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Within-lake distribution patterns of fish assemblages: the relative role of spatial, temporal and random environmental factors in assessing fish assemblages with gillnetting in a large and shallow temperate lake

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Abstract

Identifying components of variability in fish assemblage samples is important for understanding the organization of assemblages, perform ecosystem health assessment and design sampling strategy for monitoring programs. In this study, the relative role of spatio-temporal factors and associated environmental variables (water transparency and temperature) was quantified in gillnet samples in a large and shallow lake (Lake Balaton, Hungary). The majority of the variance (56.1%) in the relative abundance data (%) was related to the vertical segregation of fish. This gradient substantially affected the number-per-unit-effort (NPUE) of the dominant species, the surface-oriented bleak *Alburnus alburnus* and the benthic common bream *Abramis brama*, total NPUE, mean fish mass and species richness and diversity as well. At the lake level, horizontal habitat heterogeneity (i.e. littoral vs. offshore) accounted for only 8.3% of the total variance in relative abundance data, but was important in structuring the NPUE of the ruffe *Gymnocephalus cernua* and the pikeperch *Sander lucioperca*. The longitudinal environmental gradient (i.e. lake basin), year and season of the sampling, water transparency and temperature proved to have significant effect on relative abundance only at the habitat level, but were important component of variability of the NPUE in some species at lake level too. Since sampling schemes should consider the main gradients in fish assemblage distributions the use of surface and pelagic gillnets should be more intensively incorporated in the study and monitoring of fish assemblages in shallow lakes and lake habitats.

Key words: catch-per-unit-effort; gillnet sampling; relative abundance; spatio-temporal 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).
and the differences in ecological features of fish species and their size groups (Jackson et al., 2001; Winfield, 2004; Lund et al., 2010). Each fish species has specific habitat and food preference, environmental and competitive tolerance, behaviour, and their preferences and activity may vary by size and in time (Holmgren & Appelberg, 2000; Jackson et al., 2001; Blanck et al., 2007). These factors, together with the intra- and inter-specific interactions (Fisher, 2000; Jackson et al., 2001; Hölker et al., 2002) result non-random, within lake patterns of fish assemblages. However, fish distribution generally is also affected by at least one random component arising from the formation of fish shoals and their movements within and among resource patches (Hensor et al., 2005). Further, since most fishing gears are selective, estimation of fish assemblage structure and its response to environmental changes generally is effected by limitations of the sampling method applied.

One of the most popular sampling methods in still waters is the gillnetting. Gillnetting is a passive fishing method, which catching efficiency varies among fish species and size groups, depends on stock density, the environmental circumstances (e.g. weather, water temperature and transparency, habitat structure, feeding conditions) and the sampling conditions (e.g. net construction, time of the day, soak time) (review: Hamley, 1975; and more recently: Linløkken & Haugen, 2006; Olin et al., 2004; Pierce et al., 2010; Prchalová et al., 2011; György et al., 2012). Standardized sampling protocols control large part of the gear related variance in the samples, but generally not those being linked to random variations in sampling conditions. For example, water transparency and temperature are factors that can significantly influence gillnet catches, and may vary across sampling sites and days, especially in shallow, wind exposed waters (Hansson & Rudstam, 1995; Linløkken & Haugen, 2006; György et al., 2012). Although it is widely investigated how these factors affect fish assemblage or fish assemblage sample variability, it is still largely unknown what are their relative importance in structuring gillnet samples at the lake level.
Goal of this study was to partition the variance characterizing gillnet samples along the main dimensions of regulatory factors under a standardized sampling protocol in a large and shallow lake (Lake Balaton, Hungary). Specifically, it was examined to what extent variability of sample composition, species richness and diversity, mean fish body mass and fish abundance (measured as catch-per-unit-effort; CPUE) can be related to spatial, temporal and random environmental factors at the lake level. It was hypothesized that segregation of fish assemblages among the main habitat types (i.e. littoral vs. offshore) and water layers (i.e. benthic vs. non-benthic) will be the basic force of gillnet sample variability at the whole lake level. Although Lake Balaton is a very shallow lake with a mean depth of 3.2 m, previous studies indicated rather strong vertical patterns in the distribution of fish assemblages (Specziár et al., 2009; Specziár, 2010). It was also examined to what extent variability of different assemblage attributes could be related to spatial, temporal and random environmental factors in the benthic and surface water layers in the offshore area of Lake Balaton. Since variations of the water temperature and the water transparency are hardly controllable in large lake monitoring requiring multiple sampling days for a complete survey, it is particularly important to assess the rate of the bias they may cause in fish assemblage assessments.

MATERIALS AND METHODS

STUDY AREA
Lake Balaton is the largest shallow lake (surface area: 593 km$^2$; mean depth: 3.2 m) in Central Europe, situated at 46° 42' - 47° 04' N, 17° 15' - 18° 10' E and 104.8 m above sea level. The lake is meso-eutrophic with mean annual chlorophyll-a concentrations of 3.6-18.7 mg m$^{-3}$ (Istvánovics et al., 2007). Forty-seven percent of the lakeshore is covered by reed grass, but submerged macrophytes occur sparsely in the littoral zone. The lake is slightly alkaline, it contains about 400 mg l$^{-1}$ of Ca$^{2+}$ and Mg$^{2+}$(HCO$_3^-$)$_2$, its pH varies between 8.2 and 9.1, and has a conductivity of 550-671 μs cm$^{-1}$. In general the lake is turbid with a Secchi depth varying between 0.2 m and 0.8 m, although in exceptional cases (e.g. under ice cover) water transparency may reach 1.5-1.8 m. Oxygen deficiency has never been registered in the lake, and concentrations of pollutants are low or insignificant. Detailed information on the limnology and fish fauna of the lake can be found in reviews by Herodek et al. (1988), Bíró (1997) and Istvánovics et al. (2007).

**SAMPLING**

This study is based on methodically fully compatible gillnet surveys conducted between July 2005 and October 2010. For samplings, multi-mesh gillnets compatible with the European standard EN 14 757 (CEN, 2005) and made by Nippon Verkko oy (Finland) were used. In order to assess characteristic depth strata of the lake, the following gear set up was used. The standard benthic gillnet (BG) composed of 12 conventional mesh-sizes between 5 and 55 mm (43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35 and 29 mm; knot to knot) supplemented with 65 and 80 mm mesh-sizes, being 1.5 m high and in total 35 m long (length of each mesh panel is 2.5 m) was the basic gear of sampling and was used at each sampling occasion (i.e. site × date) in triplicate. Weighting of the BG (linear density of the buoyancy line in water: 7 g m$^{-1}$; linear density of the lead line in air: 22 g m$^{-1}$) was set to ensure dipping
of the lead line to the bottom. At sites with ≥2 m water depth, the surface-set version of the standard gillnet (SG) was also used in triplicate. Weighting of the SG (linear density of the buoyancy line in water: 31 g m\(^{-1}\); linear density of the lead line in air: 22 g m\(^{-1}\)) was set to ensure floating of the buoyancy line on the water surface.

Fish assemblages were sampled at 16 sites distributed across the four basins of the lake (Fig. 1). Gillnets were set in the morning (after sunrise). Nets were positioned linearly with one net length gap between them adjusted with a rope to ensure that the nets do not influence each other's performance. In order to avoid the saturation of nets by fish and the related biases (Olin et al., 2004; Prchalová et al., 2011), soak time must be kept short in Lake Balaton (Specziár et al., 2009). Therefore, sampling intervals of 1 to 4 hours were applied based on our experience on expected CPUE values by sampling sites and seasons. Altogether, 96 sampling occasions yielded catch data from 468 net sets.

Catch of each net was processed separately. Captured fish were identified, counted by species, measured to the nearest millimetre standard lengths and gram wet mass. Gillnet catches were expressed in both NPUE (number of fish captured per one hour per net) and BPUE (mass of fish captured per one hour per net). Note, that for brevity only the results based on NPUE are presented here. Altogether, 35,606 specimens of 18 fish species and three hybrids [roach Rutilus rutilus (L. 1758) × common bream Abramis brama (L. 1758), bleak Alburnus alburnus (L. 1758) × A. brama and silver carp Hypophthalmichthys molitrix (Valenciennes 1844) × H. nobilis (Richardson 1845)] comprised the samples (Table I).
Water depth and Secchi depth to the nearest 1 cm and water temperature to the nearest 0.1 °C were also measured at each sampling. Water depth, Secchi depth and temperature ranges covered by this study were 1.30-4.80 m, 0.19-1.12 m and 12.4-26.2 °C, respectively.

STATISTICAL ANALYSIS

Data evaluation was performed at both the assemblage (i.e. relative abundance, species richness and diversity data) and the species levels (i.e. NPUE by species), and for all samples and the offshore BG and SG samples only.

For statistical analyses, the three parallel samples by gillnet types (i.e. for BG and SG) were merged (averaged for density related indices and pooled for species richness data) for each sampling occasion (i.e. site × date). The main reason of merging these parallel samples by sampling occasions was to eliminate the high within sample variability in catch composition that would substantially increase the error term in analyses, and to enable a robust multivariate analysis (see also Lek et al., 2011). High within sample variability could be a joint effect of small-scale patchiness of fish distribution (i.e. fish form shoals by species and size class) and the relatively short soak time.

Rare species (i.e. <0.1% representation in the whole data set) were excluded from relative abundance analyses, but were considered in analyses exploring patterns of the total NPUE, mean fish mass, and species richness and diversity. Hybrids were excluded from species
richness and diversity estimates, but included to calculations of the total NPUE and mean fish mass. Species diversity was expressed by the Shannon-Wiener index.

Explanatory variables considered in the analyses were: 1) lake basin (four lake basins representing a trophic gradient; Istvánovics et al., 2007), 2) horizontally structured habitat type (offshore, littoral north and littoral south), 3) sampled water layer (BG, SG), 4) year of the sampling (2005-2010), 5) season of the sampling (spring, summer and autumn), 6) water depth, 7) Secchi depth and 8) water temperature. Explanatory variables were classified to three main variable groups as follows: 1) space (lake basin, habitat and water layer), 2) time (year and season), and 3) environment (water depth, Secchi depth and water temperature).

At the lake level, variations of relative abundance data and their relationships with the spatial, temporal and environmental factors were investigated with redundancy analysis (RDA) using CANOCO version 4.5 (ter Braak & Šmilauer, 2002). The method of RDA was chosen, because a preliminary detrended correspondence analysis (DCA) indicated a relatively short gradient length (≤2.10 in standard deviation units, see Lepš & Šmilauer 2003).

Response variables (i.e. relative abundance data) were arcsin($x^{0.5}$) transformed prior to analyses. Of explanatory variables, lake basin, habitat, water layer, sampling year and season were treated as categorical factors and re-coded into binary dummy variables (Lepš & Šmilauer, 2003); whereas water depth, Secchi depth and water temperature were treated as quantitative variables and were log$_{10}$(x+1) transformed. Since water depth strongly correlated with lake basin and habitat, it was excluded from the model building.
Firstly, a preliminary overall RDA model was built, which included all potential explanatory variables (Lepš & Šmilauer, 2003). The relative contribution of each variable to the model was assessed by using the forward stepwise selection procedure, and their significance was tested with Monte-Carlo permutation test with 9,999 permutations under the full model. Based on this selection procedure, only significant explanatory variables (P < 0.05) were retained in the final RDA model. Similarly, statistical significance of ordination axes and the whole model (i.e. including all axes) were tested using the Monte Carlo permutation test with 9,999 permutations. Next, a series of RDA and partial RDAs were conducted to partition the effects of spatial, temporal and random environmental factors on gillnet sample composition (Cushman & McGarigal, 2002).

To assess how much of the variances of NPUE data of the dominant fish species and of total NPUE, as well as of species richness, Shannon-Wiener diversity and mean fish body mass was explained by the investigated spatial, temporal and environmental variables, variance component analysis (VCA) was performed using Statistica 8.0 software (StatSoft, Inc.). For the analyses, the restricted maximum likelihood method (all factors are random-effects factors) was chosen because of the unbalanced distribution of data (Robindson, 1987). This method iteratively optimizes parameter estimates for the effects in the model (Searle et al., 1992). Since the VCA requires categorical explanatory variables, values of the Secchi depth and the water temperature were categorized into four evenly distributed ranges of ≤40 cm, 41-60 cm, 61-80 cm and >80 cm, and ≤15.0 °C, 15.1-20.0 °C, 20.1-25.0 °C and >25.0 °C, respectively. Due to its close relatedness to lake basin and habitat type, water depth was excluded from VCA analyses.
All analyses (i.e. RDA and VCA) were conducted also for offshore samples only, and separately for BG and SG samples.

RESULTS

ASSEMBLAGE COMPOSITION

At the lake level, the vertical segregation of fish assemblages in the water column was the most important factor structuring the gillnet catches (Fig. 2). This gradient associated with the first RDA axis that explained 62.6% of the total variance in the relative abundance data. The benthic layer of the water column was dominated by the *A. brama*, and the upper layer by the *A. alburnus*. All other fish species positioned left from the origin of the plot suggesting their closer link to the benthic layer than the surface layer. The second RDA axis (4.7% of the total variance) represented the littoral-offshore habitat gradient. Specifically, the ordination showed the predominance of razor fish *Pelecus cultratus* (L. 1758) and *A. brama* in the offshore catches, and the higher share of the *R. rutilus* and the white bream *Blicca bjoerkna* (L. 1758) in the littoral samples. Overall, 69.3% of the total variance of relative abundance data was described by the RDA model (Table II). Variation partitioning procedure showed that time (i.e. year and season) and environmental factors (i.e. temperature and water transparency) had little influence on relative abundance data. Most of the variance was associated with spatial factors, where the water layer sampled was the most important variable. Pure water layer effect accounted for 81.0% of the total explained variance (Fig. 3).
Significant RDA models were obtained for both the offshore BG (total explained variance: 33.1%) and the offshore SG samples (total explained variance: 36.6%). Redundancy analysis identified both seasonal and space related gradients in the percentage composition of the BG catches [Fig. (4a)]. Autumn samples were characterized by a higher proportion of the *A. brama*, while the opposite end of the gradient (i.e. spring) was associated with the *A. alburnus*. The second RDA axis characterized changes along the longitudinal gradient of the lake, with higher abundance of the *B. bjoerkna* in the shallowest and most productive Basin I. However, a substantial part of the variance remained unexplained (66.9%) [Fig. (5a); Table II]. Composition of SG samples varied mainly among lake basins and sampling years (RDA axis 1). This variability was associated with the relative importance of *A. alburnus*, *P. cultratus* and *A. brama* [Fig. (4b)]. The second RDA axis explained only 3.8% of the total variance and reflected a weak association of higher shares of the *P. cultratus* with lower temperatures and higher shares of the *A. brama* with higher temperatures in the samples, respectively. However, a substantial part of the variance remained unexplained (63.4%) [Fig. (5b); Table II].

**SPECIES RICHNESS, DIVERSITY, AND MEAN FISH MASS**

At the lake level, most of the variance in the species richness and the diversity, as well as in the mean fish mass was associated with the water layer (Fig. 6). For offshore assemblages, the contribution of the explanatory variables to the variability of these fish metrics varied by water layers. In SG samples, most of the variance in the species richness occurred among lake basins, and most of the variance in the species diversity occurred among sampling years. Whereas, mean fish mass varied among basins and with water transparency [Fig. (7a)]. In BG
samples, most of the explained variance in these assemblage metrics was related to among basin differences, but the majority of the variance remained unexplained [Fig. (7b)].

Variance component analysis showed that lake level total NPUE, NPUE values of the dominant *A. brama* and *A. alburnus* most importantly depended upon the water layer sampled. However, other species responded differently; littoral versus offshore habitat gradient was important component of variability in the NPUE of the ruffe *Gymnocephalus cernua* (L. 1758) and the pikeperch *Sander lucioperca* (L. 1758), NPUE values of the asp *Aspius aspius* (L. 1758) and the common carp *Cyprinus carpio* L. 1758 varied chiefly among lake basins, among year variance was high in the *R. rutilus* and the monkey goby *Neogobius fluviatilis* (Pallas 1814), NPUE values of the *R. rutilus* and the gibel *Carassius gibelio* (Bloch 1782) varied substantially among seasons, Secchi depth proved to be important in the *B. bjoerkna* and the *C. gibelio*, and temperature affected NPUE values of the Volga pikeperch *S. volgensis* (Gmelin 1789) and the *N. fluviatilis*. Explained proportion of variance of the NPUE was high and varied by fish species between 47.3-97.6% (mean ± S.D., 86.2 ± 15.4) (Fig. 6).

Although some among basin, season and temperature related variations could be identified in the benthic layer samples of the offshore area, most of the variance of the NPUE data, with the exception of the *B. bjoerkna* and the *A. brama*, remained unexplained [Fig. (7a)]. In the surface water layer of the offshore habitat, the water transparency had a predominant influence on the NPUE both at the species level and for all fish [Fig. (7b)].
In this study, the relative contribution of spatio-temporal heterogeneity and environmental factors to the variability of gillnet samples was investigated in the large and shallow Lake Balaton. As hypothesized, the majority of the variance was associated with habitat gradients. However, contrary to the generally accepted dominance of the littoral versus offshore gradient in shallow habitats (Romare et al., 2003; Winfield, 2004), it was found that the vertical segregation of fish was the most important factor shaping fish assemblage attributes. Lake basin, temporal and random environmental factors were important factors only at the habitat level, but not at the lake level.

Vertical segregation of fish species within the water column and its effect on gillnet sample composition is well known in deep lakes and reservoirs (Hansson, 1988; CEN, 2005; Prchalová et al., 2008; Vašek et al., 2009), but it is much less investigated in shallow waters (but see Deceliere-Vergés & Guillard, 2008; Lauridsen et al., 2008; Lund et al., 2010). Moreover, in shallow lakes (i.e. <10 m water depth; CEN, 2005), fish monitoring programs generally focus on benthic fish assemblages, and largely neglect the sampling of the upper water layers. However, majority of the variance observed in gillnet samples was associated with the vertical heterogeneity of fish distribution in Lake Balaton. Characteristic vertical trends were found in the NPUE of the two dominant species, total NPUE, mean fish mass, species richness and diversity and percent composition of samples. The benthic water layer of Lake Balaton could be characterized with an *A. brama* predominated species rich fish assemblage, while the surface water layer with an *A. alburnus* dominated species poor assemblage (see also Specziár et al., 2009; György et al., 2012).
It is a common phenomenon in most lakes with well-oxygenated bottom region, that fish diversity is higher in the benthic than in the upper water layers (Deceliere-Vergés & Guillard, 2008; Deceliere-Vergés et al., 2009). However, total fish abundance and biomass not necessarily follows the same trend. For example, in Lake Balaton, the total density of fish in the surface water layer is as high as in the benthic water layer (Specziár et al., 2009; Specziár, 2010). Similarly, Prchalová et al. (2008) and Vašek et al. (2009) found that most fishes occurred in the upper water layers in the Želivka and Římov Reservoirs, respectively. The few other studies which dealt with vertical patterns of fish assemblages in shallow lakes or shallow lake habitats also pointed out that surface-oriented species may reach high densities, which are comparable to that of benthic fish (Mous et al., 2004; Olin & Malinen, 2003; Olin et al., 2009). Therefore, surface-oriented fish assemblages can be important components of lake food webs and ecosystem productivity, and thus should be more intensively included in shallow lake monitoring.

At the lake level, horizontal habitat heterogeneity played a secondary role explaining only 8.3% of the total variability in the percentage composition of catches. This factor explained however most of the variance in the NPUE of the S. lucioperca, which species is more abundant in the offshore area. Further variables, like lake basin, temporal and random environmental factors proved to be important components of sample variability mainly at species level. However, the total share of these factors in the observed variance was well below 10% for most assemblage attributes. Therefore, one of the lessons of this study is that the evaluation of long-term changes of the fish fauna should be primarily done at the habitat level (i.e. littoral/offshore × water layer). Lake level conclusions may be then refined based on the knowledge of habitat level processes.
When samples were controlled for the habitat effect and offshore samples were analysed separately by water layers, relative roles of lake basin, time of sampling and random environmental factors increased. However, their importance depended on assemblage attribute, fish species, and water layer examined. The low consistency in the observed patterns indicates the variable sensitivity of particular fish species and assemblage attribute estimates to different environmental factors and seasonality. In addition, the share of the explained variance generally was much lower than at the lake level.

In Lake Balaton, there are characteristic gradients of trophic state (Istvánovits et al., 2007), food resource density and composition (Specziár & Vörös, 2001; Istvánovits et al., 2007), and water depth (Herodek et al., 1988) from basin I towards basin IV, which were found significantly affect fish assemblage composition and stock density in most of previous studies (Bíró, 1997; Tátrai et al., 2008; Specziár, 2010) as well as in this one. However, present results show that this component on average explains less than 20% of the total variance in gillnet samples, except the lake level variability in the NPUE of the A. aspius and the C. carpio. In contrast, such factors may be more important in waters exhibiting more marked gradients. For example, in long canyon-shaped reservoirs significant trophic, depth, temperature and oxygen concentration gradients may exist from the tributary towards the dam, which basically influence fish assemblage composition and density as well as the vertical distribution pattern of fish within the water column (Prchalová et al., 2008; Vašek et al., 2009). Further, the role of temporal (both seasonal and among years) components of sample variability proved to be moderate or low, which was in agreement with other studies (Holmgren, 1999; Prchalová et al., 2008). This indicates the stability of fish assemblages and the sampling efficiency over these time scales both at the lake level and in the offshore area.
In contrast, in the littoral zone, a significant seasonal trend was documented in the CPUE, characterized by a higher fish density during the spring and early summer (Specziár, 2001), which corresponds well with the small-scale reproductive migration of fish in this season (Winfield, 2004).

An increasing number of examples shows that gillnet CPUE is a poor indicator of fish abundance, and that several environmental factors can basically affect the efficiency of gillnetting (Hansson & Rudstam, 1995; Peltonen et al., 1999; Mehner & Schulz, 2002; Linløkken & Haugen, 2006; Dennerline et al., 2012). Water temperature is undoubtedly one of the most important factors, which influences the activity and behaviour of fish, and thereby the performance of passive fishing gears. Fish activity and swimming speed supposedly increase with water temperature, and accordingly the efficiency of gillnetting is expected to increase as well (Linløkken & Haugen, 2006). In contrary to the above hypothesis, but in accordance with the observations of Hansson & Rudstam (1995), here no significant temperature effect was identified in gillnet catches neither in assemblage level indexes nor in the NPUE of most fish species. Linløkken & Haugen (2006) showed that the effect of temperature is most decisive at extreme ranges (e.g. below 5 °C or above 20 °C in perch and roach). However, extreme temperature ranges were not investigated here.

Similarly, transparency of the water can affect gillnetting efficiency at least via two ways. Firstly, in turbid water the probability that a fish observes the net before being entangled is lower than in transparent water. Secondly, activity of most fishes is influenced by light intensity, being highest at low light but not in complete darkness (Gjelland et al., 2004 and references therein). Since a wind over 1 to 4 m s⁻¹ can disturb the sediment of the shallow Lake Balaton, even day-to-day or site-to-site variations in the water transparency can be
considerable in this lake (Herodek et al., 1988). However, a significant effect of water
transparency existed only in SG samples of the offshore area, where it influenced the NPUE
of the dominant species (*A. alburnus* and *P. cultratus*) and all fish, as well as the mean fish
size (see also György et al., 2012), and at lake level in the NPUEs of the *B. bjoerkna* and the
*C. gibelio*. Hansson & Rudstam (1995) also found correlation between the water transparency
and gillnet CPUE in the Baltic Sea herring *Clupea harengus* L. 1758 and the sprat *Sprattus
sprattus* (L. 1758). In addition, Mous et al. (2004) showed that the water transparency affects
the vertical distribution pattern of the light-sensitive European smelt *Osmerus eperlanus* (L.
1758) in the shallow Lake IJssel. Considering the high light attenuation within the water
column of Lake Balaton, where more than 90% of the light attenuates within the upper 1 to 3
m water layer (Herodek et al., 1988; V.-Balogh et al., 2009), it is not surprising that water
transparency proved to be important in the uppermost water layer, but not in the deeper
layers. Recently, Prchalová et al. (2010) established some justifications and standards for
comparable gillnet sampling among different lowland European fish species and waterbodies
under variable turbidity.

The high proportion of the unexplained variance, especially in the habitat level analyses,
cautions that the monitoring of the effects of specific environmental gradients on the fish
fauna might require multiple sampling surveys to equalize (control) the effect of
uncontrollable (random) factors influencing sampling efficiency. However, when discussing
gillnet sample variability, the effect of two other factors, the time of the day when the
sampling is done and the saturation of the nets with fish should not be surpassed. Due to
cycles of fish activity and light condition, gillnet samples generally show marked diurnal
variability regarding both their composition and CPUE (Olin & Malinen, 2003; Vašek et al.,
2009). This effect was controlled in the present study by choosing a short and standard
sampling interval. However, controlling or adjusting the effect of the gillnet saturation is
much more problematic (Prchalová et al., 2011), and generally, this issue is still largely neglected by monitoring protocols. Although relatively short sampling intervals were applied in this study, and, in addition, they were adjusted to habitat specific capture rates (see also Olin et al., 2004, 2009), this factor likely to contribute to the unexplained variance in samples.

To conclude, our study proves that the vertical habitat gradient may have significance over both the horizontal habitat gradient and temporal variations in structuring gillnet samples in shallow lakes. However, the high proportion of unexplained variance reflects the importance of random and generally uncontrollable factors in gillnet monitoring. These results demonstrate that sampling schemes should be planned carefully when considering the main factors organizing the distribution of fish in the particular system. Since sampling protocols should consider the main gradients in fish assemblage distributions the use of surface and pelagic gillnets should be more intensively incorporated in the study and monitoring of fish assemblages in shallow lakes and lake habitats.

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632  and directives of the modern utilization of the fish stock. Acta Biologica Debrecina
634  (In Hungarian with an English summary)


Table I. List of species and hybrids, their abbreviations used in figures and number of individuals captured ($N$).

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

Number of species (hybrids) 18 (3)
TABLE II. Results of the redundancy analyses describing the relationship between relative abundance data (%) and forward selected, significant (at $P < 0.05$) explanatory variables in Lake Balaton, for all sites included (all sample), and for specific water layers of the offshore habitat only.

<table>
<thead>
<tr>
<th>Significant explanatory variables</th>
<th>First axes</th>
<th>All axes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Eigen value</td>
<td>$F$ (d.f. num., d.f. den.)</td>
</tr>
<tr>
<td></td>
<td>Eigen value</td>
<td>$F$ (d.f. num., d.f. den.)</td>
</tr>
<tr>
<td>All sample</td>
<td>0.626</td>
<td>247.54 (7,148)</td>
</tr>
<tr>
<td>Bas-I, 2008, Autumn, Temp</td>
<td>0.140</td>
<td>8.46 (6,52)</td>
</tr>
<tr>
<td>Offshore, benthic layer</td>
<td>0.325</td>
<td>18.78 (5,39)</td>
</tr>
<tr>
<td>Offshore, surface layer</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

d.f. num. = degrees of freedom of the numerator, d.f. den. = degrees of freedom of the denominator, BG = benthic gillnet, Offsh = offshore habitat, Lit-N = littoral habitat along the northern shoreline of the lake, Bas-I = lake basin I, Bas-IV = lake basin IV and Temp = water temperature.
Figure captions

**FIG. 1.** Distribution of the sampling sites (Ο, littoral sites; Φ, offshore sites) in Lake Balaton.

**FIG. 2.** Redundancy analysis plot describing the relationship between the relative abundance data (%) of fish species (→) and forward selected, significant (at $P < 0.05$) explanatory variables (¬→, continuous variables; Ω, binary dummy variables) in Lake Balaton. Percentage variances represented by axes are indicated in brackets (of species data; of species-explanatory variables relation) after the axis name. Scale factor for biplotting and characteristic environmental gradients represented by the axes are also indicated (for a more detailed statistics see Table II). Species and explanatory variables with scores close to the centre of the graph are clarified on the small graph in the upper right corner. Species name abbreviations are given in Table I, while abbreviations of explanatory variables are as follows: BG = benthic gillnet, Offsh = offshore habitat, Lit-N = littoral habitat along the northern shoreline of the lake, Bas-I = lake basin I, Temp = water temperature.

**FIG. 3.** Results of the variation partitioning among the main groups of explanatory variables (a), and among space related variables only (b) influencing relative abundance (%) data. The area of each rectangular cell is proportional to the variance accounted for by that component.
Fig. 4. Redundancy analysis plots describing the relationship between the relative abundance data (%) of fish species (―) and forward selected, significant (at $P < 0.05$) explanatory variables (→, continuous variables; ○, binary dummy variables) for the benthic (a) and the surface (b) water layers of the offshore habitat in Lake Balaton. Percentage variances represented by axes are indicated in brackets (of species data; of species-explanatory variables relation) after the axis name (for a more detailed statistics see Table II). Scale factor for biplotting and characteristic environmental gradients represented by the axes are also indicated. Species scores close to the centre of the graph (a) are clarified on the small graph in the upper right corner. Species name abbreviations are given in Table I, while abbreviations of explanatory variables are: Bas-I = lake basin I, Bas-IV = lake basin IV, Temp = water temperature.

Fig. 5. Results of the variation partitioning among the main groups of explanatory variables influencing relative abundance data (%) in the benthic (a) and the surface (b) water layers of the offshore habitat in Lake Balaton. The area of each rectangular cell is proportional to the variance accounted for by that component.

Fig. 6. Results of the variance component analysis describing the percentage of the variation of the number-per-unit-effort (NPUE) of the abundant species, total NPUE, mean fish mass ($M$), species richness ($S$) and Shannon-Wiener diversity ($H$) accounted for by explanatory variables (💧, water layer; 🌿, habitat; 🌊, lake basin; ☀, year; 🌞, season; 🌡️, Secchi depth; 🌡️, water temperature), along with the unexplained variance proportion (□).
Results of the variance component analysis describing the percentage of the variation of the number-per-unit-effort (NPUE) of the abundant species, total NPUE, mean fish mass ($M$), species richness ($S$) and Shannon-Wiener diversity ($H$) accounted for by explanatory variables (■, lake basin; ☉, year; ☄, season; ☁, Secchi depth; ☼, water temperature) along with the unexplained variance proportion (□) in the benthic (a) and the surface (b) water layers of the offshore habitat in Lake Balaton. Species name abbreviations are given in Table I.
Axis 1 (62.6%; 90.3%)

Axis 2 (4.7%; 6.8%)
(a) space 66.5%  
    temperature 0.9%  
    time 1.9%  
    unexplained 30.7%

(b) water layer 56.1%  
    habitat 8.3%  
    interaction 0.3%  
    basin 2.1%