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Spatial distribution of fish in reservoirs and lakes

Ph.D. Thesis

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ANNOTATION

This thesis is focused on the fish spatial distribution and its changes mainly during the diel cycle. In the first part, I described the fish spatial distribution in the tropical lake ecosystem of Lake Turkana. The second part deals with the fish spatial distribution in a temperate reservoir on the different spatial scales from in/offshore habitats over the fine-scale to the level of individuals. The linkage of fish distribution patterns with selected environmental variables was also evaluated.

DECLARATION [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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LIST OF PAPERS AND AUTHOR'S CONTRIBUTION

The thesis is based on the following papers (referred as PAPER I-IV in the text):

I. **Muška, M.**, Vašek, M., Modrý, D., Jirků, M., Ojwang, W.O., Malala, J.O., Kubečka, J. (2012) The last snapshot of natural pelagic fish assemblage in Lake Turkana, Kenya: A hydroacoustic study. Journal of Great Lakes Research. 38: 98-106. (IF$_{2012}$ = 2.309).
Milan Muška was responsible for sampling arrangement, hydroacoustic survey, data processing, statistical analysis and writing the manuscript.

II. **Muška, M.**, Tušer, M., Frouzová, J., Draštík, V., Čech, M., Jůza, T., Kratochvíl, M., Mrkvička, T., Peterka, J., Prchalová, M., Říha, M., Vašek, M., Kubečka, J. (2013) To migrate, or not to migrate: Partial diel horizontal migration of fish in a temperate freshwater reservoir. Hydrobiologia 707: 17–28. (IF$_{2012}$ = 1.985).
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III. **Muška, M.**, Tušer, M., Frouzová, J., Mrkvička, T., Kubečka, J. Diel changes in fine-scale spatial distribution patterns of offshore fish assemblage (unpublished manuscript).
Milan Muška was responsible for sampling arrangement, hydroacoustic survey, data processing, statistical analysis and writing the manuscript.

IV. Mrkvička, T., **Muška, M.**, Kubečka, J. (2012) Two step estimation for Neyman-Scott point process with inhomogeneous cluster centers. Statistics and computing. Accepted DOI10.1007/s11222-012-9355-3 (IF$_{2012}$ = 1.977).
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CONTENTS

SPATIAL DISTRIBUTION OF FISH IN RESERVOIRS AND LAKES

INTRODUCTION

Spatial distribution is the result of interactions between organisms and their biotic and abiotic environment and as such remains the central issue of ecological research (Begon et al. 2006). In other words, spatial distribution is a realization of many individually optimized strategies of resource exploitation headed towards increase of individual fitness (Parker and Smith 1990). Distribution of all animals is not random in a space but exhibit spatial patterns, in dependence of scale of observation, and fish are no exception (Levin 1992). Understanding what drives and maintain these patterns of spatial heterogeneity is besides the basic research problem on its own also requirement for understanding of fish communities relationships and its role in the whole ecosystem. Further, the knowledge of fish occurrence is essential for determination of appropriate management when fish are the object of commercial, biomanipulation or conservation interest (Hölker et al. 2007; Jansen 2012; Kanno et al. 2012).

The various controls on fish spatial distribution can be both, extrinsic and intrinsic. The external factors are shaping the distributions mainly by environmental factors in a form of various gradients and are being summarized in the suitability of habitat (Elshout et al. 2013; Jeppesen et al. 2006; Prchalová et al. 2009; Prchalová et al. 2008; Ward et al. 2010). On the other hand, intrinsic controls such as age structure, population size, individual fish condition and motivation and diversity in behavioral patterns are modulating fish spatial distribution such as density dependence, age-dependent habitat preferences, different migration capacities, and so on (Brodersen et al. 2011; Brodersen et al. 2008; Persson et al. 1999; Čech et al. 2005). It is generally accepted that the extrinsic (environmental) parameters are acting on a larger scale while intrinsic (biological) processes are more relevant to local scales (van Moorter et al. 2013). Together with this is going the increasing importance of stochastic processes over the deterministic processes (Caruso et al. 2012).

Reservoirs and lakes as lentic waters share some general characteristics. The majority of its volume is represented by the pelagic zone in contrast to shallow,

structured and limited in space littoral zone, and thermal stratification often develops during part of a year (Duncan and Kubečka 1995; Kalff 2002). On the other hand, the reservoirs possess also unique features. Owing to its artificial and recent origin, most reservoirs are morphologically similar, with narrow and elongated or canyon-shaped morphology, closed within a deep valley of dammed river(s). Due to many of their purposes and utilization of the retained water, they have on average lower retention time, higher water level fluctuations and the longitudinal gradient of productivity is mainly driven by the river inlet (Hejzlar and Vyhnálek 1998). This gradient is consequently followed by all components of the trophic levels (Prchalová et al. 2008; Rychtecký and Znachor 2011; Seďa and Devetter 2000; Vašek et al. 2004). Reservoirs also host the original riverine fish fauna (Fernando and Holčík 1991), however the fish community underwent fundamental changes in species composition and its representation but no species has been documented to switch to the pelagic life cycle completely (Kubečka 1993a; Říha et al. 2009).

The most obvious changes of fish spatial distribution happens in reservoirs and lakes as a result of light intensity changes during the diel cycle. Diel migrations are widespread phenomena observed in freshwater ecosystems and are explained mainly with bioenergetics efficiency, predator avoidance and feeding opportunities (Gliwicz and Jachner 1992; Hasler and Villemonte 1953; Mehner et al. 2007; Zaret and Suffern 1976). The diel vertical migrations (DVM) consist of fish occurrence deep in the water column during day, subsequent ascend to the upper layer at dusk, residence near the surface during night and return to the deep waters during dawn (Mehner 2012). This behavioral pattern, typical for small zooplanktivourous fish, has been documented from vast number of water bodies in temperate zone (Hrabik et al. 2006; Mehner 2012; Scheuerell and Schindler 2003; Čech et al. 2005) and rarely in tropical waters (Getabu et al. 2003; Goudswaard et al. 2004; Prchalová et al. 2003). The most important proximate trigger of DVM is the intensity of light (Appenzeller and Leggett 1995; Probst and Eckmann 2009) acting together also with the temperature, oxygen and resources gradients (Kramer 1987; Kratochvíl et al. 2008; Wurtsbaugh and Neverman 1988). The ultimate causes bioenergetics efficiency, predator avoidance and feeding opportunities acting synergistically explained this behavioral pattern reasonable (Donner and Eckmann 2011; Mehner et al. 2007).

Less attention has been paid to the diel horizontal migrations, albeit they represent the principal component of fish spatiotemporal relationships in water

bodies where the vertical movements are restricted by depth and other physical factors, such as anoxic and cold hypolimnion, typical for euthrophicated temperate or shallow lakes and reservoirs (Comeau and Boisclair 1998; Gaudreau and Boisclair 1998; Järvalt et al. 2005; Prchalová et al. 2009). Furthermore, DHM was frequently studied in juvenile or small zooplantivorous fish in lakes. The widely accepted hypothesis to explain this migratory behavior is a diurnal variation in habitat specific trade-offs between predation risk and growth rate (Gliwicz et al. 2006). At the daytime, the structured littoral areas or the edge zone between littoral and pelagic habitats serve as refuge from predation for small fish but the resources may be quickly depleted in these limited habitats (Eklöv and Persson 1996; Romare et al. 2003; Savino and Stein 1989). On the other hand, pelagic habitats present more risky place, especially in presence of pelagic predators like asp (*Leuciscus aspius*) and pikeperch (*Sander lucioperca*), and juveniles and small bodied species enter to the open water only under decreasing light intensity following the "antipredation window" at dusk (De Robertis et al. 2003; Gliwicz et al. 2006). The relationship of decreased contrast during twilight is steeper for larger objects, which allows the small fish "to see and not be seen" (De Robertis et al. 2003). During the dawn they return again back to the littoral habitat with increasing light intensities.

On the contrary to this frequently studied behavior, the inverse night migrations of subadults and adults to the inshore habitat have been described in reservoirs, lakes and rivers (Blackwell and Brown 2005; Kubečka 1993b; Kubečka and Duncan 1998; Říha et al. 2011). The daytime occurrence of these fishes is less documented, but higher fish biomass with significant proportion of large fish was documented in pelagic habitats (Draštík et al. 2009; Vašek et al. 2009), even under pelagic predators occurrence (Brabrand and Faafeng 1993; Lammens et al. 1992; Schulze et al. 2006). The horizontal shifts between pelagic and littoral habitats were documented by telemetric studies for adults of the dominant species in lakes and rivers (Jacobsen et al. 2004; Schulz and Berg 1987; Zamora and Moreno-Amich 2002). As proximate causes for these migrations were suggested generally more profitable pelagic zooplankton resource (Hölker et al. 2007; Vašek and Kubečka 2004) and changing feeding efficiency with light intensities on pelagic (zooplankton) and littoral food resource (zoobenthos) (Imbrock et al. 1996; Schulz and Berg 1987) or termination of activity when foraging is inefficient or saving of energy in slower flows nearshore in rivers (Wolter and Freyhof 2004). Predators have been shown to be gape limited in freshwater systems and predation is therefore not likely the main cause for DHMs in larger fish (Nilsson and Brönmark

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2000; Skov et al. 2011) and convincing explanation is missing. Those two concepts of adult and juvenile DHMs, however seem completely opposite on the first view, are rather complementary and may provide the opportunity for niche partitioning (Specziar and Rezsu 2009).

Recently, the partial migration theory has come into prominence in fish ecology (Chapman et al. 2011a; Chapman et al. 2012a). Increasing reports have revealed that partial migration is extremely widespread and is rather the rule than exception (Chapman et al. 2012b). At first, partial migration was described among seasonally migrating diadromous fish species (Ker et al. 2009; McPhee et al. 2007) but includes also potamodromous fish (Brodersen et al. 2008) and lately was observed also among diel vertical migrants (Mehner and Kasprzak 2011). This theory, which is based on individual behavioral decisions, defines the partial migration as a migration in which less than 100% of the population participates (Chapman et al. 2011b). This point of view on migration behavior allows or even requires different approach focused more on individual fish.

The current expansion of Geographic Information Systems (GIS), remote sensing methods and spatial modelling creates ideal opportunity for mapping and modelling of the real spatial distribution of fish based on its geographical position, spatial relationships and its direct accounting to relevant environmental variables (Kery 2011). Nevertheless, its direct accounting to relevant environmental variables is scarce in lakes and reservoirs (Brosse et al. 1999; Rinke et al. 2009) and the usage of the spatial models for predictions of fish occurrence is infrequent even in freshwaters (Joy and Death 2004). The correct approach to deal with spatial data must include some methods to deal with autocorrelation, which is widely distributed natural ecological phenomena at all scales (Beale et al. 2010). This higher similarity of nearby localities and therefore non-random distribution cause serious problem with proper statistical testing by violation the assumption of independence of samples of most standard statistical procedures (Legendre 1993) and neglecting this can increase type I error, bias estimate of model parameters or even invert the relationships in observed dataset (Kühn 2007).

For clarification and understanding of ultimate causes for fish spatial distribution is essential to focus to the distribution of individuals which act as a basic unit in evolution (DeAngelis and Mooij 2005). From both, the increase importance of partial migration and its extremely limited knowledge of ecological and evolutionary consequences justified by individual difference of cost and demands and the lack of biological factors being included into spatial models lead to the

huge demand of construction individual based models (Chapman et al. 2012a). Such a model can elucidate the role of evolutionary processes in ecosystem of large freshwaters, which have been studied mainly on the scale of assemblage or community.

This dissertation is focused on the fish spatial distribution and its changes under diel cycle produced by changes of fish behavior. In the first part, I described fish spatial distribution in the unique well-mixed deep lake ecosystem of Lake Turkana and tried to summarize the development of its pelagic assemblage (PAPER I). The second part is focused on the cyclic movements between in/offshore habitats and brings novel insight of partial migration theory into Diel Horizontal Migrations concept (PAPER II). Next part is concerned spatial model of fine-scale fish distribution in pelagic habitat (PAPER III). Moving even to the smaller scale, the individual based model was developed with intentions to assess individuals linkage to the heterogeneous pelagic habitat, shoaling behavior and individuals interactions and preliminary results are shown (PAPER IV).

RESULTS

This dissertation is composed of four original papers – three of them already published (PAPERS I, II, IV) in impacted international scientific journals, one is in a form of unpublished manuscript (PAPER III).

PAPER I – The last snapshot of natural pelagic fish assemblage in Lake Turkana, Kenya: A hydroacoustic study

Muška, M., Vašek, M., Modrý, D., Jirků, M., Ojwang, W.O., Malala, J.O., Kubečka, J. (2012) The last snapshot of natural pelagic fish assemblage in Lake Turkana, Kenya: A hydroacoustic study. Journal of Great Lakes Research. 38: 98-106.

A hydroacoustic survey and supplementary gillnet investigation were carried out in the open water of the central part of Lake Turkana in September 2009. Overall acoustic fish density and biomass were assessed as 1381 ind./ha and 30 kg/ha, respectively. The fish density estimate was lower than the results from two previous investigations in the 1970s and 1980s (long-term average 3739 ind./ha), but the biomass remained relatively unchanged (long-term average 25.4 kg/ha). A decreasing gradient in pelagic fish density from the western to eastern shore of the lake was observed. Fish were distributed unevenly within the water column. During the day, a majority of fish aggregated in the mid-water layers (10–12 m below the water surface), creating on echograms the so-called Midwater

Scattering Layer. This feature dissipated completely during dusk and the majority of fish occurred in the surface layers at night. These diel vertical fish migrations influenced day and night hydroacoustic estimates of the total fish abundance. *Synodontis* spp., *Lates* spp. and *Schilbe uranoscopus* dominated the catch of both mid-water and bottom gillnets installed in open water areas. *Hydrocynus forskalii* and *Brycinus* spp. contributed significantly to the catch of mid-water gillnets while *Bagrus bayad* and the endemic *Haplochromis macconneli* occurred only in the catch of the bottom gillnets.

PAPER II – To migrate, or not to migrate: partial diel horizontal migration of fish in a temperate freshwater reservoir

Muška, M., Tušer, M., Frouzová, J., Draštík, V., Čech, M., Jůza, T., Kratochvíl, M., Mrkvička, T., Peterka, J., Prchalová, M., Říha, M., Vašek, M., Kubečka, J. (2013) To migrate, or not to migrate: Partial diel horizontal migration of fish in a temperate freshwater reservoir. Hydrobiologia 707: 17–28.

The diel horizontal migration (DHM) of fish between the inshore and offshore zones of the Římov Reservoir (Czech Republic, deep, stratified,meso-eutrophic) was investigated by a combination of horizontal and vertical hydroacoustic surveys at 3-h intervals over 48 h and day/night purse seining in August 2007. An overwhelming majority of fish were aggregated within the epilimnetic layer. Considering only the horizontal surveys, cyclic diel fish movements between inshore and offshore habitats were apparent, while the total fish biomass remained constant between day and night. A higher fish biomass was detected in the offshore zone during daytime by both hydroacoustics and purse seining. In contrast, a higher fish biomass was recorded at night in the inshore zone. Bream *Abramis brama*, roach *Rutilus rutilus*, and perch *Perca fluviatilis* dominated the daytime offshore fish assemblage whereas bleak *Alburnus alburnus* prevailed at night. Bream and roach decreased in abundance at night while perch completely disappeared from the offshore habitat. The diel differences in size distributions and direct catches suggested the population-wide horizontal offshore migration of bleak and inshore migration of all perch during dusk. On the other hand, partial inshore migration of bream and roach adults was observed during dusk (52 and 80%, respectively). The different proportions of offshore residents among species and size classes suggested that differences in size, and, therefore, predation vulnerability, contributed to the observed migration patterns.

PAPER III - Diel changes in fine-scale spatial distribution patterns of offshore fish assemblage

Muška, M., Tušer, M., Frouzová, J., Mrkvička, T., Kubečka, J. Diel changes in fine-scale spatial distribution patterns of offshore fish assemblage (unpublished manuscript)

1/ Understanding how spatial distribution is generated and maintained, and how this phenomenon unfolds in a temporal scale and in dependence on environment, remains a central issue in ecological research. In freshwater ecosystems is the information about real-time fish spatial distribution, its changes during diel cycle and dependence on environmental covariates in the offshore areas nearly lacking.

2/ In this work, we analysed patterns of spatial distribution of freshwater offshore fish assemblage, mostly bream *Abramis brama*, roach *Rutilus rutilus*, bleak *Alburnus alburnus* and perch *Perca fluviatilis*, during 48 hours in a temperate reservoir. The real-time spatial distribution of undisturbed fish was recorded during the detailed hydroacoustic surveys for two days at 3-h period and the distance from the bank (DFB), underwater light intensity, bottom slope, depth and zooplankton density were used as environmental proxies. The Simultaneous Autoregressive (Spatial Lag) model was used to evaluate the correlation of fish occurrence and predictors.

3/ After accounting for spatial autocorrelation, the correlations between fish occurrence and extrinsic factors attained inverse trends in day and night spatial distributions in most cases. The amount of fish was positively correlated with DFB, light intensity and depth while decreased with slope during the day. During the night DFB correlated with amount of fish negatively. Further, bottom slope and depth have significant positive correlation with night fish distribution. Zooplankton was distributed homogenously within the studied area and therefore probably did not influence fish distribution.

4/ We showed DFB as the most significant factor that the difference between day and night fish spatial distribution is mainly driven by. This result suggests prominent movements of assemblage between offshore and inshore areas on the diel bases. The pattern of spatial distribution during the crepuscular period, when is huge translocation of diurnal and nocturnal species realized, resulted in no significant relationships in the model. After all, spatial regression models represent

valuable tool which should be used for explaining and predicting fish distribution for effective stock assessment and management.

PAPER IV – Two step estimation for Neyman-Scott point process with inhomogeneous cluster centers

This paper is concerned with development of individual based model approach capable to assess basic parameters of individual fish distribution. This approach can address important questions of fish ecology like how the fish interact with each other on a small scale and how fish density is influenced by recorded covariates (i.e. distance to the bank, underwater light intensities, steepness of bottom and depth). Methods for parameter estimation for the Neyman-Scott point process with inhomogeneous cluster centers are described. Inhomogeneity depends on spatial covariates. The regression parameters are estimated at the first step using a Poisson likelihood score function. Three estimation procedures (minimum contrast method based on a modified K function, composite likelihood and Bayesian methods) are introduced for estimation of clustering parameters at the second step. The performance of the estimation methods are studied and compared via a simulation study. The results clearly show the significantly nonrandom distribution of individual fish. The more frequent shorter nearest-neighbor distances, than it should under random distribution, the fish shoaling behavior is evident. From simulation study is further deduced that range of individuals interaction is similarly important to environmental covariates. This suggests that if the scale of individuals is considered the biological characteristics like shoaling or predator avoidance become more important.

GENERAL DISCUSSION & CONCLUSIONS

The presented dissertation substantially contributes to the knowledge of fish spatial distribution in freshwaters. It has been shown that fish distribution patterns are rather heterogeneous in studied lake and reservoir in both vertical and horizontal plane and on different scales, from kilometers over tens of meters to

individuals. The prominent changes in fish distribution patterns during the diel cycle are also demonstrated.

The horizontal and vertical distributions of pelagic fish assemblage in Lake Turkana were not homogeneous. The horizontal pattern revealed, confirms the results of previous studies, which showed a decreasing gradient in fish density from the western to the eastern shore of the central sector of Lake Turkana (Hopson 1982; Lindem 1986). This spatial pattern is directly opposite to the surface water mass movements induced by the regularly blowing south-west winds prevailing in this region. The abundant pelagic assemblage was concentrated near the western shore where the abundant zooplankton drifts within the shifting upper layers of water column (Ferguson 1982). The similar concentration of zooplanktivores in place where wind induced seiche brings abundant zooplankton was observed in studies from temperate lakes (George and Winfield 2000; Rinke et al. 2009).

The vertical distribution of pelagic fish in Lake Turkana agreed with a general distribution pattern defined for the pelagic fish assemblage (Hugie and Dill 1994), where small zooplanktivorous species avoid the highly illuminated surface water layers dominated by predators therein during day. These zooplanktivors, mainly aggregating small pelagic characids, create very distinct segregated thin layer (7 m) in depths around 10 m, which is typical for Lake Turkana openwater assemblage (Kolding 1992). Nowhere else in African Great Lakes is observed such concentrated layer, small zooplanktivores usually create dense schools during day (Beadle 1974). An analogous thin condensed layer of *Rastrineobola argentea* in Lake Victoria has been described only during the stratified period when fish were excluded from the anoxic bottom layers and aggregated near the thermocline (Getabu et al. 2003; Tumwebaze et al. 2002). The vertical position in the water column of the scattering layer was observed to respond to changes in light intensity driven by changing turbidity or even crossing clouds similarly to vertically migrating perch in temperate reservoir (Čech et al. 2005). A predation threat is the likely factor leading to the formation of the scattering layer because piscivorous *Lates* spp. inhabit deep offshore areas underneath while other predatory fish *Hydrocynus forskalii* occupies the surface layer and small characids are their principal prey (McLeod 1982). The vertical migration of small characids to the surface layer occurring in open water (Hopson et al.1982) resemble the DVMs of small fish upward to the surface described also in other great lakes (Allison 1996; Goudswaard et al. 2004; Mehner 2012). The unique isothermal conditions and common predatory fish under and over the migrating characids clearly suggest the

predator avoidance and probably feeding opportunities on the drifting zooplankton as ultimate causes for the DVMs in Lake Turkana. Further we can reject the bioenergetical causes for DVM based on behavioral thermoregulation according the isothermal conditions here. However our study was limited in coverage due to the very remote location and complicated transportations it documented changes in little studied ecosystem of this largest desert lake.

The diel changes of fish spatial distribution and its stability between consecutive days was investigated in PAPER II. It has been shown that adult fish DHM is the main reason for the significant cyclic variation of fish biomass in the offshore and inshore zones during the diel cycle in the Římov Reservoir. The vertical component of the observed fish movements can be excluded due to nearly deserted layers deeper than four meters, similar to the results in other studies in stratified reservoirs and lakes (Brosse et al. 1999; Draštík et al. 2009; Knudsen and Sægrov 2002; Kubečka and Wittingerová 1998). In deep eutrophic water bodies, thermal and oxygen stratification exclude fish from deeper layers, so that no or only a very few fish occur under the thermocline in such systems (Jarolím et al. 2010; Järvalt et al. 2005; Prchalová et al. 2009; Prchalová et al. 2008). However, the decreases of only 33 or 52% of biomass in offshore zone at night, according to hydroacoustic and direct catch estimates, respectively, suggest that the night inshore migration does not encompass the entire day assemblage. This disproportion between acoustic and direct catches can be associated with selectivity of purse seine (Říha et al. 2012), however this influenced our results only marginaly. The diel changes of fish biomass demonstrated that a substantial part of the day offshore assemblage exhibit a resident strategy at night, which resembles the pattern of diel partial vertical migration in coregonids described by (Mehner and Kasprzak 2011). Partial migration was confirmed in populations of bream and roach, while perch and bleak seem to act via population-wide horizontal migration. Contrary to the situation in rivers, under lentic reservoir conditions the night inshore migration seems to represent an extra cost for the migrating part of bream and roach populations compared to their offshore resident conspecifics. This migrating behavior appears not to be of any evident advantage and seems to be, therefore, maladaptive. Individual phenotypic plasticity in the tendency to rest near structures, or a behavioral syndrome related to inshore migration of originally riverine populations (Fernando and Holčík 1991; Sih et al. 2004) may probably explain the maintenance of partial migration of adults. The results suggest predation risk for subadults and smaller adults as the main factor in the decision to migrate or not. However, other individual traits, such as body conditions

(Brodersen et al. 2008), behavioral syndromes (Sih et al. 2004), or phenotypic polymorphism (Chapman et al. 2011b) may also be important drivers of partial DHM. The observed apparent increase of small fish abundance in the offshore zone at night, together with a coincident decrease of small fish representation in the inshore zone, corroborate the model of juvenile DHM, with an extension for bleak adults, where predation also plays much more important role (Bohl 1980; Gliwicz and Jachner 1992).

The local spatial distribution of offshore fish in the Římov Reservoir was proved as autocorrelated and appropriate for spatial modeling in PAPER III. The correlations between fish biomass and extrinsic factors attained inverse trends in day and night spatial distributions in most cases. The diel changes in fish biomass patterns on the in/offshore scale are the most apparent explanation of the highest significance of DFB with opposite direction of regressions during day (+) and night (-). This well corresponds with the model of adult DHM between offshore and inshore habitats (Järvalt et al. 2005; Kubečka 1993b; Vašek et al. 2009). The amount of fish was positively correlated with the light intensity which has been shown as essential for visually orientated particulate feeding or gulping large strictly zooplanktivorous cyprinids (Vašek and Kubečka 2004). The intensity of light has been also shown as important factor whether pursue or not the sinusoidal swimming pattern which improves the detectability of transparent zooplankton in offshore reservoir habitats (Čech and Kubečka 2002). The high importance of solar radiation has been demonstrated by decreased proportion of the individuals performing sinusoidal swimming even when small decreases of solar radiation caused by crossing clouds occurred (Jarolím et al. 2010). At daytime, the fish biomass increased over the gentle bottom slope and opposite effect was observed at night. This is in congruence with the described generally higher fish aggregation over mild sloped habitats in natural lakes (Scheuerell and Schindler 2004). The night positive effect of steep sloped habitats is probably consequence of the night horizontal movement close to the shore. Part of the daytime offshore assemblage migrate to the shallow inshore habitat at night (Říha et al. 2011) but the substantial proportion remains in the offshore and here the steep sloped areas represent the nearest "impression" of littoral for the originally riverine (semipelagic) fish with residual need of night association with shore. Because these habitat turns nearly immediately to offshore habitat, fishes staying here overnight migrate shorter distances and reach the profitable pelagic habitat earlier than conspecifics migrating to the shallow inshore. The depth was the less important factor positively correlated with fish biomass both during day and night. The variability in

coefficients of determination suggest that although the selected environmental variables are significant in explaining the fish biomass variability there are probably other factors behind.

The increasing resolution of observing window focused on the spatial processes implies the higher influence of biological factors and individuality of fish behavior (Planqué et al. 2011). The preliminary results of our individual based model proved the spatial distribution of individuals as nonrandom with evident clusters or patches. It has been also demonstrated, that the interactions of individual are more important than environmental covariates. This well corroborates with studies suggesting increasing importance of biological processes on the smaller scale (Levin 1992; Rinke et al. 2009).

It is essential to state that correlation of spatial distribution pattern with environmental covariates is dependent on selection of appropriate variables, its nature and sampling density. The latter is probably the crucial because there are only few easily available variables on comparable spatiotemporal scale with continuous and detailed hydroacoustic data. Certainly, increasing of the number of relevant covariates, especially more dynamic parameters sampled on the similar temporal scale can improve the prediction performance of spatial model in the future. Incorporation of internal triggers such as population size, age structure, fish conditions, diversity and behavior that are too complex to be included in current distribution models but can be helpful in future (Planqué et al. 2011) and together with usage of individual based models to comprise individuals interaction is highly promising and can help to uncover the ultimate causes underlying partial migration in fishes, which are currently vague and ecological and evolutionary consequences are extremely limited (Chapman et al. 2012a).

PERSPECTIVES

Holistic studies of fish population distribution and their changes are often limited by methodology. To a great extent, this thesis was based on hydroacoustics that is a largely accepted method for fish observations (Thorne 1998). Despite recent progress in understanding of horizontal acoustic application, further research is necessary to solve the actual limitations of methodology. At the time, we did all the best representing state of the art of horizontal mobile acoustic research. Both split beam and DIDSON (acoustic camera) echosounders, the latter employed also

during the experiments but not processed thoroughly, had showed some limitations in mobile horizontal survey (Tušer 2013). One of the findings is that data from horizontal acoustics contain some degree of uncertainty in detection of smaller fishes in dependence of their aspect orientation (PAPER II) and determination of exact size of particular detected fish (Godlewska et al. 2012). Clarifying of these issues represents challenge for further studies and will highly improve the assessment of pelagic fish distribution patterns in future. So far, this study presents the most detailed observation of pelagic fish ever made within reservoirs by mobile horizontal acoustic.

Our effort to develop theories about how the freshwater ecosystems or fish communities are organized must revolve around attempts to discover patterns that can be quantified and compared across scales. If such patterns are detected and described we should try to discover the determinants of the pattern and mechanisms that generate and maintain those patterns. With understanding of the mechanism we have opportunity to predict the studied feature either in space or time. Results of our studies (Paper II, III) showed that the description of fish distribution patterns vary across scales from in/offshore through fine-scale (15 m squares) to individual level. On the comparison from the fine scale study (Paper III) and preliminary results from individual based model (Paper IV) is obvious that observed patterns are probably driven by different factors on different scales. In the Paper III, all environmental factors that were employed were significantly important; however on the individual scale only one factor (slope of bottom) was proved significant. This suggest more pronounced influence of biological factors in formation of spatial distribution patterns of individual fish such as shoaling behavior, predator-prey interactions, density dependent habitat selection or individual differences in behavior. To elucidate these questions, the combination of hydroacoustic methods with other approaches providing information about individuals and its endogenous conditions is required. Part of these questions could be answered by telemetric methods or experimental studies.

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PAPER I

The last snapshot of natural pelagic fish assemblage in Lake Turkana, Kenya: A hydroacoustic study

Muška, M., Vašek, M., Modrý, D., Jirků, M., Ojwang, W.O., Malala, J.O., Kubečka, J. (2012)

The last snapshot of natural pelagic fish assemblage in Lake Turkana, Kenya: A hydroacoustic study

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ABSTRACT

A hydroacoustic survey and supplementary gillnet investigation were carried out in the open water of the central part of Lake Turkana in September 2009. Overall acoustic fish density and biomass were assessed as 1381 ind./ha and 30 kg/ha, respectively. The fish density estimate was lower than the results from two previous investigations in the 1970s and 1980s (long-term average 3739 ind./ha), but the biomass remained relatively unchanged (long-term average 25.4 kg/ha). A decreasing gradient in pelagic fish density from the western to eastern shore of the lake was observed. Fish were distributed unevenly within the water column. During the day, a majority of fish aggregated in the mid-water layers (10–12 m below the water surface), creating on echograms the so-called Midwater Scattering Layer. This feature dissipated completely during dusk and the majority of fish occurred in the surface layers at night. These diel vertical fish migrations influenced day and night hydroacoustic estimates of the total fish abundance. *Synodontis* spp., *Lates* spp. and *Schilbe uranoscopus* dominated the catch of both mid-water and bottom gillnets installed in open water areas. *Hydrocynus forskalii* and *Brycinus* spp. contributed significantly to the catch of mid-water gillnets while *Bagrus bayad* and the endemic *Haplochromis macconneli* occurred only in the catch of the bottom gillnets.

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Introduction

Pelagic fish play important role in the ecosystem of all African Great Lakes. The extensive open water areas of African Great Lakes host rich pelagic communities dominated by small species like *Rastrineobola argentea* (Pellegrin) in Lake Victoria, *Stolothrissa tanganicae* Regan and *Limnothrissa miodon* (Boulenger) in Lake Tanganyika, *Engraulicypris sardella* (Günther) together with diverse cichlids in Lake Malawi and *Brycinus minutus* (Hopson & Hopson) plus *Brycinus ferox* (Hopson & Hopson) in Lake Turkana. These small planktivores are responsible for

the relatively efficient transfer of secondary production to the higher trophic levels, as they represent an important prey to piscivorous species like native or introduced *Lates niloticus* (L.) and others (Beadle, 1974). Both small pelagic planktivores and their predators usually represent an important part of commercial fish yield in African Great Lakes. The knowledge of fish stock parameters is essential for the determination of appropriate fisheries management and definition of sustainable fish yield.

Lake Turkana is situated in the arid region of northwestern Kenya, in the eastern branch of the Great Rift Valley. With its 240 km length and 14–50 km width, it is the world's largest desert lake and also the fourth largest African lake by area (Ferguson and Harbott, 1982; Herdendorf, 1982). Since Lake Turkana was first discovered for the scientific community at the end of 19th century (von Höhnel, 1894), as the last of the African Great Lakes, only little attention was given to its environment and fish populations. The first scientific observations of Lake Turkana central sector were made by Cambridge expeditions to the East African lakes in 1930–31 (Beadle, 1932; Worthington, 1936). Later, in the 1970s, a three-year survey program (1972–75) summarized by Hopson (1982) laid the foundations of knowledge of the Lake Turkana environment. This extensive

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PAPER II

To migrate, or not to migrate: Partial diel horizontal migration of fish in a temperate freshwater reservoir

Muška, M., Tušer, M., Frouzová, J., Draštík, V., Čech, M., Jůza, T., Kratochvíl, M., Mrkvička, T., Peterka, J., Prchalová, M., Říha, M., Vašek, M., Kubečka, J. (2013)

PRIMARY RESEARCH PAPER

To migrate, or not to migrate: partial diel horizontal migration of fish in a temperate freshwater reservoir

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Jiří Peterka · Marie Prchalová · Milan Říha · Mojmír Vašek · Jan Kubečka

Abstract The diel horizontal migration (DHM) of fish between the inshore and offshore zones of the Římov Reservoir (Czech Republic, deep, stratified, meso-eutrophic) was investigated by a combination of horizontal and vertical hydroacoustic surveys at 3-h intervals over 48 h and day/night purse seining in August 2007. An overwhelming majority of fish were aggregated within the epilimnetic layer. Considering only the horizontal surveys, cyclic diel fish movements between inshore and offshore habitats were apparent, while the total fish biomass remained constant between day and night. A higher fish biomass was detected in the offshore zone during daytime by both hydroacoustics and purse seining. In contrast, a higher fish biomass was recorded at night in the inshore zone. Bream *Abramis brama*, roach *Rutilus rutilus*, and perch *Perca fluviatilis* dominated the daytime offshore fish assemblage whereas bleak *Alburnus alburnus* prevailed at night. Bream and roach decreased in abundance at night while perch completely disappeared from the offshore habitat. The diel differences in size distributions and direct catches suggested the population-wide horizontal offshore migration of bleak and inshore migration of all perch during dusk. On the other hand, partial inshore migration of bream and roach adults was observed during dusk (52 and 80%, respectively). The different proportions of offshore residents among species and size classes suggested that differences in size, and, therefore, predation vulnerability, contributed to the observed migration patterns.

Keywords Diel activity · Diurnal migration · Individual decision making · Horizontal hydroacoustics · Purse seining · Cyprinids

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Introduction

Diel habitat shifts are widespread phenomena observed in marine and freshwater ecosystems (Hasler & Villemonte, 1953; Zaret & Suffern, 1976; Axenrot et al., 2004; Mehner et al., 2007). The diel vertical migrations have received more attention even though diel horizontal migrations (DHM) represent the

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Diel changes in fine-scale spatial distribution patterns of

offshore fish assemblage

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Abstract

1/ Understanding how spatial distribution is generated and maintained, and how this phenomenon unfolds in a temporal scale and in dependence on environment, remains a central issue in ecological research. In freshwater ecosystems is the information about real-time fish spatial distribution, its changes during diel cycle and dependence on environmental covariates in the offshore areas very scarce.

2/ In this work, we analysed patterns of spatial distribution of freshwater offshore fish assemblage, mostly bream *Abramis brama*, roach *Rutilus rutilus*, bleak *Alburnus alburnus* and perch *Perca fluviatilis*, during 48 hours in a temperate reservoir. The real-time spatial distribution of undisturbed fish was recorded during 13 detailed hydroacoustic surveys for two days at 3-h period and the distance from the bank (DFB), underwater light intensity, bottom slope, depth and zooplankton density were used as environmental proxies. The spatial lag model was used to evaluate the correlation of fish occurrence and predictors.

3/ After accounting for spatial autocorrelation, the correlations between fish biomass and extrinsic factors attained inverse trends in day and night spatial distributions in most cases. The amount of fish was positively correlated with DFB, light intensity and depth while decreased with bottom slope during the day. During the night DFB correlated with amount of fish negatively. Further, bottom slope and depth have significant positive correlation with night fish biomass distribution. Zooplankton was distributed quite homogenously within the studied area and therefore probably did not influence fish distribution.

4/ We showed DFB as the most significant factor that the difference between day and night fish spatial distribution is mainly driven by. This result suggests prominent movements encompassing significant part of fish assemblage between offshore and inshore areas on the diel bases as explanation. The pattern of spatial distribution in the morning (0600-0900) overlap with the huge translocation of diurnal and nocturnal communities realized during the crepuscular period, resulted in no significant relationships in the model. After all, spatial lag models represent valuable tool which should be used for explaining and predicting fish distribution for effective stock assessment and management.

Introduction

The spatial heterogeneity of resources and environmental conditions is essential property of all biological systems on different spatiotemporal scales (Levin 1992). The spatial distribution of freshwater fish is a result of the external and internal influences i.e. physicochemical parameters (dissolved oxygen, light and temperature (Cerri 1983; Kramer 1987; Sims et al. 2006), spatial and temporal changes in food availability (Bohl 1980; Vašek and Kubečka 2004), predation risk (Diehl and Eklöv 1995; Lammens 1992; Savino and Stein 1989) and intraspecific relationships (Persson 1987; Persson and De Roos 2012). Following evolutionary theory, spatial distribution is a realization of many individually optimized strategies of scarce resources exploitation headed towards increase individual fitness (Parker and Smith 1990).

Spatial distribution of offshore fish was primarily presumed nearly homogenous or even vacant in reservoirs (Fernando and Holčík 1991), in contrast to the onshore assemblage studied in more detail, until more accurate studies described heterogeneous nature of fish distribution in this habitat (Amour et al. 2005; Gibson 1967; Mason et al. 2005; Mehner et al. 2005). Although the fish spatial distribution models have been attempted at lake or reservoir scale showing the response of fish to the large-scale pattern, e.g. nutrients, temperature and turbidity gradients (Heege and Appenzeller 1998; Muška et al. 2012; Planqué et al. 2011; Prchalová et al. 2008), less investigations were made at the finer scale taking into account the local environmental qualities. Determination of driving environmental factors responsible for the spatial distribution of offshore fish assemblage is challenging and not clarified sufficiently (George and Winfield 2000; Simard et al. 1993). Changes of spatial distribution on the local scale are assumed to be more frequent and faster than on the large scale and simultaneously responding to the faster and local changes of resource availability (van Moorter et al. 2013).

In this view, hydroacoustic methods are well-established and recognized techniques for assessment aquatic resource (Thorne 1998). In freshwater habitats, hydroacoustics has been used to describe vertical (Mehner 2006; Čech et al. 2005) and horizontal (Draštík et al. 2009; Kubečka and Wittingerová 1998; Muška et al. 2013) patterns of fish distribution and it represent nearly perfect tool for studies focused on the high spatiotemporal resolution and continuous quantitative observation of undisturbed fish populations (Draštík and Kubečka 2005; Guillard 2007; Muška et al. 2013; Rinke et al. 2009). Together with the expansion of Geographic Information Systems (GIS) and remote sensing methods it creates ideal opportunity for mapping and modelling of the spatial distribution of pelagic fish (Georgakarakos and Kitsiou 2008; Simard et al. 1993; Valavanis et al. 2008), nevertheless its direct accounting to relevant environmental variables is scarce (Brosse et al. 1999; Rinke et al. 2009).

In analysis of the spatial data plays crucial role a phenomenon known as spatial autocorrelation (Beale et al. 2010). Spatial autocorrelation occurs when the values of variable sampled in the nearby localities are more similar, and therefore not independent, than the more distant one (Sokal and Oden 1978). This general property occurs in most natural ecological phenomena at all scales and also cause serious problem with proper statistical testing by violation the assumption of independence of samples of most standard statistical procedures (Legendre 1993). If the spatial autocorrelation is neglected it can bias estimate of model parameters, increase type I error or even invert the relationships in observed dataset (Kühn 2007). Spatial lag models, applying the spatial structure by (treating autocorrelation through) the distance based spatial weight matrix, were proved as appropriate tool for regression analysis of spatially correlated data (Anselin et al. 2006; Dormann et al. 2007).

This study aimed to assess day- and night-time horizontal spatial distribution of offshore fish at local (finer) scale and identify determinants for such patterns. The

study focused on a part of Římov Reservoir, which was explored in extensive spatiotemporal detail (> 42 % study area, every 3-h). Here, the distribution of fish biomass was modeled in relation to environmental variables. Specific objectives included determination whether predictors could be generalized during day- and night-time or between different days and nights.

Materials and methods

The study was undertaken at meso–eutrophic Římov Reservoir (48°50' N, 14°30' E; South Bohemia, Czech Republic) during 7 – 9 August 2007. The reservoir represents typical canyon–shaped water body with narrow (max. width 600 m), elongated shape (length 10 km) and alternating slight and strong sloped banks (Fig. 1A). The reservoir covered area of 162 ha at the water level during the study (465.5 m a.s.l.) with maximum and mean depth of 39 and 12 m, respectively. The reservoir is dimictic, with summer stratification evident from April to October. The average retention time of this water body is approximately 91 day. The offshore fish assemblage in the Římov Reservoir was investigated simultaneously by purse seining and was represented by bream, *Abramis brama* (L.), roach, *Rutilus rutilus* (L.), and bleak, *Alburnus alburnus* (L.)) with an additional proportion of perch, *Perca fluviatilis* L. (Muška et al. 2013). Predatory fish (asp, *Leuciscus aspius* (L.), pikeperch, *Sander lucioperca* (L.), pike, *Esox lucius* L. and European catfish, *Silurus glanis* L.) represent important proportion (14.5 % of biomass) of offshore assemblage (Prchalová et al. 2009). The study site, situated in the middle part of the reservoir, represented 26 % (42 ha) of total reservoir surface. The maximum and mean depth in the study area was 31 and 16 m respectively, the bottom slope attained values up to 62° and maximum reservoir width was 320 m (Fig 1 C,D,E).

Zooplankton

Samples of epipelagic zooplankton were collected on 8th August at ten locations located within the study site. At each location, two vertical hauls through the

epilimnion were taken (net diameter 20 cm, mesh-size 200µm) from depth of 5 m during the daytime. Catches were pooled into one sample and immediately preserved in 4% formaldehyde. In the laboratory, zooplankton densities were estimated by the standard method of microscopic counting in a Sedgewick-Rafter chamber.

Acoustic equipment

The acoustic study was made by a combination of a horizontally orientated elliptical transducer (ES120_4; nominal beam angles 9.2° x 4.3°) and a circular transducer (ES120_7C; nominal angle 6.4°) aimed vertically. Both transducers were operated by a SIMRAD EK 60 split-beam echosounder at the frequency of 120 kHz via a multiplexer. Elliptical transducer was orientated starboard and tilted 4° downwards. The echosounder was driven by the SIMRAD ER 60 software (version 2.2.0), a pulse duration of 128 µs was constant and the ping rate was set at the maximum (mostly around 5 pings s-1) during the study period. Before the survey, the whole system was calibrated using a 23 mm diameter copper calibration sphere (target strength (TS) -40.8 dB) according to (Foote et al. 1987).

Survey design

The acoustic survey was performed along a predesigned dense parallel grid (Fig. 1B) with a constant speed of 1.5 m s^{-1} and was repeated with 3-hours interval during two consequent 24-h cycles.
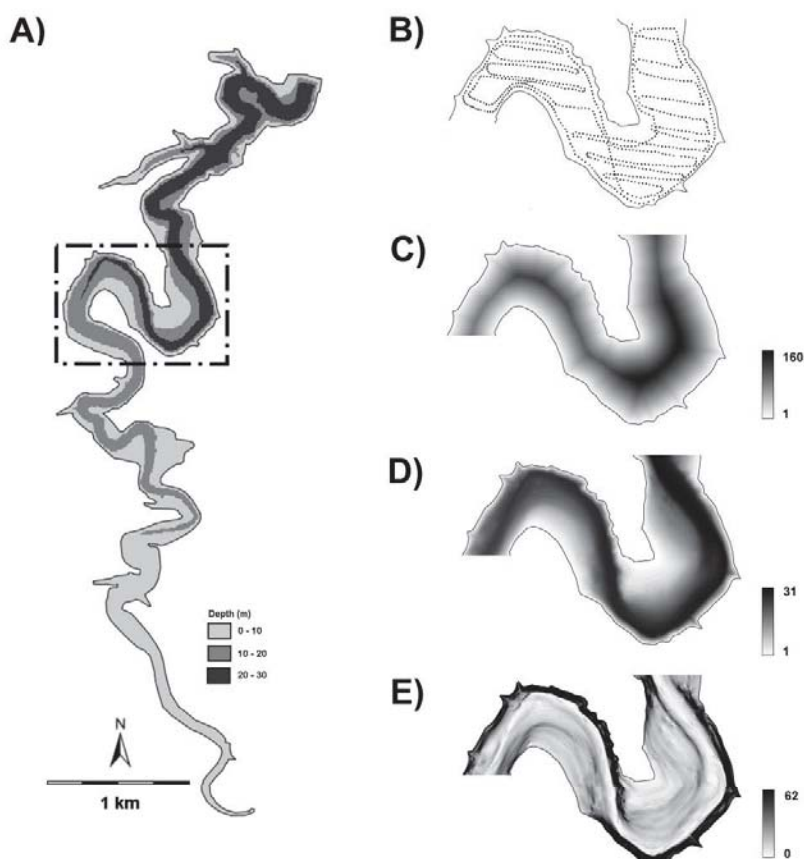
Fig. 1. Bathymetric map of the Římov Reservoir with study area highlighted by dot–dash rectangle (A). A representation of sampled points of hydroacoustic survey (B). Visualization of used covariate layers, distance to the shore (m), depth (m), bottom slope (degrees) (C, D, E).

A total number of 16 hydroacoustic surveys was performed in total. Three surveys (0600-0900 and 1800-2100 during the first day and 0300-0600 on the second day) were not processed because of the very noisy data in combination with technical problems. Each survey measured 11.5 km and trajectory included the offshore and inshore areas, with limitation to depths > 1.5 m. At this point, depending on the slope of inshore zone, the recording was filled with bottom echoes and acoustic data are unreliable. The position of the survey boat was measured using a Garmin GPSMAP 60CSx GPS receiver with an external antenna attached to transducer's

holder and the obtained geographic coordinates were embedded into the acoustic data files.

The whole survey was divided into 15 m long transects. Such a short length was chosen in order to reveal spatial distribution changes on this necessary scale. Vertical temperature and oxygen levels were measured using a calibrated YSI 556 MPS probe during the survey. The intensity of visible light was measured 1 m under the water level in lux using the LI-1400 dataloger with LI-193 sensor (LI-COR Biosciences, Nebraska, USA) at 1 s interval and averaged in each transect. Because overwhelming majority of fish was acumulated within the surface layer and negligable amount of fish occurred in vertical results (Muška et al. 2013), the vertical data were further not considered.

Data processing

Raw acoustic data were converted and analyzed with the Sonar5 Pro post-processing software (version 5.9.1; Balk and Lindem 2009). The horizontal recordings were bound by setting the upper and lower limit of the pelagic layer at 4 and 20 m from the transducer, respectively. These limits were set to avoid a bias caused by the transducer near-field (2.29 m) or far-field non-spherical spreading induced by ray distortion at the thermocline or surface layers. A manually-defined bottom line was used in order to exclude noisy parts in a record or bank echoes occurring within the pelagic layer and only data within the pelagic layer were processed. In addition, Cross Filter Detector (Balk and Lindem 2000) was used to eliminate noise in the horizontal data with the following parameters:

foreground filter: height 5 and width 1, background filter: height 55 and width 1, offset + 6 dB, perimeter length: 10 - 10 000 (Nr. of samples around the detected region), ratio: min 1 - max 270 (track length/mean echo length), max intensity: (-60 to -10 dB).

Non-fish echoes were eliminated by setting a -65 dB minimum TS threshold and all targets exceeding this threshold were echo-integrated for obtaining the volume backscattering strength (S_V; dB). The S_V values were georeferenced with transect's centre of gravity. We have used S_V value as a broadly accepted measure of fish biomass. The raster layers with environmental covariates i.e. distance from the shore, water depth and bottom slope (Fig 1 C, D, E) were prepared in ArcMAP 10, Spatial Analyst extension (ESRI Inc., CA, USA). The values were merged into the corresponding transect centres and projected to metric S-JTSK coordinate system.

Statistical methods

The spatial regression analysis was performed in the OpenGeoDa 1.0.1 software (Anselin et al. 2006). The spatial autocorrelation of the data was evaluated by Moran's *I* statistic (Moran 1950). We used the permutation test to examine whether the Moran's *I* statistic is equal to 0. The spatial regression analysis is the refined regression which takes into account the spatial correlations of the data. The spatial correlations are summarized in a spatial weight matrix computed on the basis of distance. We set up the threshold distance to be 20 m, because such distance covers all the neighbouring measurements. According to spatial diagnostics (Lagrange multiplier test statistics), we chose the spatial lag model to analyse the data. The model was concretely:

S_V = Light + Distance to bank + Bottom slope +Depth.

Since the residuals produced from spatial lag model did not show any spatial autocorrelation (no significant permutation test for the Moran's *I* statistic), we assume the distance of 20 m to be sufficient and the spatial lag model to be correctly chosen.

Summary statistics

Since we have several independent realizations of the data and thus several p-values are produced from the spatial lag models for one covariate, we used the Šidák correction to adjust the critical value of significance (Abdi 2007). For evaluation of the importance of particular covariate influence, we used the logarithmic mean of the p-values to summarize the information about the rate of significance. The logarithmic mean p-value was calculated from the sample of p-values p_i, i=1,..,n by:

$$Lp = Exp((Ln(p) + \ldots + Ln(pn))/n)$$

Results

The fish spatial distribution was not homogeneous in any of 13 hydroacoustic surveys during both days and differed between day and night (compare in Fig. 2 day vs night).

Fig. 2. Map of spatial variation in fish biomass (expressed as volume backscattering strength (S_V, -dB)) at day- and nighttime. Only survey number 15 (day) and 10 (night) were chosen for example, the pattern in other particular surveys was similar.

Moran's *I* scores, as a largely accepted measure of spatial autocorrelation, attained values from 0.26 to 0.51 in all studied fish spatial distributions and were highly significant (p < 0.001) which proved strong positive autocorrelation between fish

biomass in individual samples (table 1). The Moran's *I* scores were not significant in any residuals from all spatial lag models, that shows that autocorrelation was treated correctly and model fitted the data adequately (Anselin et al. 2006).

Further, all covariates were proved in spatial lag model as significant after Šidák's correction at alfa 0.05 (tab 2) and their correlation signs remained the same during particular daytime period. All regressions differed in correlation direction between day and night, except depth. The correlation of fish biomass and depth has the same direction during day and night.

	data		residuals	
	moran's I	p-value	moran's I	p-value
G1	0.465	p<0.001	-0.37	p=0.14
G2	0.379	p<0.001	-0.036	p=0.16
G3	0.308	p<0.001	-0.0254	p=0.246
G5	0.26	p<0.001	0.026	p=0.21
G6	0.377	p<0.001	0.005	p=0.39
G7	0.29	p<0.001	0.046	p=0.055
G9	0.401	p<0.001	-0.048	p=0.87
G10	0.475	p<0.001	0.066	p=0.026
G12	0.51	p<0.001	0.029	p=0.16
G13	0.45	p<0.001	-0.0123	p=0.354
G14	0.465	p<0.001	-0.0141	p=0.323
G15	0.427	p<0.001	-0.0238	p=0.17
G16	0.313	p<0.001	0.037	p=0.12

Tab. 1. Calculated Moran's I spatial correlation coeficient for 13 surveys in the raw data and in residuals after spatial weights application and its levels of significance obtained from the permutation tests.

Only the model for the survey from 0600-0900 (overlapping morning transitional period) did not show any significant relationship with any covariates. The highest rate of significance was proved for distance from the bank, which was positively

correlated to fish biomass during day (Tab. 2). The intensity of the underwater light and depth was also positively correlated with fish biomass. On the contrary, the bottom steepness was negatively influencing fish biomass spatial distribution, but with the smallest rate of significance, albeit still significant after Šidák's correction. The common effect of significant covariates as were collaborated on the day fish spatial distribution pattern is depicted in figure 3A. The coefficient of determination suggested that the models developed for daytime fish distribution explained significant part of the fish biomass variability (tab. 1; mean r^2 0,24; max. 0,37).
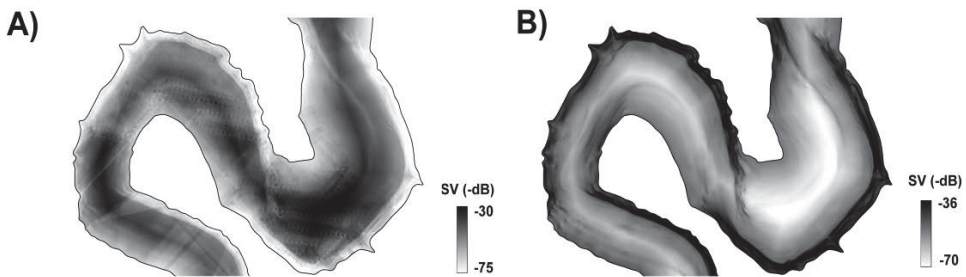

Fig. 3. Visualization of spatial lag model realization developed for one day (A) and one night (B) spatial distribution patterns of fish biomass (expressed as volume backscattering strength (S_V, -dB)). Only survey number 15 (day) and 10 (night) were chosen for example, the pattern in other particular surveys was similar.

Tab 2. Spatial lag models calculated with fish biomass as response variable and distance to the bank (DTB), underwater light intensity, bottom slope, depth as independent variables. Fish biomass expressed as back scttering strength (-dB) on the logarithmic scale. Factors passed through adjusted p-value after Šidák's correction (to the critical value of significance alfa=0.05 is 0.064 for daytime and 0.01 for nighttime models) are labeled with asterisk.

Survey no.	DTB Coefficient	DTB p-value		Light Coefficient	Light p-value		depth Coefficient	depth p-value		bottom slope Coefficient	bottom slope p-value		adjusted R^2
1	-0.042	0.003	*				0.360	0.000	*	0.147	0.000	*	0.24
2	-0.030	0.007	*				0.122	0.005	*	0.082	0.011		0.24
3	-0.060	0.000	*				0.001	0.986		0.011	0.684		0.18
5	0.017	0.329		0.001	0.714		-0.014	0.038		-0.175	0.002	*	0.12
6	0.020	0.466		0.069	0.000	*	0.263	0.006	*	-0.191	0.005	*	0.19
7	0.044	0.016		0.003	0.077		0.184	0.003	*	0.032	0.509		0.15
9	-0.027	0.101					0.079	0.223		0.098	0.002	*	0.24
10	-0.037	0.003	*				0.065	0.163		0.067	0.043		0.27
12	0.027	0.115		0.005	0.650		0.116	0.072		-0.025	0.574		0.35
13	0.076	0.000	*				0.129	0.042		-0.002	0.972		0.34
14	0.079	0.000	*	0.001	0.317		0.076	0.207		0.081	0.120		0.36
15	0.048	0.000	*	0.004	0.000	*	0.068	0.251		-0.053	0.206		0.31
16	0.066	0.000	*	0.005	0.001	*	0.053	0.153		-0.051	0.039	*	0.27
daytime rate of significance	0.0007			0.0093			0.0415			0.0651			
nighttime rate of significance	0.0011						0.0071			0.0145			

In contrast to the daytime spatial distribution pattern, the distance from the bank was related to the fish biomass negatively and remained still the most significant covariate at night (tab 2). Depth and slope correlated with fish biomass positively, the former more important than latter. For the night spatial lag models were r^2 comparable the daytime situation (tab. 1; mean r^2 0,23; max. 0,27). The common effect of significant covariates as were collaborated on the night fish spatial distribution pattern is depicted in figure 3B.

Densities of epilimnetic zooplankton attained values ranging from 63 to 182 ind. L^{-1} (CV=0.38; mean 107) at ten sampling site with the domination of large cladocerans (Fig. 4).
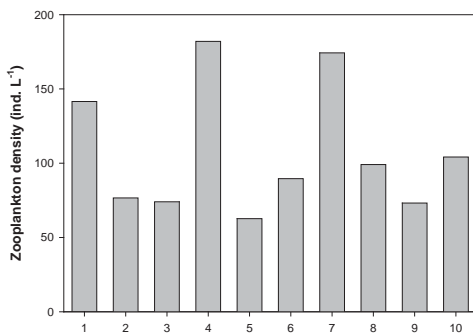

Fig. 4. Density of zooplankton at 10 sites sampled during the experiment. Sites covered the whole study area representatively.

Discussion

In this study we present the first attempt to explain and predict the patterns in offshore fish spatial distribution at local scale (15 m) in relation to accessible and relevant factors. Because the covariates proved always the same sign of the relationship with fish biomass during both days and in particular day period, we believe that they represent the characteristic grounds responsible for local fish spatial distribution in freshwater reservoir in late summer.

The heterogeneity of fish spatial distribution has been attributed to the large-scale differences in temperature, oxygen, wind, nutrients, prey distribution and

predator-prey interactions in many studies of freshwater ecosystems (Gaudreau and Boisclair 1998; George and Winfield 2000; Kratochvíl et al. 2012; Rinke et al. 2009; Vašek et al. 2004). Since we investigated the central part of the reservoir sheltered in two meanders, only small changes of above mentioned parameters would be expected and therefore acting on the local scale with observed horizontal fish distribution patterns. Morover, the effect of some factors may differ depending on the scale of observation and may change its influence (Levin 1992).

For instance, the positive or none relationship have been observed between zooplanktivorous fish and zooplankton horizontal distribution on the scale of whole-lake or reservoir (George and Winfield 2000; Romare et al. 2003; Vašek et al. 2006). On the contrary, the negative correlation of zooplanktivores and zooplankton, as a result of the direct depletion of zooplankton by active foraging fish, was observed at the local scale (George and Winfield 2000; Kalikhman et al. 1995). In this view, we expected rather negative relationship of fish biomass and zooplankton density in this study. This effect was not evident in the data, because zooplankton exhibited rather homogenous distribution throughout the sampling area.

The diel changes in fish biomass patterns in the reservoir cross section direction are the most apparent explanation of the highest significance of DFB with opposite direction of regressions during day (+) and night (-). This well corresponds with the model of partial diel horizontal migration of adults as was described by (Muška et al. 2013). The high preference to offshore habitats of large fish of dominating species in biomass was similarly observed in many studies from lakes and reservoirs during day (Draštík et al. 2009; Jacobsen et al. 2004; Schulz and Berg 1987; Vašek et al. 2009). At night, part of this daytime assemblage moves inshore, the other part still creates substantial biomass offshore and move closer to the banks (Muška et al. 2013; Říha et al. 2011). In night offshore assemblage occur also smaller species and juvenile fishes, which were hidden inshore during day (Říha et

al. subm.), but they contribute to the biomass only marginally (about 10% in direct catch; Muška et al. 2013).

The effect of lower underwater light (turbidity) on the fish distribution seems to have positive effect on the large scale (Heege and Appenzeller 1998, Jacobsen et al. 2004; Pekcan-Hekim et al. 2010) or on local scale (Helfmann 1981) by offering hiding places. The dominant zooplanktovores gain advantage under such conditions from the much steeper decrease of its visual contrast, and therefore detectability for potential predator, than the decrease of zooplankton contrast (De Robertis et al. 2003). In contrast, the underwater light has significantly positive effect on fish biomass in our study. This is in approval with studies denoted the high importance of light intensity for visually orientated particulate feeding or gulping large strictly zooplanktivorous cyprinids, which is mostly accompanied by sinusoidal swimming in reservoirs (Vašek and Kubečka 2004; Čech and Kubečka 2002). Foraging under high light intensities probably allow to detect large zooplankton individual or patches filter feeding and the sinusoidal swimming enhance this ability. The high importance of solar radiation has been demonstrated by decreased proportion of the individuals performing sinusoidal swimming even when small decreases of solar radiation caused by crossing clowds occured (Jarolím et al. 2010).

The daytime increase of fish biomass over gentle bottom slope and higher depths was unexpected and the correlation of bottom slope can be probably caused by the general preference of mild sloped habitats during day (Scheuerell and Schindler 2004). The latter, is coupled with the preference of offshore habitats during day; however the depths are in this part of reservoir distributed both, farther offshore and near highly steeped bank, because the original river bed (i.e. highest depths) is going close to the shore. The night positive effect of steep slope is probably consequence of the night horizontal movements close to the shore. Part of the openwater community migrates to the shallow inshore areas (Říha et

al. subm.), but substantial portion remains offshore and here present the steep sloped areas the nearest impresion of „littoral" which is probably by some fish still prefered at night. This movements to the structured littoral is probabaly coded in the originally riverine fish populatine but is probably maladaptive under reservoir conditions (Fernando and Holčík 1991; Muška et al. 2013). Aggregating individuals near the steep banks can probably satisfy the abovementioned needs together with decreasing the inprofitability of desertation the favourable ofshore feeding habitats by lower travel expenditures in comparison with individuals migrating to the more distant shallow littoral (Muška et al. 2013, this study).

Generally, the observed differences in regression signs of the most significant factors between day and night led us to the connection of the changes of offshore spatial distribution patterns to the diel horizontal migration as the most important driving factor.

During the standard hydroacoustic surveys focus on fish stock assessment is being usually applied larger sampling scale (Draštík et al. 2009; Emmrich et al. 2010; Guillard and Verges 2007) summing the local variability and does not allow to detect the fine scale fish distribution pattern (George and Winfield 2000; Kalikhman et al. 1995). Observing changes of spatial distribution patterns on the smaller (local) scale is assumed to be more demanding on the sampling techniques, because it is necessary to follow more frequent and faster processes than on large scale and probably derived by faster and gentle changes of resource availability (Rinke et al. 2009; van Moorter et al. 2013). Although other studies focused on the offshore assemblages in relation to environmental variables failed to found any relationship (Simard et al. 1993; Georgakaracos and Kitsiou 2008), studies using similar covariates but different model approaches and whole lake scale explained comparable amount of variability (Rinke et al. 2009).

It is essential to state that correlation of spatial distribution pattern with environmental covariates is dependent on selection of appropriate variable, its nature and sampling density. The latter is probably the crucial because there are only few easily available variables on comparable spatiotemporal scale with continuous and detailed hydroacoustic data. Certainly, increasing of the number of relevant covariates, especially more dynamic parameters sampled on the similar temporal scale can improve the prediction performance of spatial model in the future. Incorporation of internal triggers such as population size, age structure, fish conditions, diversity and behaviour that are too complex to be included in current distribution models can be helpful in future (Planqué et al. 2011).

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PAPER IV

Two step estimation for Neyman-Scott point process with inhomogeneous cluster centers

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Two step estimation for Neyman-Scott point process with inhomogeneous cluster centers

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Abstract This paper is concerned with parameter estimation for the Neyman-Scott point process with inhomogeneous cluster centers. Inhomogeneity depends on spatial covariates. The regression parameters are estimated at the first step using a Poisson likelihood score function. Three estimation procedures (minimum contrast method based on a modified K function, composite likelihood and Bayesian methods) are introduced for estimation of clustering parameters at the second step. The performance of the estimation methods are studied and compared via a simulation study. This work has been motivated and illustrated by ecological studies of fish spatial distribution in an inland reservoir.

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1 Introduction

This work has been motivated by ecological studies of spatial distribution of fish population in an inland reservoir. Important questions that can be addressed are how the fish interact with each other on a small scale and how fish density is influenced by recorded covariates. In recent years new acoustic techniques allowed to record the fish positions along a trace of boat, which can be viewed as two dimensional point process (Simmonds and MacLennan 2005). One dimension corresponds to the trace of the boat and the second is the horizontal distance of the fish to the boat measured by acoustics. The data covariate consists of four parts: depth, distance from the bank, steepness of the bottom and light radiation.

In this paper, we model fish positions by the inhomogeneous Neyman-Scott process. The clusters correspond to fish families or shoals which keep together (Pitcher 1979). The models of optimal shoal size suggest that they are homogeneous under similar environmental conditions (Bertram 1978). Since the investigated part of the reservoir is a central part of the reservoir where only small changes of resources occur, the sizes of shoals are assumed to be homogeneous, but the occurrence of fish shoals is assumed to be inhomogeneous. Therefore this situation is modeled by inhomogeneous cluster centers, which is introduced in Sect. 2.

Since the likelihood-based inference for inhomogeneous point process models is computationally very demanding and not straightforward to implement (Møller and Waagepetersen 2004, 2007; Waagepetersen 2007), we focus here on two-step estimation methods. This algorithm for inhomogeneous Neyman-Scott process with second order intensity reweighted stationarity (Baddeley et al. 2000) is described in Waagepetersen (2007) and Waagepetersen and Guan (2009). The possibilities for two step estimation

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CURRICULUM VITAE

Milan Muška was borned on 12 November 1981 in Příbram, Czech Republic. After he finished secondary school (Gymnázium pod Svatou Horou), he started to study at the Faculty of Science, University of South Bohemia in České Budějovice. In 2003, he successfully defended his Bachelor thesis (Phylogenetic Interpretation of Ontogeny Pigmentation Patterns in Central American Cichlids; supervisor RNDr. Jindřich Novák Ph.D.). He graduated at the same faculty in 2007 – diploma in Zoology. His Master thesis was focused on „Ontogeny of coloration patterns in Neotropical cichlids of the Tribe Heroini (TELEOSTEI: CICHLIDAE: CICHLASOMATINAE)" (supervisor RNDr. Jindřich Novák Ph.D.) and was awarded by dean's award for scientific excellence. In the same year, he started his Ph.D. study in Zoology at the same faculty (supervisor Prof. Jan Kubečka CSc.) and became the member of Fish Ecology Unit (www.fishecu.cz) established at the Institute of Hydrobiology in České Budějovice. He focused his interest mainly on fish spatial distribution, behavior, diel migrations and hydroacoustic methods. He also participated in scientific research of many freshwater reservoirs and lakes in Czech Republic, Austria and Kenya. From 2011, he also works partly at the Agency for Nature Conservation of the Czech Republic where is the responsible person for coordination of monitoring and evaluation of status of fish species under Directive 92/43/EHS.