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Environmental drivers of fish spatial distribution and activity in a reservoir with water level fluctuations

Rôle des facteurs environnementaux sur la distribution spatiale et l'activité des poissons dans une retenue soumise à marnage

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Abstract – The aquatic ecosystem structuration in human influenced environment, is closely dependent of the associated uses, which are generally fluctuant. We conducted an extended field monitoring on a reservoir under water level fluctuations (WLF), in order to study the responses of fish fauna to changes in environmental conditions. The study design was based on a monitoring of fish behaviour by telemetry in a reservoir with a particular attention to the littoral zone because of its front line position during WLF. The results of this study, which was conducted on the Bariousses reservoir, located on the Vézère river (Corrèze, France), are summarized in this article. The study revealed that WLF induced a temporal variability in the littoral zone surface. In addition, we observed a gradual decline in structural complexity of littoral habitats with a tendency towards homogenisation (dominance of fine substrates and absence of vegetation) in relation with the drop in water level. Behavioural individual responses of pikeperch, perch and pike were highly variable in relation to environmental fluctuations. Temperature and photoperiod were the two main parameters controlling fish activity and spatial distribution. Water level affected part of fish assemblage: some individuals were more mobile and left the littoral zone when inshore habitats were less complex (low water level).

Keywords – reservoir; littoral habitat; fish; water level fluctuations; acoustic telemetry.

Résumé – Le fonctionnement des milieux, aquatiques soumis à des pressions anthropiques, est étroitement dépendant des usages générant des fluctuations de l'environnement des communautés biologiques. Nous avons mené une étude sur une retenue soumise à des fluctuations du niveau de l'eau (WLF), afin d'étudier les réponses de l'ichtyofaune aux changements des conditions environnementales. Un suivi du comportement des poissons par télémétrie acoustique a été mené avec une attention particulière portée à la zone littorale car elle est fortement soumise aux WLF. Les résultats de cette étude sur la retenue des Bariousses, localisé sur la Vézère (Corrèze, France) sont synthétisés dans cet article. Nous avons mis en évidence que les fluctuations du niveau de l'eau induisent une variabilité

temporelle de la surface occupée par la zone littorale. De plus, une diminution progressive de la complexité structurelle des habitats littoraux avec une tendance à l'homogénéisation (dominance des substrats fins et de l'absence de végétation) est observée suite à un abaissement du niveau de l'eau. Les réponses comportementales du sandre, de la perche et du brochet étaient fortement variables en fonction des conditions environnementales. La température et la photopériode représentent deux paramètres structurant majeurs de l'activité et du choix des habitats. Le niveau d'eau affecte une partie du peuplement ; certains individus sont plus mobiles et ont tendance à fréquenter de façon moindre la zone littorale lorsque les habitats de bordures sont faiblement complexes (faible niveau d'eau).

Mots-clés – retenue ; habitat littoral ; poissons ; variations de niveau d'eau ; télémétrie acoustique.

1 Introduction

Reservoirs are man-made lakes constructed for different purposes: electricity production, water supply, irrigation or provision of water for domestic and industrial uses (Day & Garratt, 2006). For example, hydroelectricity supplies 16.2% of the electricity requirements worldwide (Observ'ER, 2013). At the end of the 20th century, there were 45 000 large dams built for multiple purposes in more than 140 countries (World-Commission-on-Dams, 2000). From a hydrological point of view, functioning of reservoirs differs from the one of natural lakes because of variations in water level related to flow rate control. Water level fluctuations (WLF) may be strong and irregular in reservoir, whereas they are generally weak and stable in lake (Wetzel, 1990). This parameter is a major driver controlling lake ecosystem functioning (Wilcox & Meeker, 1992; Poff *et al.*, 1997; Leira & Cantonati, 2008). Total amplitude and temporal variability constitute the two main characteristics (Poirel *et al.*, 2001).

The lowering of water level or more generally WLF has a direct impact on physical characteristics of reservoirs:

they may alter the basin morphometry (Leira & Cantonati, 2008), intensify erosion, transform sedimentation zones (Gafny & Gasith, 1993; Leira & Cantonati, 2008) or alter the thermal regime (Leira & Cantonati, 2008). The overall functioning of lake ecosystems is closely dependent on the littoral zone, which is under strong pressure induced by WLF (Wetzel, 1990; Schindler & Scheuerell, 2002; Strayer & Findlay, 2010). Several studies observed impacts of a water level drop with an alteration of littoral habitats availability and a decline in littoral habitats complexity (Gasith & Gafny, 1990; Beauchamp *et al.*, 1994; Zohary & Ostrovsky, 2011). Nevertheless, to our knowledge, none quantified precisely composition changes at a whole reservoir scale. Due to the link between biological functions and environmental conditions, these changes can also induce modifications of the biocenosis.

Among aquatic organism, fishes concentrate economic, social and patrimonial interests. Indeed, in reservoirs, angling may represent high economic value (Irz *et al.*, 2002) and they host some native species of interest like pike (*Esox lucius* (L.)) and trout (*Salmo trutta* (L.)). Because of their top position

within the food web (Ramade, 2009), they may represent the global functioning of the ecosystem. In addition, they have a long-life cycle (several years) requiring various types of habitats or functional units for each stage of their development and vital requirements (reproduction, feeding and protection) (Schlosser, 1995), which can make them more vulnerable.

Indirect effects of WLF on reservoir fish populations related to changes in habitat conditions, were well identified (Sutela & Vehanen, 2008). WLF may alter spawning habitats availability and, as a consequence, reproduction success (Gafny *et al.*, 1992; Clark *et al.*, 2008; Kahl *et al.*, 2008), with different sensitivity degrees according to species requirements in terms of spawning substrates. Analysis of time series allows to relate water level and amplitude of WLF with spawning success or failure and thus with population dynamic (Ostrovsky & Walline, 2000; Kahl *et al.*, 2008; Webb, 2008; Ostrovsky *et al.*, 2013). In addition, WLF alter number of fish refuges (Gasith *et al.*, 2000; Fischer & Ohl, 2005). Finally, alteration of trophic resources (in particular, invertebrates and plankton) for fish species is also a consequence of WLF. For example, significant changes in composition of macro-invertebrates communities were observed in relation with WLF (Smith *et al.*, 1987; Valdovinos *et al.*, 2007; Aroviita & Hamalainen, 2008; Baumgartner *et al.*, 2008; Brauns *et al.*, 2008; White *et al.*, 2008). Several studies contributed to improve knowledge of direct or indirect effects of WLF on fish fauna. They pointed towards the potential alteration of all the vital functions of fish species (survival,

growth and reproduction), *via* environmental alteration by hydraulic control of reservoirs. However, these studies generally refer to the alteration of one particular process, such as the impact on recruitment or alteration of diet for a particular species. In addition, in most of them, quantification of process intensity and evaluation of its impact on species dynamic are not assessed (Rose, 2000). Temporal dynamic of the relationships between fish fauna and its environment under hydrological pressure were rarely described.

In this context, our objective was to characterize how the fish fauna was structured by environmental changes (hydrology, water temperature and photoperiod) in a medium-sized reservoir impacted by WLF. The study design was based on a multi-scale approach, both biological (community and individual) and temporal (annual and diurnal cycles), with a particular attention devoted to the littoral zone because of its front-line position during WLF (Fig. 1). We focused on improving knowledge on links between fish assemblages and physical drivers thanks to an extended field monitoring on one reservoir.

More precisely, we first quantified the impacts of WLF on the availability and the quality of littoral habitats at the whole reservoir scale. The hypothesis tested was that complexity and diversity of littoral habitats decline with the lowering of water level due to disappearance of the shoreline vegetation and to predominance of fine substrates.

Then, we focused on the individual adult behaviour of three piscivorous species occurring in the reservoir, *i.e.* pikeperch (*Sander lucioperca* (L.)), perch (*Perca fluviatilis* (L.)) and pike.

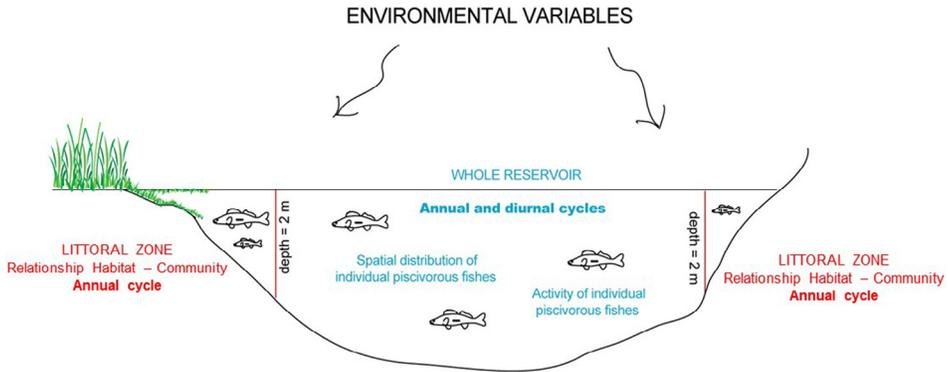


Fig. 1. Diagram of the approach adopted.

Fig. 1. Schéma de la démarche adoptée.

The effects of WLF, temperature and photoperiod on the activity and the spatial distribution patterns were studied. The presence in the littoral zone and the activity of these three species are assumed to be very strongly influenced by temperature and photoperiod (Zamora & Moreno-Amich, 2002; Horky *et al.*, 2008). Nevertheless, variations in water level are also expected to be a structuring parameter. Assumptions that the littoral zone is less attractive and that mobility is higher when habitats are more homogeneous were tested.

This study was conducted on the Bariousses reservoir, located on the Vézère river (Corrèze, France). This article presented a synthesis of all the methods, results and conclusions obtained during a PhD (Roy *et al.*, 2014).

2 Study site

Bariousses reservoir is an impoundment of the Vézère River in west central

France, located at an altitude of 516 m (45.33°N, 1.49°E) (Fig. 2). It is operated by Electricité De France (EDF). The upstream drained watershed is 229 km². The reservoir has an area of 80.9 ha, a perimeter of 9.9 km, and mean and maximum depths of 7.1 m and 18.9 m, respectively. Its volume is 5,707,290 m³, with a mean renewal time of twelve days. It is monomictic with a period of summer stratification. Its last draining was in 1997. WLF observed in this reservoir result of hydropeaking of Monceaux (upstream) and Treignac (downstream) hydroelectric powerplants. WLF total amplitude is 12 m (under normal operation, maximum and minimum water level are 513 m NGF and 501 m NGF respectively), but WLF total amplitude did not exceed 6.2 m between 1st January 2011 and 20th May 2013 (507.3–513.5 m NGF) for an average daily level of 511.4 m NGF. The Bariousses reservoir displays a large heterogeneity of water levels. WLF do not follow either a seasonal or a weekly pattern.

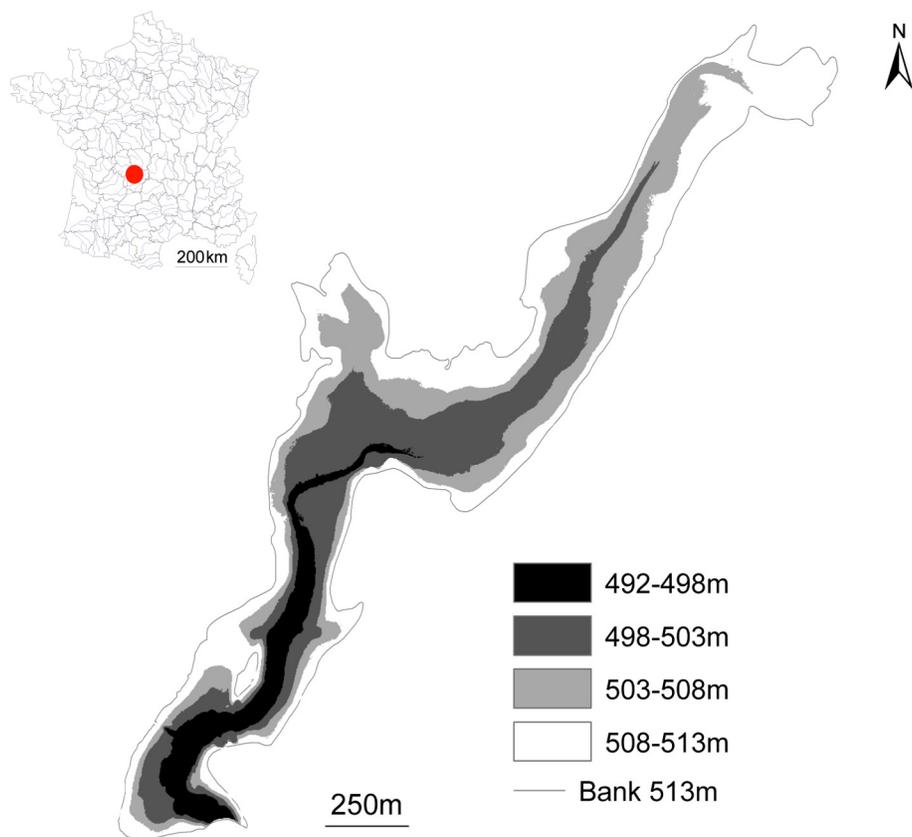


Fig. 2. Location of the Vézère River in France and map of the Bariousses reservoir with altitudinal contour lines.

Fig. 2. Localisation de la rivière Vézère en France et bathymétrie de la retenue des Bariousses.

In addition, of WLF induced by hydroelectric production, the Bariousses reservoir is located in a rural and natural environment, in a catchment dominated by forestland cover with low anthropogenic activities (Rebière *et al.*, 2012). At the average water level, this reservoir presents diversified littoral habitats and low shore degradation (except dam). Moreover, fish community is quite comparable to that encountered in many French reservoirs and two of the three piscivorous focused species (*i.e.* perch and

pikeperch) are not controlled by the fishery management authorities. The Bariousses reservoir has mean physical and hydrological characteristics that well represent a part of EDF other reservoirs, particularly in the Massif-Central.

In 2010, the fish community of the Bariousses' reservoirs was sampled with multimesh gillnets following the Nordic standardised protocol (C.E.N., 2005). Eleven species were identified: Pike, Pikeperch, Perch, Bream (*Abramis brama* (L.)), Carp (*Cyprinus carpio*

(L.), Chub (*Leuciscus cephalus* (L.)), Roach (*Rutilus rutilus* (L.)), Ruffe (*Gymnocephalus cernua* (L.)), Pumpkinseed (*Lepomis gibbosus* (L.)), Rudd (*Scardinius erithrophthalmus* (L.)), and Tench (*Tinca tinca* L.). The community was dominated by roach that represent 52% of the number of fish caught and 24% of the biomass. Then ruffe and perch were most frequent (27 and 10% of the fish caught respectively) whereas carp and tench were the most abundant in biomass (17% and 16% respectively).

During this 3 years study, additional electrofishing samplings in the littoral habitat highlight the presence of 4 additional species: Wels Catfish (*Silurus glanis* (L.)), European brook lamprey (*Lampetra planeri* (Bloch, 1784)), Dace (*Leuciscus burdigalensis* (L.)) and Brown trout.

3 Materials and methods

The extended field monitoring included a field mapping of area affected by WLF and an individual monitoring of fish equipped with acoustic tags.

3.1 Habitats

A bathymetric map was determined by a multibeam sonar in March 2012 (source Engineering unit DTG of EDF). The littoral zone was defined by areas with a depth less than 2 m. Littoral habitat (substrate and vegetation) described by the CHARLI protocol (Alleaume *et al.*, 2014) was mapped between 508 and 513.5 m NGF with a differential GPS. The variations of the littoral zone area and the proportions of

the littoral habitat types were observed between 4 water levels: 513.5, 512.5, 511.5 and 510.5 m NGF.

3.2 Spatial distribution and activity of perch, pike and pikeperch

An acoustic VEMCO telemetry system was deployed on the whole reservoir during one year. Thirty hydrophones were set close to the isobaths 507 m NGF (*i.e.* maximal depth of 6.5 m) and ten additional hydrophones were set in depth higher than 6 m in order to monitor fish in the whole reservoir.

Thirty-six adults of pikeperch, twenty-seven adults of pike and twenty-seven adults of perch were caught by anglers and multimesh gillnets set during very short period in order to limit the stress. Fifty-four fish were equipped with acoustic tag in order to analyse their spatial distribution and thirty-three to characterize their activity (Roy, 2014).

The “VEMCO Positioning System (VPS)” was used to calculate 2D positions of tagged fish (VEMCO Division, 2008, 2013; Smith, 2013). Under test conditions, mean positioning error of our system was 3.3 m (standard deviation of 3.3 m) and probability of location was 40% after filtering out aberrant positions (79% of positions maintained) (Roy, 2014).

Each fish position was associated with 7 environmental variables to characterize photoperiod, temperature and water level (Tab. I).

Spatial distribution was defined first by the presence/absence of the fish in the littoral zone then by the water column height at the fish location

Table I. Environmental variables describing each fish position.**Tableau 1.** Variables environnementales associées à chacune des positions de poissons.

Identifiant	Type	Description
PHOTOPERIOD (PP)	Category	Four phases of the day: 'Dawn' and 'Dusk' covering for two hours the sunrise and sunset and 'Day' and 'Night', corresponding to hours recorded between Dawn and Dusk.
TEMP_S (MT)	Numerical	Mean daily water temperature, 50 cm below the surface (°C) in downstream part of the reservoir
WATER_LEVEL_DAY (WL)	Numerical	Mean daily water level of the reservoir (m NGF) calculated on hourly data
ABS_AMP_DAY (WLDif_D)	Numerical	Absolute value of the difference between the mean water level of day J and day J-1 (m)
DIRECTION_DAY (WLFD_D)	Category	Direction of WLF since the previous day. This is a two-mode variable: fall and rise
ACCUM_ABS_AMP_WEEK (WLDif_W)	Numerical	Sum of the ABS_AMP_DAY over the last 7 days (m)
DIRECTION_WEEK (WLFD_W)	Category	Direction of WLF since the last 7 days. This is a two-mode variable: fall and rise

Table II. Mean values of water temperature (°C) and water level (m NGF) for each season.**Tableau 2.** Valeurs moyennes de la température de l'eau (°C) et du niveau de l'eau (m NGF) pour chacune des saisons.

	Summer	Autumn	Winter
Duration	29 June 2012 to 07 August 2012	05 October 2012 to 20 December 2012	21 December 2012 to 20 May 2013
TEMP_S (MT)	20.8	10.4	4.7
WATER_LEVEL_DAY (WL)	511.5	510.9	511.7

(HW) and its distance to the closest shore (Dr). A total of 1 168 576 positions corresponding to movement of 25 pikeperch (143–695 mm), 19 perch (320–486 mm) and 10 pike (425–629 mm), monitored over 283 days from 11 March 2012 to 20 May 2013 were analysed. These spatial distributions were analysed depending on the seasons. In terms of temperature and hydrological conditions, the different periods selected are highly contrasted (Tab. II).

Fish activity was described by two metrics. The minimal distance covered in one day was calculated when a minimum of 8 positions were observed

at dawn, 24 at daylight, 8 at dusk and 24 at night (a minimum of 64 positions per day). On average, a distance value covered by day was calculated with 314 positions. The number of distance covered per day finally available was 1765 for the pikeperch, 1110 for the perch and 308 for the pike. The home range corresponding to the area where a fish stays 95% of the time (HR95) (Parsons *et al.*, 2003; Katajisto & Moilanen, 2006) was assessed by the Brownian Bridge Movement Model (BBMM) (Horne *et al.*, 2007) using the "kernelbb" function of the R package "adehabitatHR" (Calenge, 2006, 2013). This metric was calculated at the

diurnal and seasonal scales. A total of 1512381 positions corresponding to movement of 28 pikeperch (143–695 mm), 21 perch (240–486 mm) and 14 pike (375–629 mm) during 405 days from 11 March 2012 to 20 May 2013 were considered.

3.3 Data analyses

The relationships between mean daily values of HW and Dr measurements for each species and water temperature were tested using a Spearman correlation coefficient (excluding spring period).

The influence of the 7 environmental variables listed in [Table I & II](#) (3 qualitatives: PP, WLF_D and WLF_W; 4 numericals: MT, WL, WLDif_D and WLDif_W) on the presence / absence (binary variable, 0 or 1) of fish individuals in the littoral zone (excluding spring period) was analysed by a logistical regression ($n=30$). Hierarchical partitioning was then implemented to determine explanatory power (explained variance) of each environmental variable ([Chevan & Sutherland, 1991](#)). A PCA was then applied on contribution values of each environmental variable to compare individual responses to the explanatory variables.

Multiple regressions by individual ($n=20$) were used to predict daily activity described by the numerical variable daily distance covered during the spring period in function of the 4 numerical environmental variables (MT, WL, WLDif_D and WLDif_W). Beforehand, daily distance has been transformed by $\log(x+1)$ to make the distributions more symmetrical and

each numerical variable has been normalized. A redundancy analysis has been used to do a partitioning of variance for each environmental variable ([Legendre & Legendre, 1998](#)).

All statistical analyses were performed using R software ([R.C.T, 2012](#)).

4 Results

4.1 Impact of water level fluctuations on littoral habitats

4.1.1 Littoral habitat

During the study period, WLF induced variations in surface occupied by the littoral zone. The area varied between 9 and 14 ha (between 9.3 and 14.4% of the total surface of the reservoir). Surface of the littoral zone reached a maximum at 510.9 m NGF but this level was observed only 2.1% of the time.

At maximum recorded water level (513.5 m NGF), lawn, and more characteristic of terrestrial habitats than of lake habitats, dominated the littoral zone ([Tab. III](#) and [Fig. 3](#)). The littoral zone was also characterized by a high proportion of shoreline bordered by submerged vegetation, which provided riparian shade and habitats complexity (roots and tree branches). Nevertheless, maximum water level was seldom reached (124 days between 1997 and 2013) and was thus poorly representative of the mostly encountered conditions by organisms.

The lowering of water level led to a gradual increase in the littoral habitats with sandy and silt substrates, but coarse substrates remained poorly represented ([Tab. III](#), [Figs. 3](#) and [4](#)). Vegetation, spawning substrate for pike particularly, was present above

Table III. Percentages of surface occupied by each substrate and bank vegetation categories in the littoral zone observed at 513.5, 512.5, 511.5 and 510.5 m NGF.**Tableau 3.** Pourcentages surfaciques occupés par chacune des catégories de substrat et de végétation de rive observés en zone littorale aux cotes 513.5, 512.5, 511.5 et 510.5 m NGF.

	Categories	513.5	512.5	511.5	510.5
Substrate	Silt	3.5	20.5	31.4	42.3
	Sand	5.2	12.2	19.1	24.7
	Gravel	7.9	16.8	16.5	10.7
	Pebbles	0.3	1.5	1.7	0.6
	Stones	2.1	5.6	7.1	6.4
	Boulders	0.2	0.3	0.3	0.3
	Large rocks	2.9	6.7	10.1	11.0
	Slabs	1.0	1.7	2.5	2.3
	Unknown	1.8	2.6	2.7	1.2
	Lawn	75.2	32.2	8.5	0.5
Vegetation	Submerged vegetation	72.7	41.4	17.4	4.9
	Riparian shade	71.4	40.9	17.3	5.3
	Herbaceous	12.8	9.3	6.0	1.9
	Helophytes	5.0	6.8	3.5	0.4
	Litter	0	0	0.01	0.02
	Dead ligneous	0	0	0.01	0.02

**Fig. 3.** Changes in the littoral habitat of the Bariousses reservoir with a drop in water level from 513 NGF (left) to 510 m NGF (right).**Fig. 3.** Évolution des habitats de rive de la retenue des Bariousses au cours d'un abaissement du niveau de l'eau entre 513 NGF (à gauche) et 510 m NGF (à droite).

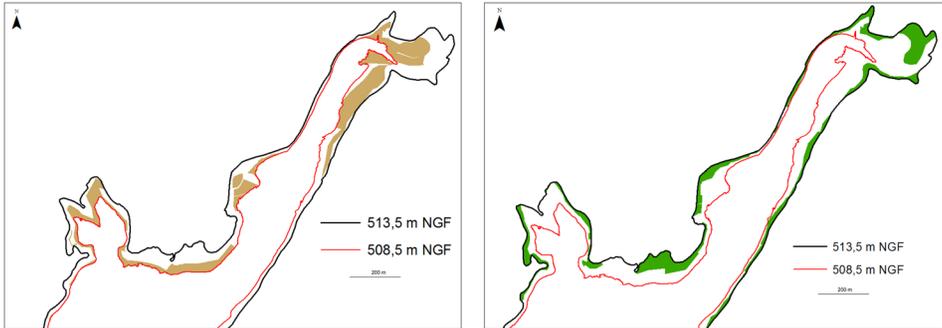


Fig. 4. Map of the area occupied by silt (left) and by submerged vegetation (right), in the upstream part of the reservoir, between 513.5 (black) and 508.5 m NGF (red).

Fig. 4. Cartographie de la surface occupée par la vase (à gauche) et par les ligneux émergents (à droite), dans la partie amont de la retenue, entre les cotes 513.5 (en noir) et 508.5 m NGF (en rouge).

511.5 m NGF and was gradually disconnected with the fall in water level. Between 1997 and 2013, in March, generally the spawning period for pike on this reservoir, this 511.5 m NGF level was only exceeded on 22.2% of days.

4.1.2 Spatial distribution of individuals

Within each species, individuals may occupy quite different areas (Fig. 5). For example, in summer, pikeperch T35 and perch T55 spent time in the whole reservoir; pikeperch T01, perch T28 and T48 and pike T46 were rather in the upstream area; pikeperch T02 and pike T16 occupied mainly the downstream area whereas pike T04 was rather confined to the intermediate area. This cartographical analysis of distribution patterns for all monitored individuals showed that the whole reservoir was well occupied.

The spatial distribution pattern of individuals of the three species differed quite distinctly between summer and winter (Tab. IV). In winter, with drop in water temperature, fish moved signifi-

cantly in areas further from the shore and deeper (Tab. V). Whatever the species and the season, there was high inter-individual variability of depth of water column and distance from the shore occupied by tracked fish (Tab. IV).

The logistical regression models correctly predicted the frequentation of the littoral zone. Method of hierarchical partitioning showed a clear influence of PP and of MT on the presence of 22 individuals in the littoral zone; their mean contributions were respectively 44% (12–95%, according to individuals) and 40% (11–83% according to individuals). In addition, the model coefficients showed that the monitored individuals were more likely to be present in the littoral zone than in the pelagic area, at night (7.9 times more on average), at dawn (4.6 times more on average) and at dusk (5.4 times more on average) than during the day. Finally, with an increase in water temperature of 1°C, individuals were on average 1.7 times more likely to be in the littoral zone than in the pelagic zone of the reservoir.

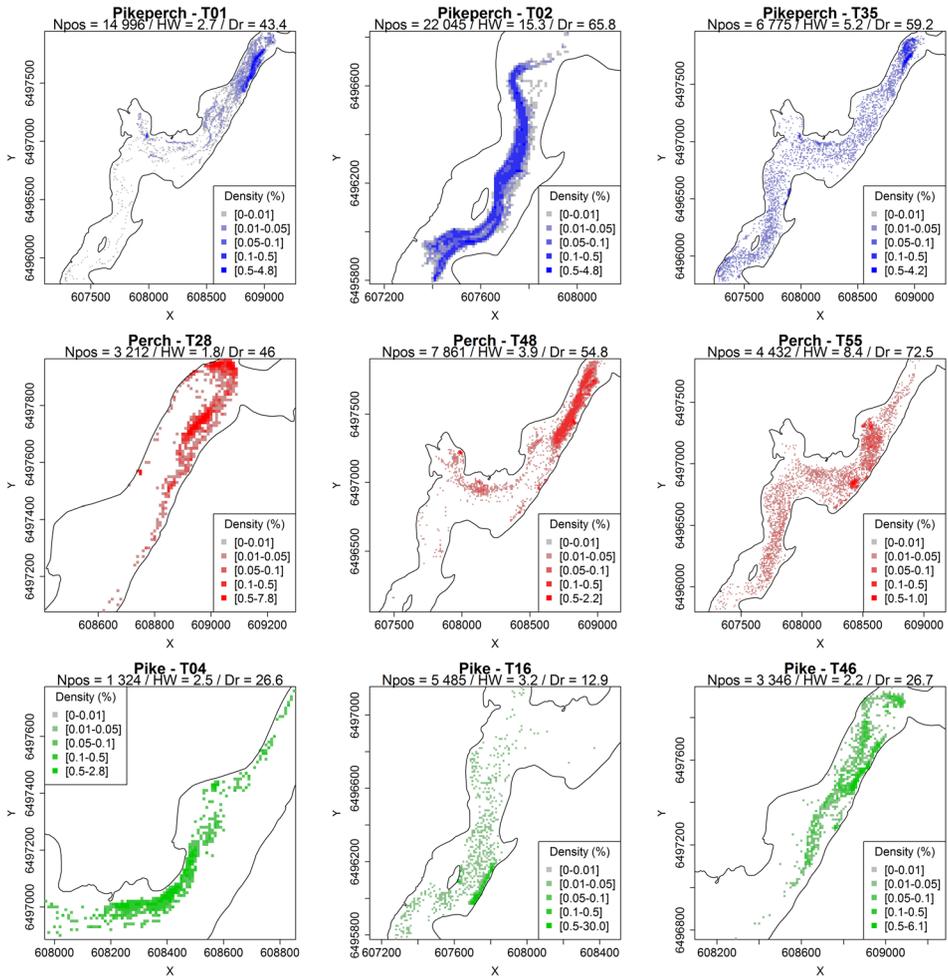


Fig. 5. Map of presence density with a square mesh of 10*10 m for 3 pikeperch individuals (T01, T02, T35, in blue), 3 perch individuals (T28, T48, T55 in red) and 3 pike individuals (T04, T16, T46, in green) during summer.

Fig. 5. Carte de densité de présence avec une maille carrée de 10*10 m pour 3 individus de sandre (T01, T02, T35, en bleu), 3 individus de perche (T28, T48, T55, en rouge) et 3 individus de brochet (T04, T16, T46, en vert) en période estivale.

The water level of the reservoir WL also had an influence on the use of the littoral zone, but to a lesser extent. Mean contribution was 31% for the mean diurnal water level ($n = 10$, 13–60%, according to individuals). The model coefficients showed that individ-

uals were on average 5.7 times less likely to be present in the littoral zone than in the pelagic zone of the reservoir with a drop-in water level of 1 m.

The descriptive parameters of the past variations in water level selected in this analyse (WLDif_D, WLF D_D, WLDif_W

Table IV. Mean values for the two metrics of spatial distribution, total depth of water column (HW in m) and distance from the shore (Dr in m), for each species, and range of variability between individuals in italics, in summer and winter (Npos = sample size and Nind = number of individuals).

Tableau 4. Valeurs moyennes des deux métriques de distribution spatiale, hauteur totale de la colonne d'eau (HW en m) et distance à la rive (Dr en m) pour chacune des espèces et gamme de variabilité inter-individuelle en italique, en été et en hiver (Npos = taille de l'échantillon et Nind = nombre d'individus).

	Pikeperch		Perch		Pike	
	Summer	Winter	Summer	Winter	Summer	Winter
Npos	118 181	149 941	59 955	187 043	15 848	44 130
Nind	20	11	12	12	6	6
HW	6.6	9.2	4.1	6.9	2.6	6.3
Dr	2–15.3	4.2–12.7	1.8–8.4	3.8–12.2	2.2–3.2	4–9.5
	51.4	87.1	44.4	53.5	22.5	52.5
	6.2–66.6	50.4–120.5	14.5–72.5	14.2–97.7	12.9–30.2	24.7–64.9

Table V. Results for Spearman correlation analysis between mean daily water temperature and the metrics depth of water column (HW in m) and distance from the shore (Dr in m).

Tableau 5. Résultats de l'analyse de corrélation de Spearman entre les valeurs moyennes journalières de la température de l'eau et des deux métriques hauteur de colonne d'eau (HW en mètre) et distance à la rive (Dr en m).

	Pikeperch	Perch	Pike
HW	$r = -0.71, P < 0.0001$	$r = -0.80, P < 0.0001$	$r = -0.57, P < 0.0001$
Dr	$r = -0.65, P < 0.0001$	$r = -0.45, P < 0.0001$	$r = -0.41, P < 0.0001$

and WLFD_W) proved to be poorly determinant and for few individuals.

We highlighted a high inter-individual variability in drivers influencing the use of the littoral zone (Fig. 5). The first axis of the PCA distinguished individuals for which, presence in the littoral zone was mainly dependent on PP and individuals for which presence in the littoral zone was mainly dependent on MT (Fig. 6). In addition, the second axis expressed a hydrological gradient with an opposition between the few individuals for which presence in the littoral zone was closely linked to amplitude of WLF (WLDif_D and WLDif_W), and the individuals for which presence in the littoral zone resulted mainly of the WL. Finally, grouping individuals by species revealed an absence of common pattern.

4.2 Activity

For the three species, the home range 95% and the mean minimum distance covered per day showed a high seasonal variability (Tab. VI). For pikeperch and perch, these two variables decreased between summer and winter. In contrast, even if the number of individuals observed was low, it would appear that home range of pike was greater in winter than in summer and that its daily activity was comparable during the two periods.

In summer, perch occupied the largest home range and pike was the least mobile. In winter, perch had the smallest home range. The highest HR 95% (42.7) was observed for a pike individual. Distances covered by perch

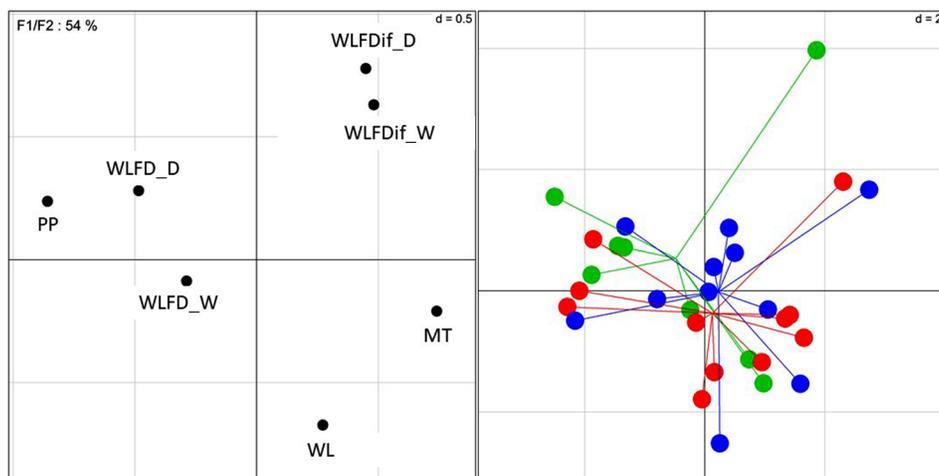


Fig. 6. Positions of variables (on left) and grouping of 30 individuals per species (on right, pikeperch in blue, perch in red and pike in green) on PCA axes F1/F2 to see the influence of the environmental variables on the presence / absence of fish individuals in the littoral zone.

Fig. 6. Positions des variables (à gauche) et regroupement des 30 individus par espèces (à droite, individus de sandre en bleu, perche en rouge et brochet en vert) sur les axes F1/F2 de l'ACP permettant d'évaluer l'influence des variables environnementales sur la présence/absence des individus en zone littorale.

Table VI. Mean values, range of variability between individuals (in italic) and sample size (in bracket) for Home Range 95 % (HR 95% in ha) and Minimum Distance Covered per Day (m) for each species, in summer and winter.

Tableau 6. Valeurs moyennes des Home Range 95 % (HR 95% en ha) et des Distance Minimale Parcourue par Jour (m) pour chaque espèce en été et en hiver, gamme de variabilité inter-individuelle en italique et taille de l'échantillon entre parenthèse.

	Pikeperch		Perch		Pike	
	Summer	Winter	Summer	Winter	Summer	Winter
Mean HR 95 %	18.1 <i>2.3–56.1</i> (n = 13)	16.3 <i>5.2–29.7</i> (n = 10)	29.8 <i>7.1–60.5</i> (n = 11)	11.0 <i>3.2–28.5</i> (n = 12)	10.4 <i>6.3–12.8</i> (n = 4)	23.2 <i>7.3–42.7</i> (n = 6)
Mean distance covered	4610 <i>1552–9135</i> (n = 17)	2395 <i>1004–3716</i> (n = 11)	5570 <i>4020–8160</i> (n = 12)	2284 <i>857–2978</i> (n = 12)	2625 <i>1724–4124</i> (n = 5)	2883 <i>1695–3946</i> (n = 5)

and pikeperch were higher in summer than in winter. They were also higher than those recorded for pike. The highest distance covered was more than 9 km for one of the pikeperch individuals. There was however a high inter-individual

variability of the level of activity within each species, both in summer and in winter (Tab. VI and Fig. 7).

For 10 individuals (6 pikeperch and 4 perch), MT was the main explicative driver of the temporal variability of

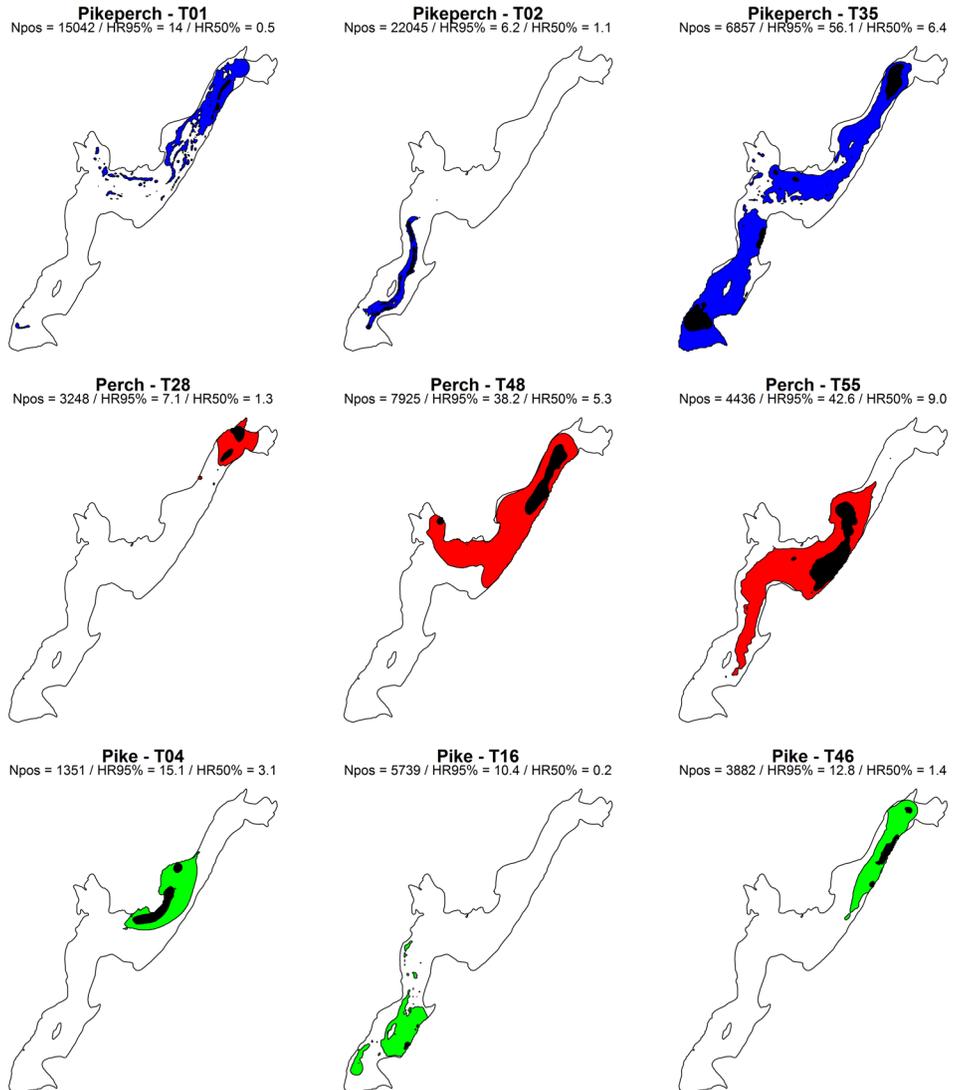


Fig. 7. Home range 95% in colour and 50% in black of 3 pike-perch individuals (T01, T02, T35, in blue), 3 perch individuals (T28, T48, T55 in red) and 3 pike individuals (T04, T16, T46, in green) during summer.

Fig. 7. Domaine vital 95 % en couleur et 50 % en noir de 3 individus de sandre (T01, T02, T35, en bleu), de 3 individus de perche (T28, T48, T55, en rouge), et de 3 individus de brochet (T04, T16, T46, en vert) en période estivale.

minimum distance covered per day. The percentage of variation associated with this parameter varied between 25

and 77% according to the individuals. The coefficient of the regression model associated with this variable, always

positive, showed that daily activity of these individuals moved in the same direction as MT.

Hydrological parameters (WL, WLDif_D and WLDif_W) contributed to explain part of variability of the daily activity but for a lower number of individuals of pikeperch and perch than MT. Activity of 6 individuals (2 perch and 4 pikeperch) was influenced by water level (contribution from 13 to 39 for WL). The coefficients associated with this variable, always negative, showed that activity and water level were negatively correlated. The responses to the amplitude of past variations (WLDif_D and WLDif_W) were more variable. For some individuals, the activity increase (positive coefficient) with the amplitude of the past variations and conversely for others (negative coefficient).

The 4 numerical environmental variables selected did not provide an explanation for the variability of the minimum distance covered per day of 8 individuals. Residual parts of the regression models were then higher than 80% and adjusted coefficient R^2 lower than 0.2.

5 Discussion

5.1 Effect of water level fluctuations on habitats

A drop in water level in the Bariousses reservoir led to a diminution of surface covered by the littoral zone. A maximum surface was observed at 510.9m NGF. In addition, a trend towards a dominance of the fine substrates (sand and silt) and an absence of vegetation was shown

confirming our initial hypothesis. The precise quantification of changes in the availability and quality of littoral habitats induced by the lowering of water level that we described here confirmed a general trend towards a reduction in habitat complexity with the lowering of water level. Similar studies are rare but our results confirmed the observations made in Lake Kinneret (Gasith & Gafny, 1990, 1998) and Lake Tahoe (Beauchamp *et al.*, 1994). Considering the interest of the littoral zone for fish fauna (Schiemer *et al.*, 1995; Schmieder, 2004; Lewin *et al.*, 2014), alterations of littoral habitats due to water level decrease are likely to affect fish community. Indeed, we could expect for example an increased exposure to predation due to loss of refuge area in the littoral zone (Kahl & Radke, 2006). Similarly, these changes could induce a decline in available food resources (Zohary & Ostrovsky, 2011). Specific study of patterns of change in littoral fish community composition sampled by electrofishing (individuals less than 250 mm) following changes in habitat conditions induced by WLF confirms this hypothesis (Logez *et al.*, 2016). In the Bariousses reservoir, the relationship between habitat complexity and fish assemblage changed along the water-level gradient. A homogenization of fish assemblages was observed when the water-level condition reached a threshold. These results suggest an effect of water-level management in structuring fish assemblages of the littoral zone of a reservoir due to a decrease of habitat complexity.

5.2 Lateral migration

The spatial distribution patterns of individuals of the 3 species were subject to high seasonal variability. Drop in water temperature resulted in movements towards deeper waters, associated with movements away from the shore. Previous studies observed similar seasonal patterns of change for pikeperch (Deelder & Willemsen, 1964; Nyberg *et al.*, 1996; Vehanen & Lahti, 2003; Lehtonen *et al.*, 2006) and pike (Rogers, 1998; Jepsen *et al.*, 2001). In addition, our study revealed the key role of water temperature in the littoral zone occupation. During cold periods, the littoral zone was more thermally unstable than the pelagic zone and that may partially explain why individuals left the littoral zone during these periods. Furthermore, decline in juvenile abundance between spring and winter, regularly observed in the littoral zone (Brosse & Lek, 2000; Brosse *et al.*, 2007), may be one of the causes of the drop in frequentation of this zone by piscivorous adults of pikeperch, perch and pike.

In addition of temperature, photoperiod was also a driver of the frequentation of the littoral zone, in the same way as water temperature. Individuals were more frequent in the littoral zone at night, dawn and dusk to take advantage either of the greater structural complexity in order to rest or to be protected from predators, or of the greater abundance of prey to feed on (Sanders, 1992; Copp & Jurajda, 1993, 1999; Horky *et al.*, 2008).

5.3 Role of water temperature and photoperiod on fish activity

Ours results highlight that water temperature and photoperiod were factors contributing to understand fish activities. Perch and pikeperch were less mobile when temperature dropped. This decline in perch activity in relation with water temperature was already observed in various hydrosystems (Craig, 1977; Eriksson, 1978; Karas & Thoresson, 1992; Huusko *et al.*, 1996; Neuman *et al.*, 1996; Jacobsen *et al.*, 2002) but for pikeperch, our observations differed from those of Koed *et al.* (2000) and Jepsen *et al.* (1999) who observed a low significant correlation between the total distance moved and water temperature. In contrast, the drop in water temperature observed between the beginning of summer and the middle of winter did not appear to clearly affect pike activity showing some species differences. There is no consensus in the literature regarding the role played by water temperature on pike behaviour: some studies showed a decline in activity between summer and winter (Casselmann, 1978; Cook & Bergersen, 1988; Rogers, 1998; Kobler *et al.*, 2008a), others an increase (Jepsen *et al.*, 2001; Koed *et al.*, 2006), or even no difference (Diana *et al.*, 1977). This absence of consensus might be explained by site differences, in particular in terms of prey availability, shore structure, availability of preferred habitats or perhaps in monitoring methods and/or triangulation techniques used (Rogers, 1998; Jepsen *et al.*, 2001).

5.4 Influence of hydrological parameters on fish position and activity

Hydrological parameters considered in this study contributed to explain only a part of the behavioural variability of pikeperch, perch and pike individuals (length greater than 250 mm). However, some individuals showed greater mobility ($n=6$, perch and pikeperch) and lesser use of the littoral zone at low water levels, when littoral habitat was more homogeneous (dominance of fine substrates without vegetation). These results are similar to those of Bruylants *et al.* (1986), who showed higher mobility for perch in homogeneous areas (similar depth, substrate and current) than in heterogeneous areas (succession of pool/riffle) of rivers. Dispersal of favourable patches when habitat is homogeneous (low water level) might explain these observations (Baras, 1992), since individuals must then cover greater distances to reach favourable habitats for accomplishing their vital functions (reproduction, rest/protection and food seeking). The lowest frequentation of the littoral zone observed at low water levels might be explained by the decline in attractiveness of this zone. By comparison, an increased frequentation of the shore when flow rate raised was regularly observed in rivers (Brenden *et al.*, 2006), as individuals sought to return to refuge zones for protection.

5.5 Methodological considerations

The implementation of experiments dedicated to individual behaviour using acoustic telemetry needs preliminary

methodological developments. In our experimental conditions, performances of VPS described by the positioning error and the probability of location were proved satisfactory (Roy *et al.*, 2014).

The present study, carried out on a large number of individuals of three species conducted in a same lake during a long period, highlights a very high variability in behavioural responses of individuals to environmental fluctuations. Therefore, we must proceed with extreme caution when behavioural characteristics are attributed to a particular species, in particular when a “mean” value of the spatial distribution and activity metrics is presented. The fish size effect was supposed to explain a part of individual variability: the largest individuals of pikeperch and perch tend to frequent areas that are deeper and further from the shore and the largest individuals of the 3 species tend to cover greater daily distances than smaller individuals, as was observed for pike by Kobler *et al.* (2008b) and for pikeperch by Jepsen *et al.* (1999). Nevertheless, further studies are required to identify precisely drivers of inter-individual variability. For example, a monitoring of individuals with the same age and sex characteristics could provide elements to explore their influence on variability among individuals.

These behavioural analyses nonetheless provided initial results that may help us to better understand factors controlling habitats, in particular, in the littoral, under water level management. Extension of these results by further studies in other lake systems impacted by different hydrological regimes might be developed. It could allow finding

efficient mitigation measures to improve the ecological potential of reservoirs.

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