, their abbreviations used in figures and number of

664 individuals captured (*N*).

665

Species and hybrid names	Abbreviation	*N*
Abramis brama (L. 1758)	Abr-bra	3075
Alburnus alburnus (L. 1758)	Alb-alb	28377
Aspius aspius (L. 1758)	Asp-asp	50
Blicca bjoerkna (L. 1758)	Bli-bjo	1309
Carassius gibelio (Bloch 1782)	Car-gib	31
Cyprinus carpio L. 1758	Cyp-carp	23
Gymnocephalus cernua (L. 1758)	Gym-cer	471
Neogobius fluviatilis (Pallas 1814)	Neo-flu	77
Pelecus cultratus (L. 1758)	Pel-cul	776
Perca fluviatilis L. 1758	Per-flu	3
Pseudorasbora parva (Temminck & Schlegel 1846)	Pse-par	5
Rhodeus sericeus (Pallas 1776)	Rho-ser	21
Romanogobio albipinnatus (Lukasch 1933)	Rom-alb	75
Rutilus rutilus (L. 1758)	Rut-rut	659
Sander lucioperca (L. 1758)	San-luc	375
Sander volgensis (Gmelin 1789)	San-vol	260
Scardinius erythrophthalmus (L. 1758)	Sca-ery	4
Silurus glanis L. 1758	Sil-gla	1
A. alburnus × *A. brama*	-	3
Hypophthalmichthys molitrix (Valenciennes 1844) × *H. nobilis* (Richardson 1845)	-	1
R. rutilus × *A. brama*	-	10
All fish		35606
Number of species (hybrids)		18 (3)

666

667   TABLE II. Results of the redundancy analyses describing the relationship between relative

668   abundance data (%) and forward selected, significant (at $P < 0.05$) explanatory variables in

669   Lake Balaton, for all sites included (all sample), and for specific water layers of the offshore

670   habitat only.

671

	Significant explanatory variables	First axis			All axes		
		Eigen value	F (d.f.$_{num.}$, d.f.$_{den.}$)	P	Eigen value	F (d.f.$_{num.}$, d.f.$_{den.}$)	P
All sample	BG, Offsh, Lit-N, Bas-I, 2008, Autumn, Temp	0.626	247.54 (7,148)	<0.001	0.693	47.69 (91,1924)	<0.001
Offshore, benthic layer	Bas-I, Bas-IV, 2008, 2009, Autumn, Temp	0.140	8.46 (6,52)	<0.01	0.331	4.28 (78,676)	<0.001
Offshore, surface layer	Bas-I, 2008, 2009, Summer, Temp	0.325	18.78 (5,39)	<0.001	0.366	4.50 (35,273)	<0.001

672   d.f.$_{num.}$ = degrees of freedom of the numerator, d.f.$_{den}$ = degrees of freedom of the

673   denominator, BG = benthic gillnet, Offsh = offshore habitat, Lit-N = littoral habitat along the

674   northern shoreline of the lake, Bas-I = lake basin I, Bas-IV = lake basin IV and Temp = water

675   temperature.

676

677 **Figure captions**

678

679

680 FɪG. 1. Distribution of the sampling sites (○, littoral sites; ◉, offshore sites) in Lake Balaton.

681

682

683 FɪG. 2. Redundancy analysis plot describing the relationship between the relative abundance

684   data (%) of fish species (⟶) and forward selected, significant (at $P < 0.05$)

685   explanatory variables (⇢, continuous variables; ○, binary dummy variables) in Lake

686   Balaton. Percentage variances represented by axes are indicated in brackets (of species

687   data; of species-explanatory variables relation) after the axis name. Scale factor for

688   biplotting and characteristic environmental gradients represented by the axes are also

689   indicated (for a more detailed statistics see Table II). Species and explanatory variables

690   with scores close to the centre of the graph are clarified on the small graph in the upper

691   right corner. Species name abbreviations are given in Table I, while abbreviations of

692   explanatory variables are as follows: BG = benthic gillnet, Offsh = offshore habitat, Lit-

693   N = littoral habitat along the northern shoreline of the lake, Bas-I = lake basin I, Temp =

694   water temperature.

695

696

697 FɪG. 3. Results of the variation partitioning among the main groups of explanatory variables

698   (a), and among space related variables only (b) influencing relative abundance (%) data.

699   The area of each rectangular cell is proportional to the variance accounted for by that

700   component.

701

702

703   Fɪɢ. 4. Redundancy analysis plots describing the relationship between the relative abundance

704   data (%) of fish species (⟶) and forward selected, significant (at $P < 0.05$)

705   explanatory variables (- -►, continuous variables; ○, binary dummy variables) for the

706   benthic (a) and the surface (b) water layers of the offshore habitat in Lake Balaton.

707   Percentage variances represented by axes are indicated in brackets (of species data; of

708   species-explanatory variables relation) after the axis name (for a more detailed statistics

709   see Table II). Scale factor for biplotting and characteristic environmental gradients

710   represented by the axes are also indicated. Species scores close to the centre of the graph

711   (a) are clarified on the small graph in the upper right corner. Species name abbreviations

712   are given in Table I, while abbreviations of explanatory variables are: Bas-I = lake basin

713   I, Bas-IV = lake basin IV, Temp = water temperature.

714

715

716   Fɪɢ. 5. Results of the variation partitioning among the main groups of explanatory variables

717   influencing relative abundance data (%) in the benthic (a) and the surface (b) water

718   layers of the offshore habitat in Lake Balaton. The area of each rectangular cell is

719   proportional to the variance accounted for by that component.
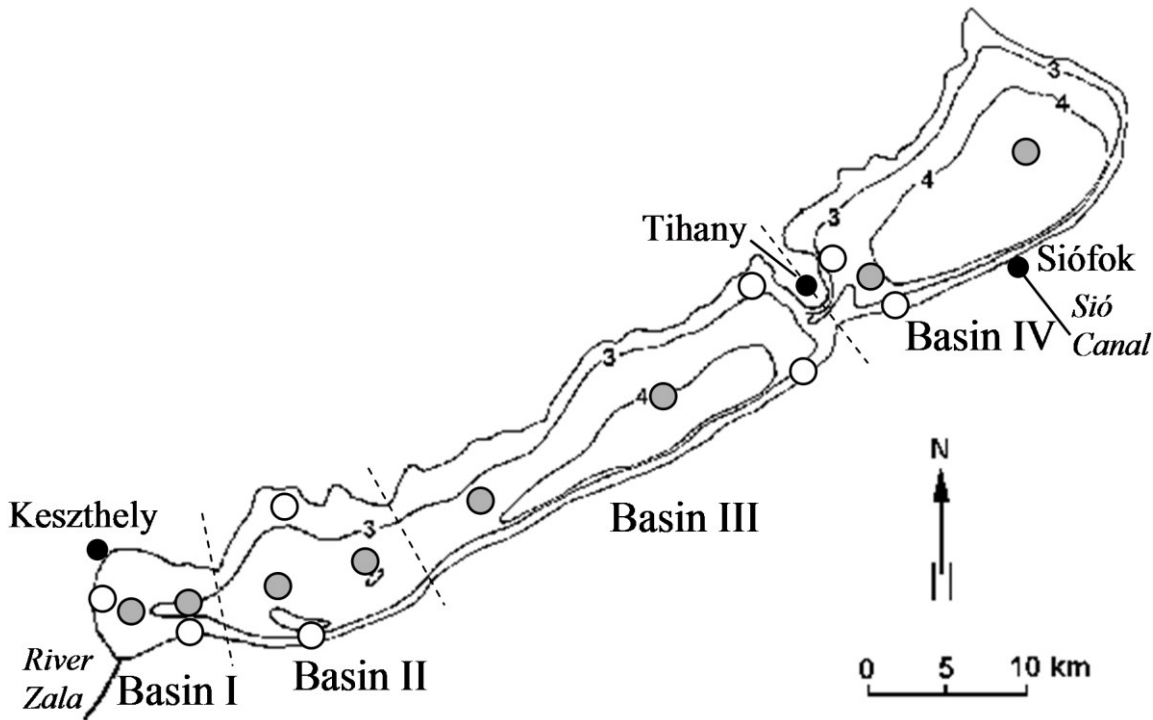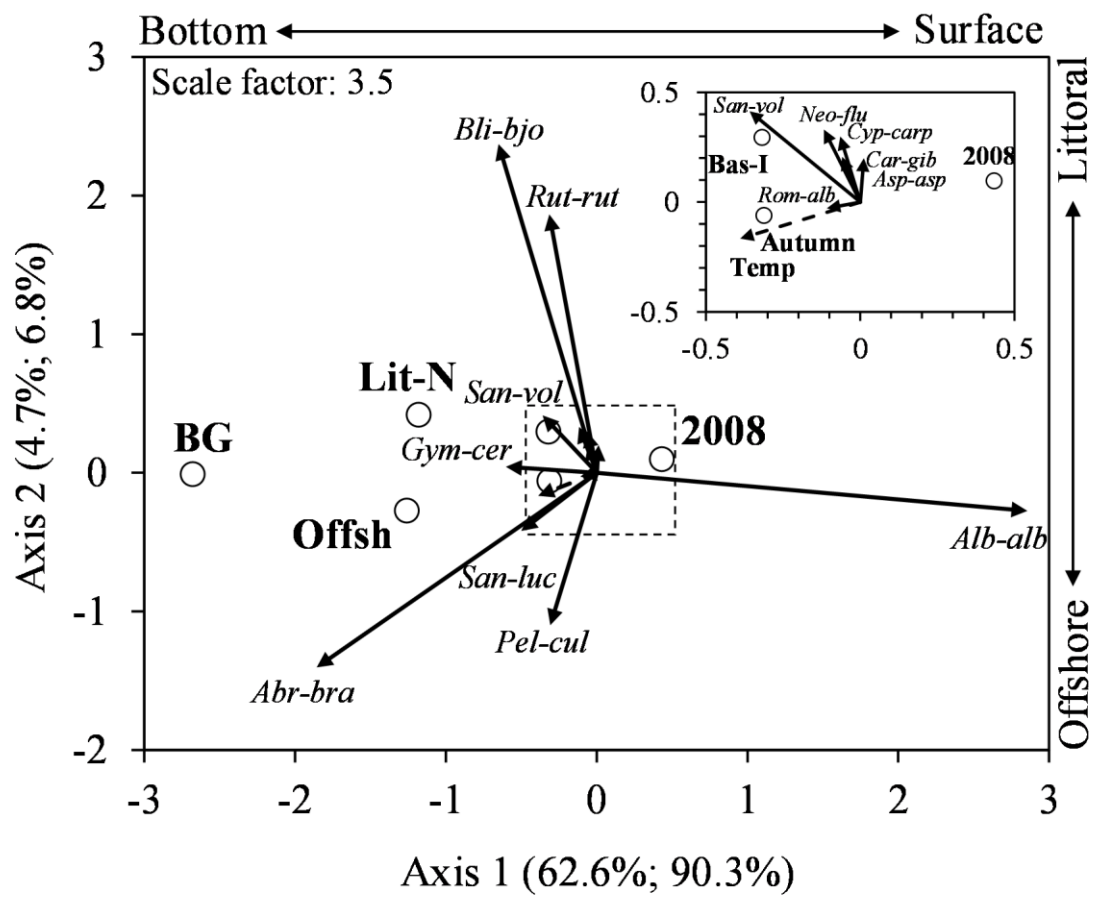
720

721

722   Fɪɢ. 6. Results of the variance component analysis describing the percentage of the variation

723   of the number-per-unit-effort (NPUE) of the abundant species, total NPUE, mean fish

724   mass (M), species richness (S) and Shannon-Wiener diversity (H) accounted for by

725   explanatory variables (⬚, water layer; ⊠, habitat; ■, lake basin; ▨, year; ◪, season; ▦,

726   Secchi depth; ▥, water temperature), along with the unexplained variance proportion (□

727   ) in Lake Balaton, for all sites investigated. Species name abbreviations are given in

728   Table I.

729

730

731   FIG. 7. Results of the variance component analysis describing the percentage of the variation

732   of the number-per-unit-effort (NPUE) of the abundant species, total NPUE, mean fish

733   mass (*M*), species richness (*S*) and Shannon-Wiener diversity (*H*) accounted for by

734   explanatory variables (■, lake basin; ◪, year; ◩, season; ▨, Secchi depth; ◫, water

735   temperature) along with the unexplained variance proportion (□) in the benthic (a) and

736   the surface (b) water layers of the offshore habitat in Lake Balaton. Species name
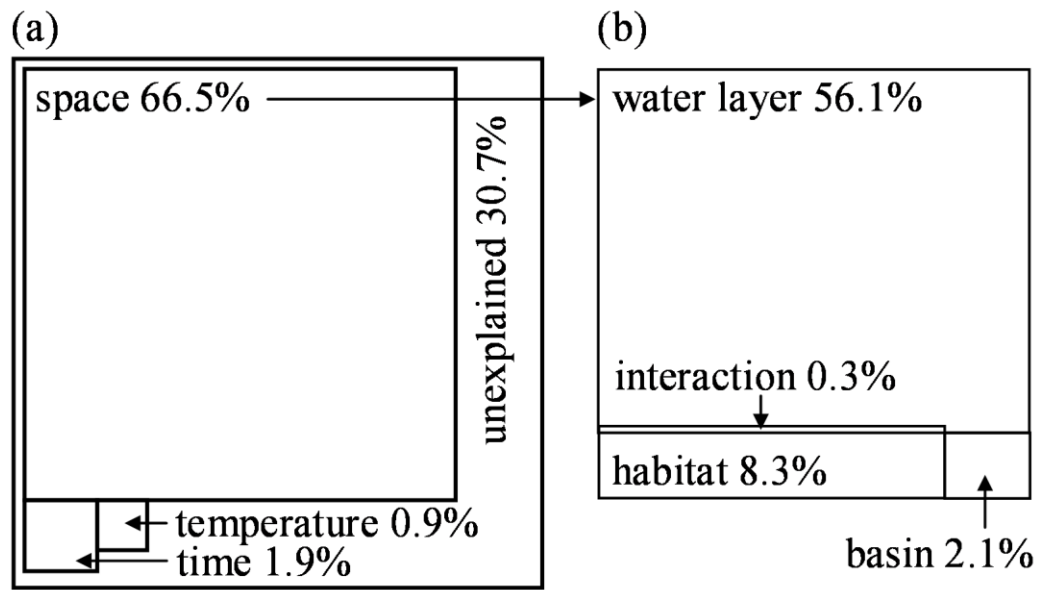
737   abbreviations are given in Table I.

738

739

740

741

(a)

space 66.5%

unexplained 30.7%

temperature 0.9%
time 1.9%

(b)

water layer 56.1%

interaction 0.3%

habitat 8.3%

basin 2.1%

746

747

748

749

750
751