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Complementarity of two high-resolution spatiotemporal methods (hydroacoustics and acoustic telemetry) for assessing fish distribution in a reservoir

Complémentarité de deux méthodes à haute résolution spatio-temporelle (l'hydroacoustique et la télémétrie) pour évaluer la distribution spatiale des poissons dans un réservoir

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Abstract – The complementarity of two high-resolution spatiotemporal acoustic methods, telemetry and hydroacoustics, was evaluated during the same time window to obtain fish distribution in a canyon-shaped reservoir, the Bariousses Reservoir (France). These methods act at an individual scale for telemetry and a community scale for hydroacoustics. The temporal scales are also different: telemetry offers continuous and long-term monitoring while a “snapshot” view is given by hydroacoustics. Day and night hydroacoustic surveys were carried out in this reservoir, during a 24-hour period in spring, using vertical and near-surface horizontal beaming. During this time window, 11 adult fish (length: 22–57 cm) from three species (roach, perch, and pikeperch) were tracked by telemetry. Four metrics were calculated with data collected by application of the two methods: distance to the nearest bank, distance to the tributary, fish depth, and bottom depth at the location. The contrasting (distance to the nearest bank, bottom depth) or partially similar results (distance to the tributary, fish depth) can be explained by the limitations associated with each method. The results obtained with telemetry are very sensitive to the species composition and the size of the tagged fish. The number of fish located in the epibenthic areas of the reservoir can be underestimated by hydroacoustics. This preliminary case study highlights that these methods act in a complementary way and their simultaneous use can provide better information on fish spatial distribution.

***Keywords* –** fish; acoustic sampling methods; spatial distribution; lacustrine ecosystem.

Résumé – La complémentarité de deux méthodes à haute résolution spatio-temporelle : la télémétrie et l'hydroacoustique, a été examinée sur une même fenêtre temporelle, pour analyser la distribution des poissons dans le réservoir des Bariousses (France), un réservoir allongé en forme de canyon. Ces méthodes agissent à l'échelle de l'individu pour la télémétrie et à l'échelle de la communauté pour l'hydroacoustique. Les échelles temporelles sont aussi différentes : acquisition en continu sur de longues périodes en télémétrie et de manière instantanée pour l'hydroacoustique. Des parcours de jour et de nuit ont été réalisés dans cette retenue, sur une période de 24 heures, au printemps, en utilisant un sondeur vertical et horizontal. Durant cette période, 11 poissons de taille adulte (tailles allant de 22 à 57 cm) appartenant à trois espèces différentes (gardon, perche et sandre) ont été suivis par télémétrie. Quatre métriques ont été calculées à partir des données collectées par l'utilisation des deux méthodes : la distance à la rive la plus proche, la distance au tributaire, la position individuelle au sein de la colonne d'eau et la profondeur du fond correspondante. Les résultats contrastés (distance à la rive la plus proche, profondeur du fond) ou partiellement similaires (distance au tributaire, position individuelle au sein de la colonne d'eau) révélés par les analyses s'expliquent par les limites inhérentes aux méthodes. Les résultats obtenus par télémétrie sont très sensibles aux espèces et à la taille des poissons marqués. La fréquentation des zones épibenthiques peut être sous-estimée par l'hydroacoustique. Cette première étude de cas montre que ces méthodes agissent de manière complémentaire et qu'une meilleure description de la distribution spatiale des poissons peut être obtenue de par leur utilisation simultanée.

***Mots-clés* –** poisson ; méthodes d'échantillonnage acoustiques ; distribution spatiale ; écosystème lacustre.

1 Introduction

Understanding the spatial distribution of fish populations remains a challenging fundamental issue in lakes ecology and a prerequisite to freshwater fishery management and conservation strategies (Cooke *et al.*, 2016).

The spatial distribution of fish within a waterbody is not random; fish exhibit spatial patterns related to the accomplishment of their vital functions –*i.e.,* reproduction, feeding, resting– requiring different environmental conditions (Lucas *et al.*, 2001).

Fish habitat selection depends on numerous abiotic and biotic factors that differ among species and ontogenic stages. First, fish search for a habitat with suitable conditions in terms of temperature and oxygen concentrations (Fry, 1971; Kubečka & Wittingerova, 1998; Brosse *et al.*, 1999b; Lucas *et al.*, 2001; Jàrvalt *et al.*, 2005); second, food availability and predation drive their distribution (Savino & Stein, 1989; Gaudreau & Boisclair, 1998; Eklov & VanKooten, 2001; Gilliam & Fraser, 2001). Finally, during the reproductive period, physiological requirements are different and impact the distribution (Gillet, 2001).

To find optimum habitat conditions, fish complete circadian migrations in both directions: diel vertical migration (DVM) and diel horizontal migration (DHM) (Lucas *et al.*, 2001). DVMs are cyclic changes in the fish position in the water column, while DHMs are their movements between inshore and offshore areas. However, the intensity and direction of migration depend on the ontogeny, species, and season. For instance, juveniles and adults generally migrate in opposite horizontal directions: juvenile fish perform night offshore migration (Romare *et al.*, 2003; Gliwicz *et al.*, 2006), whereas adults perform night inshore migration (Kubečka, 1993; Kubečka & Duncan, 1998; Zamora & Moreno-Amich, 2002; Jacobsen *et al.*, 2004; Říha *et al.*, 2011). Migration does not concern the entire population, and plasticity in the pattern of fish migration can occur (Eriksson, 1978; Busch & Mehner, 2012; Mehner & Kasprzak, 2011; Říha *et al.*, 2015).

The spatial distribution of the fish community is also structured along longitudinal and vertical gradients. In the majority of reservoirs, fish abundance and biomass decrease from the main tributary toward the dam (Brosse *et al.*, 1999a; Świerzowski *et al.*, 2000; Vašek *et al.*, 2003, 2004, 2006; Prchalová *et al.*, 2008) because of the riverine origin of fish fauna and a gradient of productivity (Vašek *et al.*, 2006). In mesotrophic or eutrophic reservoirs during spring and summer, fish are usually distributed in shallow depths, because of the attraction of warmer water and to avoid deoxygenated hypolimnion (Kubečka & Wittingerova, 1998; Čech & Kubečka, 2002; Vašek *et al.*, 2004). In cold and oligotrophic lakes, salmonid fish habitats are mainly in the deep cold water, below the thermocline (Guillard *et al.*, 2006; Yule *et al.*, 2013).

Improvements in technology have allowed scientists and managers of the waterbodies to perform more spatial behavioral fish studies (Lucas & Baras, 2000; Cooke *et al.*, 2016). All the methods dedicated to analyzing the spatial distribution of fish have intrinsic, environmental, and specific limitations. The spatiotemporal techniques available today are so diverse and with such high performances that most of the problems can be tackled by choosing the appropriate method or by combining tools and approaches (Lucas & Baras, 2000). Numerous studies have provided fish spatial distributions by coupling different methods (Tab. 1).

Telemetry, using electronic tags, is a capture-dependent method consisting in transmitting information to receivers (Cooke *et al.*, 2012), while hydroacoustics is a capture-independent method defined by the use of echosounding in water to measure the distribution and abundance of fish (Rudstam *et al.*, 2012); both methods provide high-resolution spatiotemporal data (Lucas & Baras, 2000; Arrhenius *et al.*, 2000; Belcher *et al.*, 2002; Rudstam *et al.*, 2012; Cooke *et al.*, 2012, 2013; Hussey *et al.*, 2015). Fish movements can be approached in four dimensions: horizontal (2D), vertical (depth, 3D), and over time (4D).

To our knowledge, probably because of the system perturbation or of the technical difficulty of implementation, there are only a few studies that used hydroacoustics and acoustic telemetry at the same time to describe fish spatial distribution. They can be considered as complementary methods allowing to gather better information on habitat use than each method separately. Telemetry helps locate individuals that were previously caught. Individuals are usually adults, and are limited in number. Hydroacoustics provides information

Table 1. Examples of studies using two or more different methods to study fish distributions in freshwaters.

Tableau 1. Exemples d'études reportant l'utilisation de deux ou plusieurs méthodes différentes pour étudier la distribution des poissons dans les milieux d'eaux douces.

Methods	References
Hydroacoustics and netting	Baldwin & Polacek, 2011; Muška *et al.*, 2013
Hydroacoustics, gillnetting and others (scuba diving or ichthyoplankton net)	Imbrock *et al.*, 1996; Prchalová *et al.*, 2003,
Hydroacoustics and net towing	Kratochvil *et al.*, 2010
Hydroacoustics and radio telemetry	Grimardias *et al.*, 2017
Hydroacoustics and acoustic telemetry	Lyons & Lucas, 2002; McGrath *et al.*, 2003; Dunlop *et al.*, 2010
Acoustic telemetry and gillnetting	Smith *et al.*, 2011
Radio telemetry and mark-recapture	Auer, 1999
Radio or acoustic telemetry, PIT tags	Caswell *et al.*, 2004; Binder & McDonald, 2007
Mark-recapture and PIT tags	Caroffino *et al.*, 2009
Gillnetting and electrofishing	Mehner *et al.*, 2005
Beach seining, electrofishing and purse seining	Říha *et al.*, 2015

on the distribution of the whole fish community, without distinguishing between species (Lucas & Baras, 2000). The temporal scale of the study also differs: hydroacoustics is instantaneous, acting like a "snapshot", whereas telemetry operates autonomously for extended periods (over a year), without additional maintenance need or battery change, allowing for continuous tracking (Klimley *et al.*, 1998; Heupel *et al.*, 2006; Baktoft *et al.*, 2012; McCauley *et al.*, 2014).

The main objective of this study was to test the complementarity (individual *vs.* community level) of these two methods to assess diel fish distribution during the same time window. The study was conducted in a canyon-shaped reservoir, the Bariousses Reservoir (France), with a main tributary. In this reservoir the depth variation and elongated morphology suggest an heterogeneous spatial distribution of organisms along the longitudinal axis, between littoral and pelagic zones, and a vertical distribution in the water column (Duncan & Kubečka, 1995; Jurajda & Regenda, 2004).

2 Material and methods

2.1 Site description

The study was carried out in the Bariousses Reservoir, west central France (45.33°N, 1.49°E) (Fig. 1), an 80.9 ha impoundment of the Vézère River operated by Electricité de France (EDF). It is an elongated (3500 m long and 218 m wide at the mean water level), narrow lake (mean and maximum depths are 7.1 m and 18.9 m, respectively). The reservoir is monomictic, with a thermal stratification from summer to autumn (Roy, 2014).

Fish distribution in reservoirs is usually determined by the upstream-downstream gradient of the chemical and physical parameters (Brosse *et al.*, 1999a; Świerzowski *et al.*, 2000; Vašek *et al.*, 2003, 2004, 2006; Prchalová *et al.*, 2008). We defined two subareas with specific hydrology, substratum

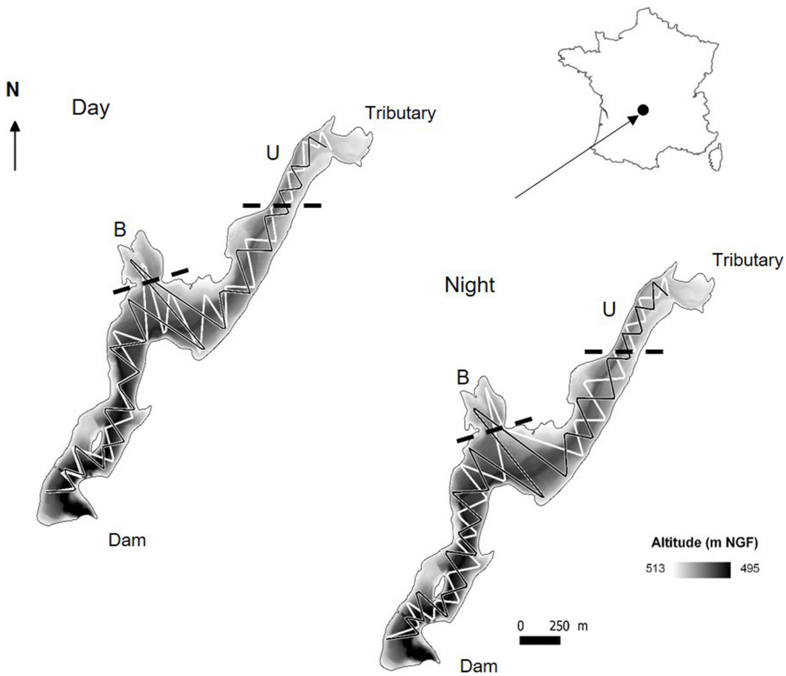

Fig. 1. Localisation and bathymetry (Altitude scale); day and night hydroacoustic zig-zag (white line: way-on; black line: way-back) and the two defined zones (U = upstream, B = Bay) and the tributary and dam positions. Maps were produced with QGIS 2.12.0, courtesy of EDF.

Fig. 1. Localisation et bathymétrie (échelle altitudinale) ; parcours en zig-zags effectués de jour et de nuit (ligne blanche : aller ; ligne noire : retour) et les deux zones délimitées (U = la partie amont, B = la baie) ainsi que les positions du tributaire et du barrage. Les cartes ont été réalisées avec QGIS 2.12.0 avec la permission d'EDF.

and low depth within the reservoir that may drive fish distribution: the upstream (sandy beach/mud with stumps) and the bay area (sandy beach/mud) (Roy, 2014) (Fig. 1).

During the survey, on 27 May 2013, the water level altitude was 512.5 m, corresponding to the 0.85 quantile over 2 years of measurements, which is high; a vertical profile of temperature was measured using a NKE thermometer installed in the deepest part of the reservoir (Fig. 2). A standardized gillnet survey (CEN, 2005) was performed at the end of August in 2010 (Roy, 2014), which described the fish population of the reservoir. The reservoir is inhabited by 12 species, four of them represent the highest catch-per-unit effort: roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernuus*), perch (*Perca fluviatilis*), and pikeperch (*Sander lucioperca*) (Roy, 2014). The fish length (TL: total length) distribution obtained by gillnetting showed a main peak at 15 cm. Electrofishing performed in the littoral zone, in spring 2011, revealed a fish length distribution mode of 10 cm (Fig. 3) (Roy, 2014). The reservoir has not been drained since 1997, and therefore

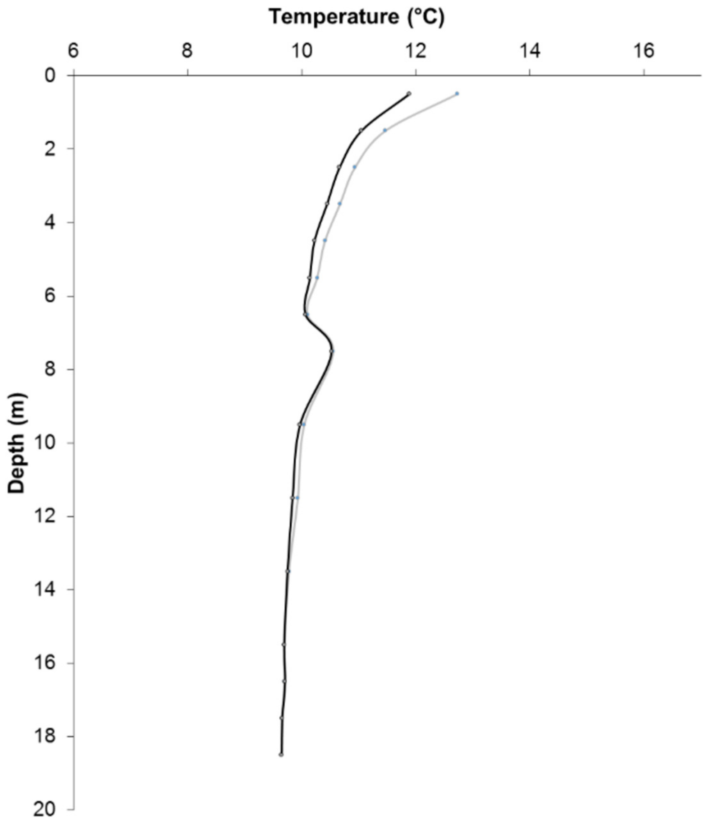

Fig. 2. Day (gray line) and night (black line) temperature profiles obtained on 27 May 2013. Each dot symbolizes the depth of an NKE thermometer.

Fig. 2. Profils de température obtenus de jour (ligne grise) et de nuit (ligne noire) le 27 mai 2013. Chaque point représente la profondeur d'un thermomètre NKE.

we assumed that the fish population has remained similar in terms of diversity and size composition.

2.2 Hydroacoustic survey

Hydroacoustic measurement was conducted on 27 May 2013 in the daytime and nighttime, at an approximate speed of 8 km.h^{-1}. Given the small size and morphology of the reservoir, day (15:19–17:16 coordinated universal time – CUT) and night (20:50–22:26 CUT) zig-zag trajectories were used, on the way-on and way-back (two replicates) (Guillard & Vergès, 2007) (Fig.1). The trajectory was determined before the study to obtain representative data according to Aglen (1989). In our case, the degree of coverage, *i.e.,* the length of all transects divided by the square root of the reservoir area, is equal to 13.23 for the day survey and 13.12 for the night one.

A Simrad EK60 split-beam echosounder, 120 kHz frequency, controlled by the Simrad ER 60 (version 2.2.0)

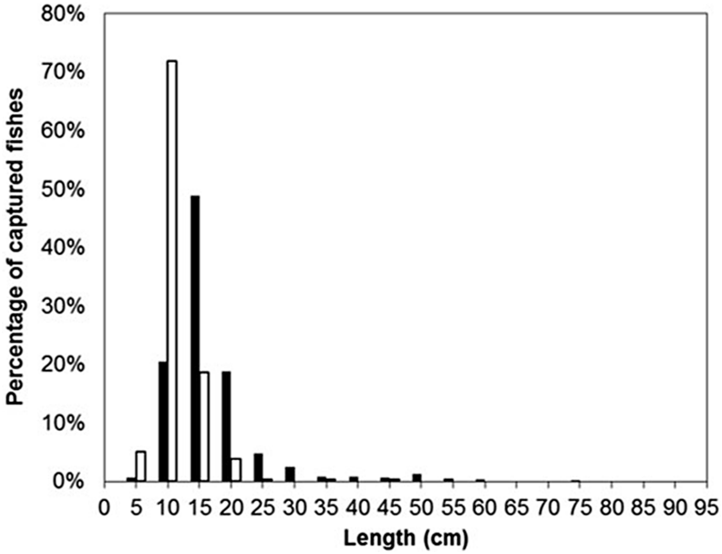

Fig. 3. Total length distribution of fish obtained by gillnetting (black) (CEN, 2005) at the end of august 2010 and by electrofishing (white) in spring 2011.

Fig. 3. Distribution des longueurs totales des poissons capturés par pêche aux filets (en noir) (CEN, 2005) obtenue à la fin du mois d'août 2010 et par pêche électrique (en blanc) au printemps 2011.

program and connected to a GPS, was used for data acquisition. Two transducers, an elliptical one (ES 120-2.5 × 10, nominal beam angle 10° × 2.5 ° at −3 dB, beaming horizontally) and a circular one (ES 120-7C, nominal beam angle of 7° at −3 dB, beaming vertically), were mounted on a platform on the side of the boat. The elliptical transducer was tilted 3° downward and the circular transducer beam was set 0.5 m below the surface. The pulse duration was 0.256 ms (Godlewská *et al.*, 2011), emitting four pulses per second, with power set at 100 W. Each transducer was calibrated once a year, using standard targets (Foote *et al.*, 1987). All acoustic data were analyzed from the echograms using post-processing software (Sonar5-Pro, version 6.0.3, Balk & Lindem, 2014). To exclude the transducer nearfield and avoid the blind area close to the sounder (Simmonds & MacLennan, 2005), acoustic data within 2 m were excluded for the vertical beaming (Yule *et al.*, 2013) and data within 4 m were excluded for the horizontal beaming, as recommended by Draštík *et al.* (2009). As the reservoir was at the beginning of the seasonal stratification process (Fig. 2), the problem of beam bending is negligible (Simmonds & MacLennan, 2005). Data were processed up to the 50-m range for the horizontal beaming, corresponding to a water layer of approximately 4.8 m below the surface. With these settings, no target was simultaneously detected by both horizontal and vertical devices. For vertical beaming, a bottom 0.5 m layer was delimited to avoid the inclusion of bottom detection in analyses and its accuracy was checked. All files were also checked for undesired non-fish echoes such as air bubbles, submerged macrophytes, debris, and buoys, and were deleted from the echograms (Emmrich *et al.*, 2012).

The hydroacoustic analysis was based on target counting, suitable for use when fish density is low, clear fish tracks are discernible within a noise, and when reliable GPS data are available (Draštík *et al.*, 2014). The latitude, longitude, and depth (m) of target positions were extracted from fish tracking.

For the vertical beaming, classic automatic tracking was applied. For the horizontal data, the cross-filter tracker (CFT) method (Balk & Lindem, 2014) was preferred instead of manual tracking, which is a labor-intensive and subjective process (Balk & Lindem, 2000), and instead of automatic tracking, which tends to generate fish-like tracks from noise echoes and to split tracks from fish. The CFT method improves automatic tracking in cases where single-echo detection (SED) echograms have low track quality combined with many noise-based detections. CFT encircles the echoes to be combined into track in an automatic way. The CFT used the cross-filter detector (CFD) (Balk, 2001) to improve track quality and to reduce erroneous detections in data with a low signal-to-noise ratio (SNR). For this survey, the CFD settings that provided the best results for tracking fish were for the detector (step1): Foreground filter = height 5 and width 1; Background filter = height 55 and width1; Offset +8 dB (Tušer *et al.*, 2009). For the evaluator (step 2), trace length and trace area were used. Minimum and maximum values for the trace length were 1–250 pings (Rakowitz *et al.*, 2008), and for the area, 8–400 samples in a detected region. The settings were chosen to find a compromise between rejected unwanted single echoes and to guarantee the maintenance of relevant parts of the fish traces containing a sufficient number of unaffected single echoes to size the fish properly. All fish tracks were manually checked.

For the vertical beaming, fish lengths were estimated using Love's (1971) equation (Emmrich *et al.*, 2012). To correct the target detection angle during mobile horizontal surveys, the deconvolution method is mainly used, based on a random distribution of fish (Kubečka *et al.*, 2009; Godlewská *et al.*, 2012), but does not allow access to the individual information, only to the length structure. However, this assumption is not true in the narrow parts of reservoirs, similar to a riverine environment, which then can lead to TS (target strength) over-estimations (Tušer *et al.*, 2009). In these parts, fish are mainly distributed with a side-aspect to the acoustic beam (Tušer *et al.*, 2009). The Bariousses Reservoir is smaller than the Rimov Reservoir (Czech Republic) where fish distribution was assessed to be in a non-random way and then positioned 90° to the beam. Owing to the riverine morphology of the Bariousses Reservoir, the fish distribution was considered to be generally positioned at 90° to the beam angle, and thus the horizontal side-aspect equation (TS side) for all the European fish species was used

(Eq. (1)) (Frouzová *et al.*, 2005). Each detected fish position was calculated using the following equation:

Equation (1): $TS_{side} = a \log_{10} TL + b$, where TS is in dB, and TL is the total length (mm), *a* is 24.71 and *b* is −89.63.

TS was recorded by echosounding and TL was calculated from the inverse equation.

Thresholds were applied to both horizontal and vertical beaming for comparability of the two sampling modes. As the data were very noisy, the TS threshold was set at −50 dB to avoid fish less than 5 cm in size; according to Love (1971), dorsal aspect regression (Simmonds & MacLennan, 2005) was chosen for vertical beaming, and according to Frouzová *et al.* (2005), side-aspect regression was chosen for horizontal beaming. This threshold was also chosen to avoid coarse suspended particles. Disproportionately strong echoes from acoustic phenomena were not identified as outliers by CFD (Rakowitz *et al.*, 2008). These outliers were removed so as not to oversize the fish, which were identified by a boxplot graphical technique (Tukey, 1977).

Prior to the hydroacoustic survey, we checked that the hydroacoustic system did not affect the telemetry system or make it collapse because of the possible interferences between the echosounder pulse emission and the tags of the telemetry system.

2.3 Telemetry survey

The telemetry dataset was considered on the same time windows as the hydroacoustics.

2.3.1 Tracking system

An array of 40 underwater VR2W 69-kHz omnidirectional acoustic receivers (VEMCO) was deployed in January 2012 throughout the reservoir. The receiver deployment took into account the bathymetry, the shape of the reservoir, and the maximum intensity of water-level fluctuations to avoid the receivers being beached. The receivers were positioned at an average of 150 m apart (range was 72–223 m) and at an average depth of 6 m (range from 2 m to 15 m) (Roy *et al.*, 2014).

The VEMCO Positioning System (VPS) (Smith, 2013) was used to calculate the fish positions in the horizontal plane. Only positions with an HPE (Horizontal Position Error, a parameter provided by the VPS, Smith, 2013) less than 20 were retained to filter false locations. This corresponded to about 86% of the full position dataset with a mean error of 3.5 m (Roy *et al.*, 2014). The depth of the VPS positions was measured with a pre-calibrated hydrostatic pressure sensor (accuracy: 2.5m).

2.3.2 Fish tagging

A total of 143 fish, mainly adults (22.0–62.9 cm), were tagged during January 2012-April 2013 period with VEMCO V9P-2L or V8-4L acoustic transmitters (mean interval burst of 90 or 120 s) in the context of a fish habitat analyze (Roy, 2014). Fish were captured in Bariousses Reservoir with gillnets set at dawn, day, and dusk for maximally 2 hours or by specialist anglers. Due to the low catch of pike-perch, the sample was completed with fish from an extensive pond aquaculture and introduced into the reservoir after marking. Once caught, fish were individually anesthetized, and the transmitter was surgically inserted in the peritoneal cavity. Then, fish were placed in an oxygenated tank to recover during at least a few hours to one night which also enabled to highlight abnormal behaviours (details in Roy, 2014) before being released close to their capture site. Not to bias the analysis with behaviors that could be linked to the surgery, only positions recorded at least 2 days after the release were retained (Bridger & Booth, 2003).

Given the theoretical battery lifetime, fish mortality and the definitive exit of some individuals from de detection zone, only 21 of the 143 fish were potentially detectable during the hydroacoustic campaign. Individual tracked during the time window of the hydroacoustic survey and belonging to the most represented species in the fish community according to gillnetting (Roy, 2014) were retained in the analysis *i.e.* three roach, six perch, and two pikeperch. Due to the low number of individuals detected during the hydroacoustic campaign, the species analysis was performed for illustrative purposes only.

2.4 Spatial data

The fish spatial distributions were described using R 3.3.1 statistical software (R Development Core Team, 2016). All the fish positions retained in the analysis were mapped. The percentage of fish positions in two areas, the upstream part and the bay part, was calculated for the two methods. To obtain the bottom depth at the fish positions, the reservoir was discretized into squares of $10\,m \times 10\,m$ and the percentage of the positions per square was calculated. For these squares, the bottom depth was calculated with bathymetric data measured *via* a multibeam sounder giving a $2\,m \times 2\,m$ resolution map (EDF). When the position of the square center was discriminated to be out of the water surface, the depth was approximated by replacing the missing value with the mean bottom depth of the 5% lowest values of the water column height. The Euclidian distance of individual fish to the bank and to the tributary was calculated with the rgeos package (Renard & Bez, 2005).

2.5 Split of fish community by length

The fish marked by telemetry were mainly adults, whereas those recorded by hydroacoustics covered all the range size of the community. As fish have different ecological preferences, but also behavior, based not only on species but also on ontogeny (Říha *et al.*, 2015), especially between juveniles and adults, the fish detected by hydroacoustics were split into two groups: fish < 20 cm and fish ≥ 20 cm.

2.6 Fish positioning and statistical analyses

Four metrics related to fish position were calculated using the two datasets (hydroacoustics and telemetry): distance between the individual position and the nearest bank, distance to the tributary, fish depth, and bottom depth at the location. The fish distribution from hydroacoustic data was analysed for small and large fish groups, and for

Table 2. Number of hydroacoustic-tracked fish obtained with horizontal and vertical beaming during the day and night survey. The number of fish with TL < 20 cm and TL ≥ 20 cm is also shown.

Tableau 2. Nombre de poissons détectés en hydroacoustique avec les sondeurs horizontaux et verticaux pendant les campagnes de jour et de nuit. Le nombre de poissons avec une LT < 20 cm et LT ≥ 20 cm est aussi présenté.

	Horizontal		Vertical		Total	
	Day	Night	Day	Night	Day	Night
All fish	489	563	23	16	512	579
Fish < 20 cm	357	461	22	13	379	474
Fish ≥ 20 cm	132	102	1	3	133	105

the telemetry data the fish distribution was set according to species identification. All distributions being not normal, Wilcoxon non-parametric tests were used to compare the different spatial metrics.

The statistical analyses were performed with R 3.3.1 statistical software (R Development Core Team, 2016).

3 Results

A total of 1,091 individual fish (Tab. 2) were detected during the day and the night surveys *via* the hydroacoustic method, mainly recorded by horizontal beaming (96% of detections). The method showed a 13% increase in the number of fish detected during the night owing to an increase in the detection of small fish compared with large fish that are detected less often.

By using telemetry, 361 individual positions from the three roach, six perch, and two pikeperch were recorded during the hydroacoustic survey period (Tab. 3). At night, the total number of recorded positions decreased (two perch not detected).

Fish length distributions obtained during the day and night from hydroacoustic surveys (Fig. 4) showed a mode at 10 cm. They were analogous to the one obtained by electrofishing (Fig. 3) performed during a similar period. The mode obtained by gillnetting survey performed later, in autumn, was higher by only 5 cm.

3.1 Global fish distribution

Fish distributions (number of individual positions recorded by hydroacoustics and by telemetry) were shown using repartition maps (Fig. 5). With hydroacoustics, fish were detected in all parts of the lake, *i.e.,* in littoral and pelagic zones of the reservoir. During the day, a higher percentage of fish was observed close to the tributary in the upstream part of the lake (35.9% during the day and 10.9% during the night). At night, the highest proportion of fish (22.4%) was recorded in the bay, in the intermediate part of the reservoir.

Telemetry positions were less homogeneously distributed than with hydroacoustics. Indeed, no position was recorded by the telemetry method in the center of the reservoir. During the day, the telemetry positions were scattered along and close to the left bank and no fish was observed in the upstream part, while during the night

Table 3. Total length (TL, cm) and number of individual positions of fish recorded by the telemetry method during the hydroacoustic surveys. The presence (yes) or absence (no) of a pressure sensor allowing the fish position in the water column to be defined is noted.

Tableau 3. Longueur totale (LT, cm) et nombre de positions individuelles de poissons enregistré par télémétrie pendant la campagne d'hydroacoustique. La présence (oui) ou l'absence (non) d'un capteur de pression permettant de déterminer la position du poisson au sein de la colonne d'eau est renseignée.

Transmitter (mean burst interval (s), type of transmitter)	Species	Pressure sensor	Total length (cm)	No. Posit. Day	No. Posit. Night
T123 (120, V8-4L)	roach	no	25.4	27	26
T124 (120, V84L)	roach	no	23.6	7	12
T125 (120,V8-4L)	roach	no	22	17	14
T56 (90, V9P-2L)	perch	yes	43	44	/
T112 (120, V9P-2L)	perch	yes	48.6	18	18
T114 (120, V9P-2L)	perch	yes	37.9	1	/
T115 (120, V9P-2L)	perch	yes	41.5	26	15
T117 (120, V9P-2L)	perch	yes	32.2	20	10
T118 (120, V9P-2L)	perch	yes	40.5	15	38
T15 (90, V9P-2L)	pikeperch	yes	42.8	4	1
T111 (120, V9P-2L)	pikeperch	yes	57	25	23
			Total	204	157

one individual was detected in this part and accounted for 24.2% of the telemetry positions. Two fish were positioned in the bay at daytime and one during the night (accounted for 31.86% of positions during the day and 14.68% during the night).

3.2 Distance to the tributary

The results obtained with the two methods were different according to the period considered.

During daytime, distances to the tributary estimated by telemetry were higher than those calculated with hydroacoustics, whatever the size group considered ($p < 0.05$) (Fig. 6).

During nighttime, distances calculated with the whole hydroacoustic dataset and for hydroacoustic data of fish smaller than 20 cm were significantly higher than those estimated with telemetry. Conversely, the distribution of fish larger than 20 cm assessed with hydroacoustic survey did not differ to the distribution of fish obtained with telemetry ($p > 0.05$).

The diel direction pattern also differed; the telemetry positions were further away from the tributary in the day than at night ($mean_{day}$: 1,568.0 m ± 24.7; $mean_{night}$: 1,300.4 m ± 51.3). The opposite was shown with hydroacoustics; statistical tests confirmed a higher fish density in the areas close to the tributary in the daytime (Fig. 6) ($p < 0.05$; $mean_{day}$: 1,090.4 m ± 31.8; $mean_{night}$: 1,449.1 m ± 24.7) than during the night.

There was no significant difference in the distribution of hydroacoustic-detected fish sized < 20 cm and ≥ 20 cm, in the day nor at night, even if the distribution of fish ≥ 20 cm was in both cases (day and night) more spread out close to the tributary.

Regarding the distance to the tributary of the different species, only perch showed a significant diel pattern by being closer to the tributary during the day than at night (Tab. 4, $p < 0.05$).

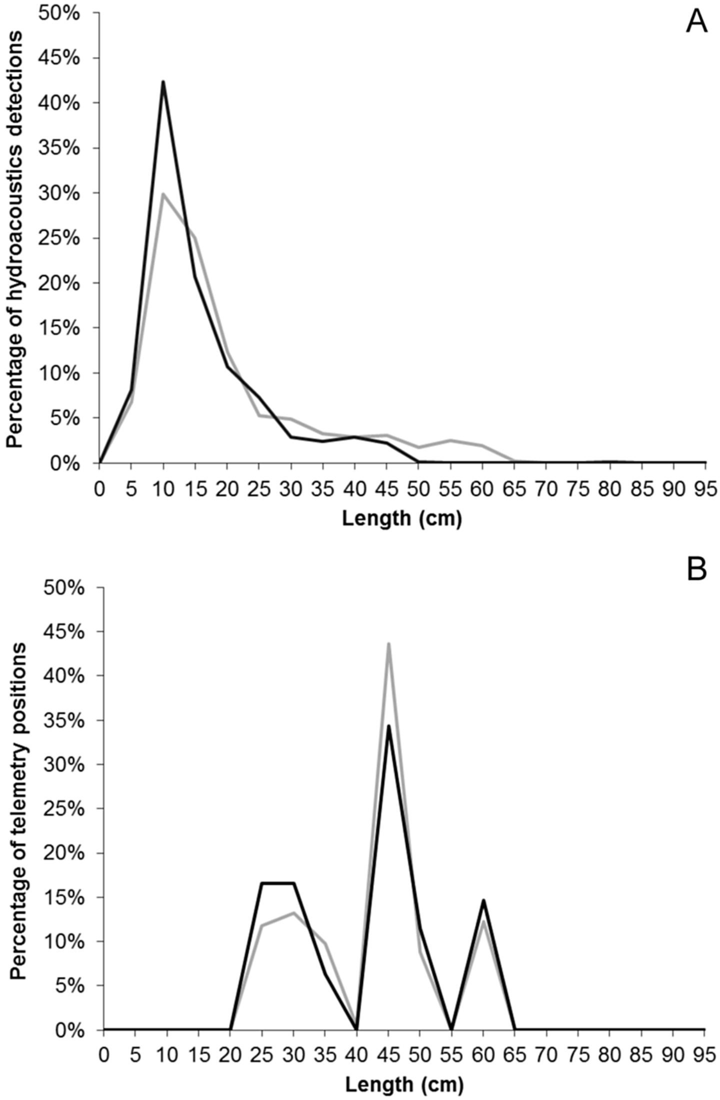

Fig. 4. Length distribution of (A) fish detected by hydroacoustics and (B) by telemetry during day (grey) and night (black) on 27 May 2013.

Fig. 4. Distribution en taille (A) des poissons obtenue à partir des données d'hydroacoustique et (B) obtenue à partir des positions en télémétrie pendant le jour (gris) et la nuit (noir) le 27 mai 2013.

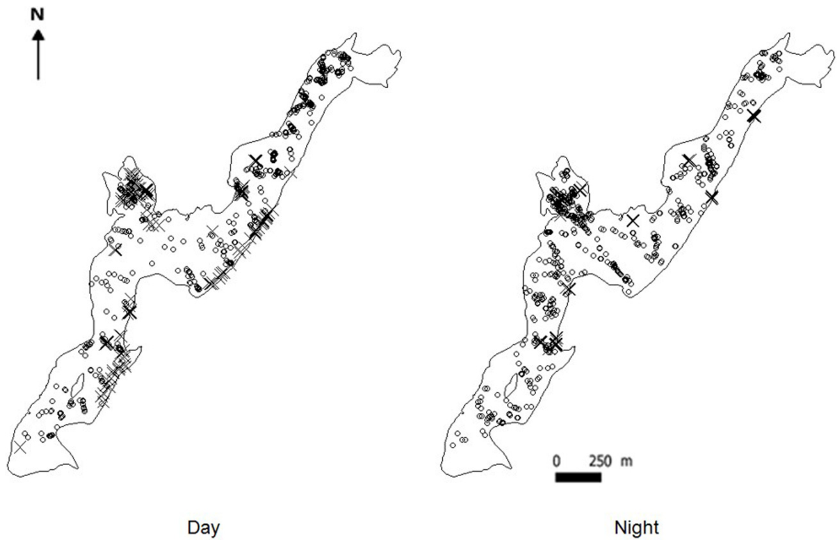

Fig. 5. Day and night spatial distribution of fish in the Bariousses Reservoir in May 2013 obtained with hydroacoustics (empty black circles) and telemetry (black crosses) methods.

Fig. 5. Distribution spatiale des poissons dans le réservoir des Bariousses obtenue de jour et de nuit par hydroacoustique (cercles noirs vides) et télémétrie (croix noires).

3.3 Distance to the bank

Statistical analysis showed that fish positions obtained with the telemetry method were closer to the bank than the ones obtained with hydroacoustics, for all the datasets considerated ($p < 0.05$) (Fig. 7). The two methods provided opposite diel patterns. Indeed, with telemetry, a greater distance was observed between the fish and the bank during the day compared with the night ($mean_{day}$: 45.5 m ± 2.1; $mean_{night}$: 38.9 ± 2.8), and the opposite was observed for hydroacoustics except in the case of large fish. The distribution of fish larger than 20 cm detected with this method did not differ significantly between day and night ($mean_{day}$: 62.0m ± 2.33; $mean_{night}$: 65.6 m ± 3.1), even if the distribution was more spread out toward the bank at night.

Global species diel pattern for marked individual was different: Perch were closer to the bank at nighttime while roach moved in the opposite direction (Tab. 3, $p < 0.05$).

3.4 Depth

Most of fish positions detected with the two methods were located in the upper water layer (< 6 m depth) and similar patterns for the diel distributions were found with the two methods; fish were deeper during the day than at night ($p < 0.05$) (Fig. 8).

Differences in depth distribution were highlighted. Most of fish detected with the hydroacoustic method were closer to the surface (for all fish: $mean_{day}$: 2.2 m ± 0.1, $mean_{night}$: 1.5 m ± 0.1) (Fig. 8) compared with the

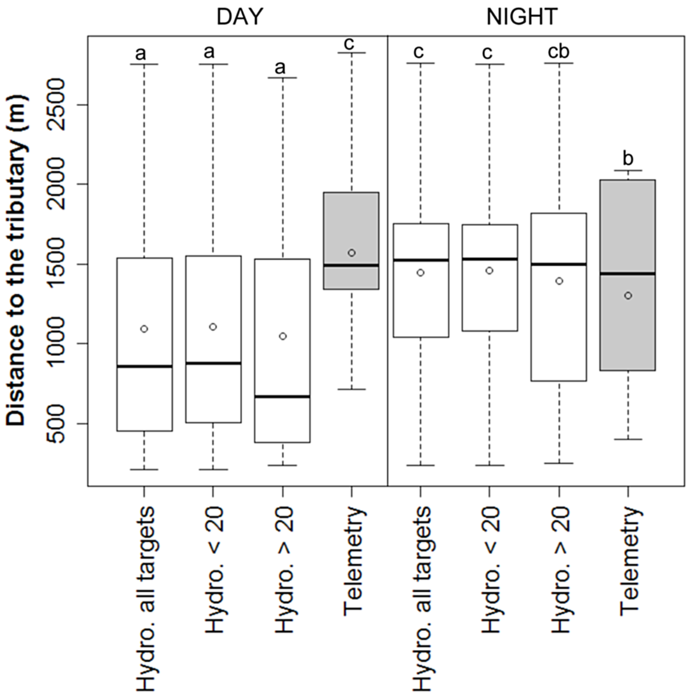

Fig. 6. Boxplots of the fish distance to the tributary obtained with hydroacoustics ("hydro.") and telemetry surveys during the day and at night. Median = dark horizontal line in bold; boxes represent 25th and 75th percentiles. Horizontal lines = maximum and minimum values. Black circles = mean values. The results of Wilcoxon test are given (variables that do not share the same letter are significantly different).

Fig. 6. Boîtes à moustaches de la distance des poissons au tributaire obtenues en hydroacoustique (« hydro. ») et en télémétrie pendant le jour et la nuit. Médiane = ligne noire horizontale en gras ; les boîtes représentent les 25 et 75$^{\text{ème}}$ percentiles. Lignes horizontales = valeurs maximale et minimale. Cercles noirs = valeurs moyennes. Les résultats du test de Wilcoxon sont donnés (les variables qui ne partagent pas la même lettre sont significativement différentes).

Table 4. Mean ± standard error distance (m) to the tributary, to the bank, and depth for each detected species by telemetry. No data are available for roach depth. The number of individuals is in parentheses.

Tableau 4. Moyenne ± erreur standard de la distance (m) au tributaire, à la rive et profondeur de chaque espèce détectée par la télémétrie. Les données concernant la profondeur ne sont pas disponibles pour le gardon. Le nombre d'individus est indiqué entre parenthèses.

		Roach	Perch	Pikeperch
Distance to the tributary (m)	Day	1,552.0 ± 81.0 (3)	1,593.9 ± 35.8 (6)	1,485.2 ± 19.6 (2)
	Night	1,578.1 ± 74.5 (3)	1,078.1 ± 79.8 (4)	1,449.1 ± 6.5 (2)
Distance to the bank (m)	Day	69.5 ± 3.9 (3)	34.6 ± 2.6 (6)	50.1 ± 0.5 (2)
	Night	81.6 ± 2.5 (3)	8.94 ± 0.8 (4)	47.4 ± 1.6 (2)
Depth (m)	Day	/	4 0. ± 1 (6)	6.4 ± 0.2 (2)
	Night	/	2.5 ± 0.1 (4)	5.8 ± 0.2 (2)

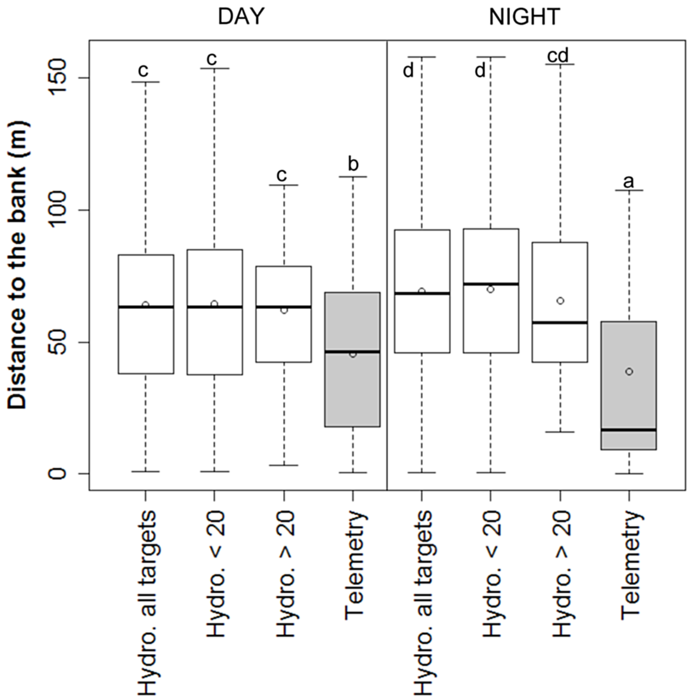

Fig. 7. Boxplots of the fish distance to the bank from hydroacoustics ("hydro.") and telemetry surveys during the daytime and at night. Median = dark horizontal line; boxes represent 25th and 75th percentiles. Vertical lines = maximum and minimum values. Red circle = mean values. The results of Wilcoxon test are given (variables that do not share the same letter are significantly different).

Fig. 7. Boîtes à moustaches de la distance des poissons à la rive obtenues en hydroacoustique (« hydro. ») et en télémétrie pendant le jour et la nuit. Médiane = ligne noire horizontale en gras ; les boites représentent les 25 et 75ème percentiles. Lignes horizontales = valeurs maximum et minimum. Cercles noirs = valeurs moyennes. Les résultats du test de Wilcoxon sont donnés (les variables qui ne partagent pas une même lettre sont significativement différentes).

depth distribution obtained *via* telemetry (mean$_{day}$: ±0.1, mean$_{night}$: 3.2 ± 0.2). In addition, fish followed with telemetry were located in epibenthic habitats whereas the hydroacoustic-detected targets were close to littoral/surface areas. The intensity of the diel shift was more pronounced for the hydroacoustic targets with no distinction between length and for fish smaller than 20 compared with the distribution of fish larger than 20 cm from telemetry and acoustics data. The < 20 cm and ≥ 20 cm distribution of hydroacoustic-detected fish did not significantly differ in the day but there were differences at night.

Compared to perch distribution in the water column, pikeperch stayed deeper whatever the time of day considered (Tab. 4, $p < 0.05$). Only perch showed a significantly different pattern between day and night ($p < 0.05$).

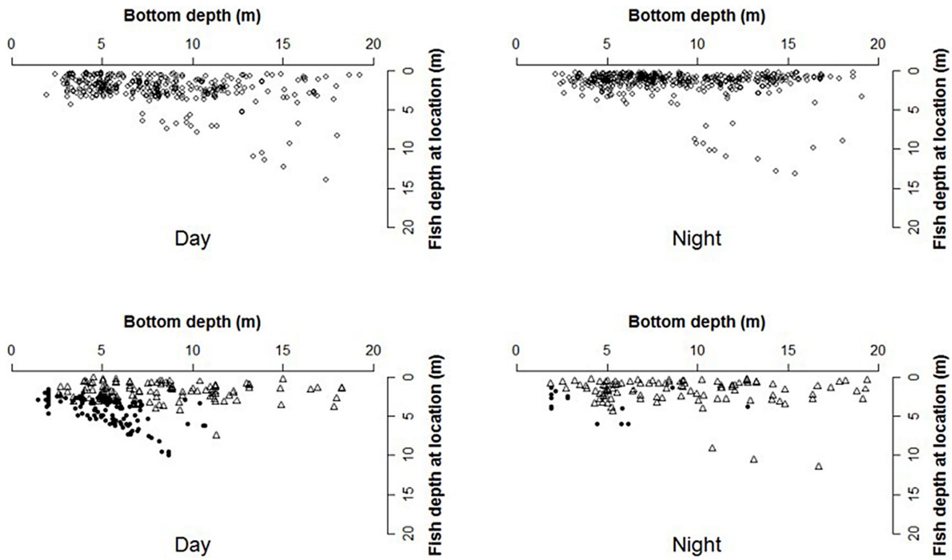

Fig. 8. Day (left) and night (right) depth plots indicating the fish position depth and bottom depth obtained with telemetry (black circles) and hydroacoustics (empty items). For the hydroacoustic method, the upper plots represent the positions of fish with a length of < 20 cm (white circles) and the bottom plots represent the positions of fish with a length of ≥ 20 cm (white triangles).

Fig. 8. Graphique représentant la profondeur des poissons et la profondeur du fond à la position des poissons, pour le jour (à gauche) et la nuit (à droite) en télémétrie (cercles noirs pleins) et en hydroacoustique (cercles blancs). Pour la méthode hydroacoustique, les graphiques du haut représentent les positions pour les poissons avec une taille < 20 cm (cercles blancs) et les graphiques du bas représentent les positions pour les poissons avec une taille ≥ 20 cm (triangles blancs).

4 Discussion

4.1 Fish horizontal distributions

In elongated reservoirs, during summer, a longitudinal gradient is generally observed with a higher fish abundance in the upstream part (main tributary area) (Pont & Amrani, 1990; Urabe, 1990; Fernando & Holčík, 1991; Brosse *et al.*, 1999a; Świerzowski *et al.*, 2000; Vašek *et al.*, 2003, 2004). This was also observed the day with hydroacoustics in our study site. Different hypotheses about this common gradient were posited by Vašek *et al.* (2004). The first one states that because fish fauna in reservoirs have a riverine origin, they are not completely adapted to lacustrine conditions and find their habitats in shallow inshore areas, close to the tributary in the upstream part (Fernando & Holčík, 1991). Second, the upstream part is generally more productive (Straskraba, 1998) with a gradient of chlorophyll-a concentrations and zooplankton densities from the tributary to the dam (Urabe, 1989; Fernandes-Rosado *et al.*, 1994; Dohet & Hoffmann, 1995; Fernandes-Rosado & Lucena, 2001; Vašek *et al.*, 2003). As a result, zooplanktivorous fish have a higher density in this area and their distribution may reflect the longitudinal gradient of productivity: Urabe (1990) and Siler *et al.* (1986) reported that the abundance of planktonivorous fish during summer decreased from the tributary to the dam. This is probably what we observed in our study. Indeed, the community is dominated by roach (Roy, 2014) and it was shown that, in conditions similar to those observed in the Bariousses, this species is able to forage most exclusively on crustacean zooplankton (Vašek *et al.*, 2003).

Hydroacoustics data revealed that the distances of the fish to the tributary and to the bank are greater at night than during the day. Small fish are generally associated with a structured habitat within the littoral during daytime (Lewin *et al.*, 2004; Gliwicz *et al.*, 2006), and at dusk small fish migrate to the pelagic zone where zooplankton prey are more abundant (Romare *et al.*, 2003; Gliwicz *et al.*, 2006).

As the tributary area is a shallower part, we can hypothesize that at dusk zooplanktivorous fish migrate to open waters to follow food supply (Bohl, 1980; Romare *et al.*, 2003; Gliwicz *et al.*, 2006) and to reduce the risk of predation as light intensity decreases (Cerri, 1983).

The telemetry method did not reveal a significant difference in the diel distribution to the tributary, whereas the opposite distribution was seen during the day with a greater distance to the tributary and to the bank. Only three roach were recorded by telemetry during the hydroacoustic survey; however, one individual showed the classic diel pattern of zooplanktivorous fish. The majority of tagged fish were perch and the distribution obtained by telemetry may reflect the spatial distribution of this species. Perch switch predominantly to piscivory when they reach two years of age and they exploit the open water zone (Parker *et al.*, 2009). Unlike cyprinids, perch are efficient competitors and predators in clear water (Diehl, 1988; Radke & Gaupisch, 2005) and this species has a higher biomass in less productive, downstream areas (Vašek *et al.*, 2016). Perch swim continuously parallel to the bank during the day and get close to the littoral zone to rest at night, exhibiting routine homing behavior (Zamora & Moreno-Amich, 2002).

The distribution of the large-sized group was closer to the one obtained with telemetry at night, and similar results were found by Lyons and Lucas (2002) in The River Trent. At night, the majority of fish are dispersed in the water column, whereas during daytime fish aggregate in schools or are close to the bottom making them less accessible to acoustics methods. Consequently, echosounding cannot easily be used to quantify the fish distribution during daytime (Duncan & Kubečka, 1993; Kubečka & Wittingerova, 1998; Ye *et al.*, 2013).

4.2 Fish depth

The two methods showed convergent patterns with fish mainly located in the warmer water (< 6 m deep). Vertical beaming alone underestimated the total amount of fish in Bariousses Reservoir by 96%. This result is in agreement with other hydroacoustic studies where the exclusive use of vertical beaming has led to underestimate fish density by 5100% (Kubečka & Wittingerova, 1998; Knudsen & Sægrov, 2002; Djemali *et al.*, 2009). In thermally stratified reservoirs, fish densities or biomass sampled with horizontal beaming are higher than those determined with vertical beaming

(Kubečka & Wittingerova, 1998; Draštík *et al.*, 2009). In the surface layer, the fish population is virtually undetectable when using only vertical beaming owing to the near field of the transducer. During our survey the process of thermal stratification had just begun; however, the slight difference in temperature observed between layers was sufficient to drive the spatial distribution of the fish. These results confirm the importance of horizontal beaming for assessing the spatial distribution of fish in thermally stratified reservoirs. A typical diel vertical shift with an ascent at dusk and a descent at dawn was also revealed with the two methods.

This distribution is explained by the multifactorial hypothesis of the "antipredation window" (Clark & Levy, 1988) and also by the thermal niche hypothesis for zooplanktivorous fish. During the day, prey fish find refuge in deeper zones with darker conditions and move within this antipredation window. To minimize the cost of swimming (Ohlberger *et al.*, 2008) and speed up the digesting rate during the nonfeeding phase at night (Wurtsbaugh & Neverman, 1988; Neverman & Wurtsbaugh, 1994), fish find temperatures close to their preferendum (Mehner *et al.*, 2010). For predators, such as perch that dominated the telemetry dataset, the risk of predation is not an issue (Mehner, 2012). The foraging and bioenergetics hypotheses have also been most successful at explaining DVM (Bevelhimer & Adams, 1993).

Predator avoidance and feeding opportunities should explain the distribution of small planktivorous fish that stay in deeper layers during the day. At night, differences are highlighted when fish distribution is driven by bioenergetic efficiency and when each ontogenic stage seeks optimum temperature layers.

In our study, fish from the telemetry dataset were found to be deeper than fish detected by hydroacoustics. Apart from measurement uncertainty (2.5 m), fish seeking energetically optimum temperatures could explain the difference (Mehner *et al.*, 2010). Perch dominated the telemetry sample but the community is dominated by roach. The location of perch in deeper layers compared with roach has been reported in numerous studies in lakes and reservoirs (Persson, 1986; Horppila *et al.*, 2000; Kahl & Radke, 2006).

Stronger diel differences in fish depth were observed for small size fish in hydroacoustics compared with large size fish using the two methods implemented here. Ontogenic differences in the thermal niche of fish (Portner & Farrell, 2008) could explain the difference in the observed amplitude of migration.

4.3 Methodological considerations

This study highlights the differences between results provided by the two methods that can be interpreted by the different biological scale (community or individual), as discussed in the previous section and temporal scale (punctual or continuous). Hydroacoustics provides an image of the repartition of the fish community during the survey, over a short time scale, whereas telemetry reflects the detailed tracks of some individuals, adults in our case, detected during the survey.

We have shown that the importance of the upper part of the reservoir highlighted by the hydroacoustic survey can be underestimated with telemetry data, even if specimens of the dominant fish species are included in the survey. The results of telemetry were highly dependent on the species and the number of tagged fish that were considered. Major disadvantages of this method are the cost of the system and the burdensome tagging procedure that often limits the number of fish tracked. Atypical movement can greatly affect telemetry results when a small number of fish are tagged. Some individuals can move a great distance, for example, when seeking for a new home range (Ebner & Thiem, 2009), and a proportion of moving individuals have been reported for perch (Zamora & Moreno-Amich, 2002). Therefore, for the various metrics discussed in the previous part, results obtained in telemetry are based on a small number of individuals and are presented here for information only. Results of the two methods would probably be in better agreement if the sample of tagged fish was more important, more representative of the composition of the whole community and the ecospecies dominance in the system. In the future, the use of micro-transmitters will make this easier.

Environment plays also a major role in the efficiency of the system (Gjelland & Hedger, 2013; Kessel *et al.*, 2014, 2015; Ottera & Skilbrei, 2016) and needs to be estimated, which was done in the present study (Roy *et al.*, 2014) but is generally still uncommon.

Conversely, regarding the depth distribution obtained with telemetry, the use of the epibenthic habitat is probably undervalued by hydroacoustics. Indeed, fish close to the bottom cannot be easily discriminated from bottom echoes and submerged macrophyte or tree roots also cause difficulties in the use of the hydroacoustic technique in shallow waters. However, the total volume sampled by this method is still very large and high-resolution spatial records of fish distribution can be created to inform on the fish distribution at the community level.

In addition, the method does not allow for the determination of species composition and must be complemented by other techniques: trawling, purse seining, and gillnetting are commonly used (Parkinson *et al.*, 1994; Yule, 2000; Baldwin & McLellan, 2008; Winfield *et al.*, 2009; Yule *et al.*, 2013). Studying the distribution of different size-classes has other limitations. Fish sizing is relatively simple with vertical echosounding because the fish are viewed from above and appropriated relationships are generally available (Love, 1977; Foote *et al.*, 1987; Simmonds & MacLennan, 2005). With horizontal mobile beaming, the angle of the fish position to the beam axis is unknown, and then the conversion to length is difficult (Godlewská *et al.*, 2012). Deconvolution does not provide information on the individual position and subsequent attributed size. We hypothesize that fish are not randomly distributed but oriented at 90° to the acoustic axis, because of the small width of the Bariousses Reservoir. However, deviation biased the distribution, and the number of large individuals is probably underestimated.

Conversely, in noisy environments, small fish can also be underestimated (Draštík *et al.*, 2009). However, in this study, the length distribution obtained by gillnetting and electrofishing is close to the one obtained by hydroacoustics. By selecting the fish size, the distribution pattern becomes similar. These results are encouraging for future studies on fish distribution taking into account ontogeny.

Even if the estimation of fish size is still a challenging limitation in the hydroacoustics horizontal scan, this study confirms that, in this type of reservoir (shallow, elongated and monomictic) at the start of the thermal stratification, horizontal beaming is crucial to study fish distribution (Kubečka & Wittingerova, 1998; Knudsen & Sægrov, 2002; Draštík *et al.*, 2009).

To conclude, the spatial distribution of fish in an elongated reservoir has the potential to be better described, using two high spatiotemporal methods – telemetry and hydroacoustics – in parallel to complement each other. Hydroacoustics gives a "snapshot" at the community level and telemetry gives continuous data at the individual and species level. The differences in the results obtained could be limited by tagging a more representative sample of the community in terms of sizes, with the use of microtransmitters, and species and by improving the detection of fish in epibenthic areas with hydroacoustic data acquisition. More experiments are needed with several time and space repeated echosounding to improve robustness (different sampling in a similar environment within a season) and to allow better generalization of the results (different sampling in other sites, at different seasons). However, we can draw preliminary conclusion about the utility of the complementation of these two high spatiotemporal acoustic methods for assessing fish spatial distribution in a reservoir and proposed typical metrics to do that. In using these two methods simultaneously, new knowledge is provided that could be very useful for fish management (Prado & Pompeu, 2014).

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