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# Behaviour of two predator fishes *Esox lucius* Linnaeus, 1758 and *Silurus glanis* Linnaeus, 1758 during two successive floods in the French Aisne River

by

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**Abstract.** – French rivers are subject to winter floods. The northern pike (*Esox lucius*) needs these, as it performs lateral migrations for breeding. On the contrary, the allochthonous European catfish (*Silurus glanis*) is known to be less active in winter. However, very few studies have focused on the behaviour of these two predatory fishes during winter floods. Thus, we propose to characterize their respective responses to high waters, using a radio telemetry approach: thirty northern pikes and seven European catfish were tagged with radio transmitters in the Aisne River (northern France) and monitored between October 2020 and May 2021. As a result, some northern pikes and at least one catfish were recorded in the major bed, in various habitats, during two major floods. A “preferential zone” was identified for the northern pike and defined from the pre-flood positions; three types of behaviour were identified: “sedentary” pikes never left these zones, “returned” pikes left during floods but returned when the water level dropped, and “departed” pikes did not come back at all. Individuals from the departed group were significantly larger than those from the other two groups (5% threshold), and those in the sedentary group significantly smaller (10% threshold), suggesting a greater exploration capacity in experienced northern pikes. Meanwhile, the supposed winter quiescence of the European catfish can be questioned, as our observations highlight an adaptability to various conditions. These results also underline the importance of taking the major bed into account in riverine management policies.

## Key words

Northern pike  
Riverine management  
Telemetry  
European catfish  
Floods  
Flood zone

**Résumé.** – Comportement de deux poissons prédateurs *Esox lucius* Linnaeus, 1758 et *Silurus glanis* Linnaeus, 1758 lors de deux crues successives dans l’Aisne (France).

Les rivières françaises sont sujettes aux crues hivernales, et ces périodes d’inondation sont des événements importants pour le comportement du brochet commun (*Esox lucius*), qui effectue des migrations latérales pour se reproduire. Le silure glane (*Silurus glanis*), allochtone, est quant à lui connu pour être plutôt moins actif pendant l’hiver. Cependant, peu d’études ont été réalisées sur le comportement de ces deux poissons prédateurs lors des crues hivernales. Nous avons donc cherché à caractériser leurs réponses respectives à la montée des eaux à l’aide d’une approche de radio télémétrie. Trente brochets communs et sept silures glanes ont été marqués à l’aide d’émetteurs radio dans la rivière Aisne (Nord de la France), et suivis entre octobre 2020 et mai 2021. Un nombre important de brochets ainsi qu’au moins un silure ont été enregistrés dans le lit majeur, dans divers habitats inondés, lors des deux crues les plus importantes. Concernant les brochets, une “zone préférentielle” a été identifiée, et définie à partir des positions des individus avant les inondations. Trois types de comportements principaux ont été identifiés : les brochets “sédatifs” ne quittaient jamais ces zones, les brochets “explorateurs” les quittaient mais revenaient à la décrue, et les brochets “délaisseurs” n’y revenaient pas du tout. Les individus du groupe des délaisseurs étaient significativement plus gros que ceux des deux autres groupes au seuil de 5 %, et ceux du groupe des sédatifs significativement plus petits au seuil de 10 %. Ceci suggère une plus grande capacité d’exploration chez les brochets plus expérimentés. Concernant le silure glane, nos observations remettent en cause sa supposée quiescence et mettent en évidence l’adaptabilité de l’espèce à diverses conditions. Ces résultats soulignent l’importance de la prise en compte du lit majeur dans les politiques de gestion fluviale.

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## INTRODUCTION

Climate change and human activities have a strong negative impact on the freshwater fish biodiversity (*e.g.*, Nagelkerken *et al.*, 2017; Su *et al.*, 2021). Moreover, the increasing frequency of natural disasters highlights the importance for aquatic environment managers to learn how to adapt their practices. In particular, it has been shown that global warming increases the atmospheric water-holding capacity and, consequently, induces heavy precipitation (Min *et al.*, 2011; Pall *et al.*, 2011; Alfieri *et al.*, 2017). This translates into a disruption of the cycles of floods and droughts, in terms of frequency and magnitude (Fowler and Hennessy, 1995). There is no doubt that these climate changes will impact species communities with, for example, the spread of invasive species (Rahel and Olden, 2008).

Major French rivers have undergone many human-induced transformations since the Middle Ages to satisfy social demands, in particular to rein their unpredictable level variations and allow navigation (Bravard *et al.*, 1999). This changed their natural dynamics and impacted their fish populations and assemblages (Boët *et al.*, 1999; Craig, 2008; Maire *et al.*, 2015). However, parts of their course, usually upstream, are less modified by those modifications and can thus still be subject to significant seasonal floods. Studying these particular environments may give us an insight into the consequences of the increasingly severe floods and droughts that are already observed there. This could help us apprehend the challenges we will face, as it will most likely affect the full length of watercourses in the near future. The use of telemetrics, with electronic tagging technology, is a modern approach that allows to follow their movements continuously and, over several months or years, learn fish behaviour in their environment (Hockersmith and Beeman, 2012; Cooke *et al.*, 2013; Donaldson *et al.*, 2014; Hussey *et al.*, 2015). This approach has been recognized as a source of new data about life-history variations (timing of migrations, reproductive investment and spawning behaviour) as well as survival-determining factors (DeCelles and Zemeckis, 2013; Crossin *et al.*, 2017). For these reasons, this tool is often used for fisheries and riverine management (Cooke *et al.*, 2013, 2016; Donaldson *et al.*, 2014; Hussey *et al.*, 2015; Crossin *et al.*, 2017; McGowan *et al.*, 2017; Brownscombe *et al.*, 2019).

Two top predators that constitute a strong interest for recreative fishing are present in the Aisne River (northern France), among others (Keith *et al.*, 2020). A native one, the northern pike *Esox lucius* Linnaeus, 1758, has a diurnal activity (Lucas *et al.*, 1991; Kobler *et al.*, 2008). It lives in low-velocity zones, often near the shores (Casselman and Lewis, 1996), where it can hide in aquatic plants or other structures (tree trunks, rocks, etc.) (Eklöv, 1997; Keith *et al.*, 2020). Moreover, it is a potamodromous fish, migrating at the end of winter to flooded grass fields for spawning between Feb-

ruary and April in most French regions (Keith *et al.*, 2020). And an introduced one, the European catfish *Silurus glanis* Linnaeus, 1758 that is predominantly nocturnal (Boujard, 1995; Carol *et al.*, 2007; Slavík and Horký, 2012). It lives in calm, turbid and deep waters as well as grassy areas (Saat, 2003; Valadou, 2007; Proteau *et al.*, 2008; Copp *et al.*, 2009; Cucherousset *et al.*, 2018). Finally, it is regarded as a potential invasive species in France (Proteau *et al.*, 2008; Copp *et al.*, 2009; Cucherousset *et al.*, 2018), even if some populations have sedentary behaviours (Carol *et al.*, 2007; Slavík and Horký, 2009; Brevé *et al.*, 2014; Capra *et al.*, 2014; Cucherousset *et al.*, 2018). As its presence in the Aisne River is attested since the beginning of the 2010s (Duntze, 2012), it is supposed to display a new invader's behaviour (Carol *et al.*, 2007, 2009; Gago *et al.*, 2016; Ferreira *et al.*, 2019; Vagnon *et al.*, 2022). Both species have also been used in previous telemetric studies (*e.g.*, Andersen *et al.*, 2008; Capra *et al.*, 2014; Pauwels *et al.*, 2017; Lenhardt *et al.*, 2021).

This paper describes the behaviour and the niches of both fish species in the Aisne River during highest flows of the 2020-2021 winter. A better understanding of their adaptation to extreme hydraulic events may provide answers to both environmental and sociological challenges.

## MATERIALS AND METHODS

### Study area

Our study area is a section of the wild or non-shipping Aisne River, belonging to the Seine drainage, about 120 km north of Paris. This section of 17.5 km stretches between two dams: Evergnicourt, upstream and Berry-au-Bac, downstream (Fig. 1).

The lower part, influenced by the Berry-au-Bac weir, is slightly wider than the upper part. The minor riverbed width ranges from 20 to 56 m, with an average of *ca.* 35 m measured in summer. Depth measured in May varies between 1 and 5 m in the deepest pits, mostly located downstream. The river essentially follows its original stretch, apart from some former arms that have been rectified. Its environment is rural with numerous fields, particularly cereals, as well as pastures for cattle and equines (Moreau *et al.*, 2016). It also passes through several small towns (200 to 700 inhabitants): upstream to downstream: Evergnicourt, Neuchâtel-sur-Aisne, Variscourt, Condé-sur-Suippe, and Berry-au-Bac.

A channel built in 1842 runs along the river to allow navigation (Matton, 1871). However, there is no connection between those two water bodies in the study section, even during floods, because of the dyke between them (Fig. 1).

This section of the Aisne River has characteristics of the grayling to barbel zones *sensu* (Huet, 1954) including rheophilic species (*Leuciscus leuciscus* (Linnaeus, 1758), *Barbus barbus* (Linnaeus, 1758), *Cottus perifretum* Freyhof,

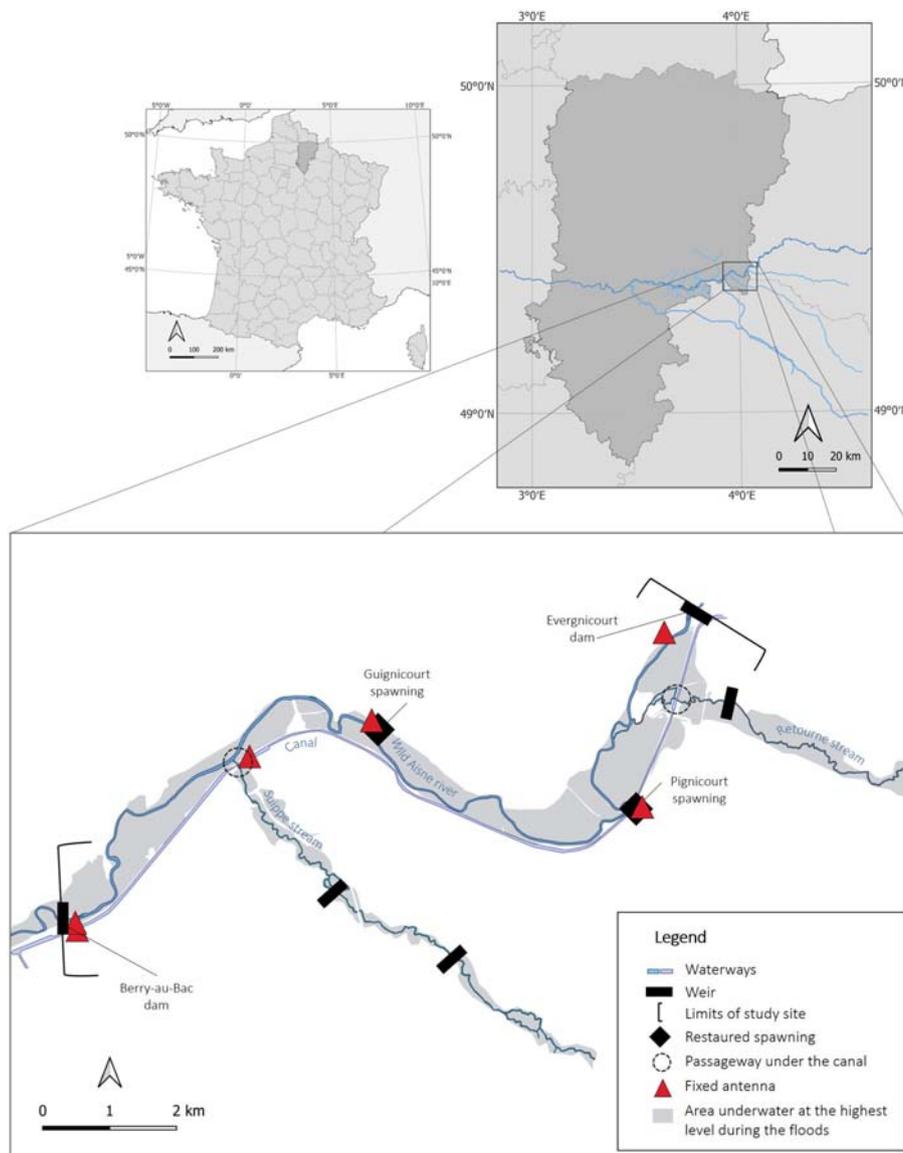


Figure 1. – Map of the study site and locations of fixed antennas, points of interest, and maximum extension of the flooded area estimated from field observations, GPS recordings and analysis of the contours of the land.

Kottelat & Nolte, 2005, *Squalius cephalus* (Linnaeus, 1758), *Pungitius* sp., *Gobio gobio* (Linnaeus, 1758), *Barbatula* sp., *Cobitis taenia* Linnaeus, 1758 and *Lota lota* (Linnaeus, 1758)), as well as some limnophilic species (*Esox lucius*, *Silurus glanis* and also *Alburnus alburnus* (Linnaeus, 1758), *Rutilus rutilus* (Linnaeus, 1758), *Anguilla anguilla* (Linnaeus, 1758) and *Perca fluviatilis* (Linnaeus, 1758)) (Duntze, 2012).

The European catfish was not yet formally recorded in this part of the river but was already reported in the channelized section situated about 50 km downstream (Duntze, 2012). However, the presence of this species has since been regularly reported by anglers, and several individuals were indeed caught in September 2020 for this study.

Two tributaries supply the river in this section, the Retourne stream and the Suippe stream, taking their water

mainly from rainwater and groundwater, respectively (Cao *et al.*, 2018). They share the particularity to run under the channel before joining the Aisne River, using two passages of about 12 m long on the Suippe stream and 35 m on the Retourne stream (estimated from satellite images).

For northern pike, two spawning areas of the main river were recently restored by the local angling Federation (FAPPMA 02) in Pignicourt in 2018 and Guignicourt in 2019. They are side arms, which have been cleared of their timber and bushes, and whose slopes have been levelled to maximize usable surfaces.

#### Definition of the concept of flood

We defined the notion of “flood” as the moment when the river was perceptibly expanding out of its minor bed. According to our in-field observations, this consistently hap-

pened when the waterflow reached about  $70 \text{ m}^3 \cdot \text{s}^{-1}$  according to measures by the French Navigable Waterways society (VNF) and the website vigicrues (<https://www.vigicrues.gouv.fr>). This flow rate is estimated using a linear regression and the water level recorded at the Berry-au-Bac weir. The flood was accordingly considered over under this limit, when the river visually came back to its original course (Fig. 1).

### Sampling, tagging and tracking

The experiment took place between October 2020 and March 2021 in the wild Aisne River. The channel running along its side was not included. Northern pikes and European catfish were marked in three sessions: September 21<sup>st</sup> and 22<sup>nd</sup> and October 15<sup>th</sup>, 2020. The captures were carried out by an electrofishing-boat with 5 operators that captured 10 northern pikes and 7 catfish in 16 hours, and 37 anglers who caught 20 northern pikes for an average of 5.5 hours per angler.

Individuals of both species were transported from their capture zone to a marking area located in the middle of the study section and placed in an 800 L-oxygenated tank. They were anaesthetized using eugenol (4-allyl-2-methoxyphenol) at a concentration of  $0.04 \text{ ml} \cdot \text{l}^{-1}$  (Zaikov *et al.*, 2008). They were then weighted, measured, and tagged with a unique identification number, attached below their dorsal fin. For northern pikes, sexes were determined according to the genital papillae (Raat, 1988), and ages were estimated by scalimetry (Baglinière and Le Louarn, 1987). Northern pikes and European catfish of less than one meter in length were then implanted with Sigma TX-PSC-I-450-M Radio Transmitter (length 46 mm, diameter 12 mm, weight 8.5 g in water) and larger European catfish with Sigma TX-PSC-E-1200-M Radio Transmitter (length 57 mm, diameter 17 mm, weight 18.0 g in water) (Sigma Eight Inc., Aurora, Canada; <https://sigmaeight.ca/>). This choice was made following Winter's law that recommends that a tag should not exceed 2% of the total weight of an individual (Winter, 1996). These tags emit a signal specific to each individual every three seconds, and have already been proven efficient to monitor the movement of wild fish (Kock *et al.*, 2021). Fish were then transported back and released as close to their capture zone as possible.

All operations were carried out by a specialized operator, in accordance with European directive no. 2010/63/EU of 22 September 2010, with articles L214-3 and R.214-87 to R.214-137 and R.215-10 of the Rural Code, and with the Decree in Council of State of the 1<sup>st</sup> February 2013, relating to the protection and well-being of animals used for scientific purposes.

Between October 2020 and March 2021, the tagged fish were located using 7 antennas (Sigma Eight Inc., Aurora, Canada): six "fixed" Orion three-element Yagi antennas split between particular positions of the study zone (the two dams, the two tributaries and the two spawning areas, cf. Fig. 1)

and one Orion "mobile" omni-directional monopole whip antenna carried along the shores once a week. This particular antenna was chosen because of its practicality, in particular when walking through areas of dense vegetation.

All Orion receivers also recorded the signal strength of every detection in decibels per milliwatt (dBm). This allowed to pinpoint the moment when a fish was the closest to an antenna. However, it proved impossible to accurately estimate the distance of detection from antennas: significant differences were observed whether the weather was dry or rainy ( $-2.87 \text{ dBm}$  on average). The most substantial loss of range was observed during windy weather ( $-9.91 \text{ dBm}$  on average).

The "fixed" antennas continuously recorded the passage of fish in front of them and in their immediate surroundings. The records were gathered into daily passages, which means that a fish which stayed  $n$  days in front of an antenna appeared to have been recorded  $n$  times. This method was used to reduce the differences between the fixed and mobile antennas in order to use the two types of detections together and not to over-represent the former in our data.

In addition, to avoid false detections due to outside noises, individuals were only considered to have been effectively near the antenna if they had been recorded twice in a day, less than 30 s apart.

Routine monitoring with the "mobile" antenna consisted of covering the whole study zone once a week, mostly by alternatively walking the two shores. The tributaries were also surveyed at the same frequency, approximately on their first 3 km. However, only about half of their length was effectively reachable because of the many private properties surrounding them.

During the floods, the walks were conducted in wading boots, as close to the minor riverbeds as possible, given the level and flow of water.

When a fish was detected with the mobile antenna, its position and the signal strength was recorded using the Orion Listener application (Sigma Eight) and a GPS (Garmin eTrex Touch 35). We also noted whether the fish was located in the minor riverbed, the in Suippe or in the Retourne streams, at their confluence with the Aisne River, in flooded fields, flooded pastures or meadows, flooded forests or undergrowth, flooded gardens, or in one of the two restored spawning areas (Fig. 1).

If the fish was in the minor riverbed or in one of the tributaries, only its position reported on the midline of the river (kilometric point from the confluence with the Oise River, noted KP) was used to avoid any hazardous estimation of its lateral position (Masters *et al.*, 2005; Pauwels *et al.*, 2014). However, when detected in flooded lands, its exact position was estimated by approaching it as much as possible, and using triangulation from several points within the flooded

area. Positions were plotted and analyzed using QGIS (QGIS Development Team, 2009).

### Data treatments

We made the hypothesis, based on field observations, that within the two months before the floods, northern pikes and European catfish stayed mostly in “preferential zones”, which can be seen as a particular case of “core areas” as defined by Skov *et al.* (2018), with some occasional short excursions out of them. Catfish seemingly maintained this behaviour throughout the whole study, whereas northern pikes tended to modify their behaviour when waterflow increased.

The average width of those zones “before flood” was estimated for both species using data collected between October 1, 2020 and December 23, 2020. For catfish, this width was computed a second time for comparison with data collected during the floods, between December 24, 2020 and February 24, 2020. Data from the first two weeks after tagging were deleted, to avoid potential unusual behaviour following tag implantation (Beaumont *et al.*, 2002). Positions recorded with the fixed antennas were also dismissed in this calculation, due to their imprecision compared to the mobile antenna.

The number of individual fixes before flood was not sufficient to estimate a reliable home range for each fish before the flood (Knight *et al.*, 2009). Instead, we opted for an approach at the dataset level of estimating an average home range for each species. In a day, fish were considered able to entirely cross the space within and around their relative “preferential zones”, as supported by their respective swimming capacities (Carbine and Applegate, 1946; Jones *et al.*, 1974; Carol *et al.*, 2007; Skov *et al.*, 2018). Thus, the positions recorded before the flood for northern pikes, and during the whole study for European catfish, were regarded as biologically independent of each other (Silva-Opps and Opps, 2011), insofar as the individual performs the majority of its movements within a preferential zone that it is able to cover several times in a day, given his swimming abilities.

For each fish we used the distance from median point at a day  $i$  ( $DM_i$ ) defined as the distance between the recorded kilometric point on day  $i$  ( $KP_i$ ) with the median kilometric point  $KP_m$  recorded for this fish. Distribution of  $DM_i$ s downstream and upstream were comparable before flood for both species, and also during the floods for catfish (verified with Mann-Whitney U tests at the 0.05% threshold). We thus used absolute values to treat them together:  $DM_i = |KP_i - KP_m|$ . The width of a zone was defined as the 90<sup>th</sup> percentile of  $DM_i$ s. Above this threshold, the  $DM_i$  cumulative frequency curve seemed to approach a plateau, and we assimilated these positions to occasional “exploratory” movements out of preferential zones.

For northern pikes, we then analysed the departure of the “preferential zones” during floods in order to categorize the behaviour of each individual in reaction to the change in waterflow. A fish was considered to have left its original zone if it at least half of its fixes during the floods were outside of it. It was considered back as soon as a position is recorded within the zone after the floods.

Finally, movements were categorized according to their direction, upstream or downstream. The cumulative distance and number of movements downstream and upstream was computed, and the difference between those values was analysed against the waterflow with a generalized linear regression (GLM) to identify eventual reactions to flow in terms of amplitude and direction of the movements.

Data treatments and statistic tests (Kruskal Wallis and Mann-Whitney tests) used R (R Core Team, 2020) and the package “riverdist” (Tyers, 2021). Graphic representations were made with “ggplot2” (Wickham, 2016).

## RESULTS

The Aisne River was subject to a first major flood from 24<sup>th</sup> December 2020 to the 05<sup>th</sup> January 2021 that reached a flow of  $130 \text{ m}^3 \cdot \text{s}^{-1}$ , which is not uncommon for this region. A second lasted longer, from 15<sup>th</sup> January 2021 to 23<sup>rd</sup> February 2021, reached a waterflow of  $260 \text{ m}^3 \cdot \text{s}^{-1}$ , making it a 5-year flood event (Anonymous, 2008). No other flood occurred during the study (Fig. 2).

Between 21<sup>st</sup> September 2020 and 31<sup>st</sup> March 2021, 535 fish positions were recorded with the mobile antenna while 482 daily passages were recorded by the fixed antennas.

### Tracking

Thirty northern pikes (6 males and 24 females, 44 to 82 cm fork length, age 2.8 to 5.8) and seven European catfish (unsexed, 68 to 155 cm) were caught by electrofishing or angling in three sessions, on September 21<sup>st</sup> and 22<sup>nd</sup> and then on October 15<sup>th</sup>, 2020 (Table I). Of the 30 northern pikes caught, only one (a female no. 135) has not been detected since November 2020 and was not included in our analysis.

All movements recordings are available in the Supplementary file 1.

### Northern pike

#### Longitudinal movements

Throughout the study, the number of movements recorded downstream or upstream appeared very similar, with a total of 275 and 273, respectively. However, in the first half of the study, more movements were recorded directed upstream, while this tendency changed after December. The

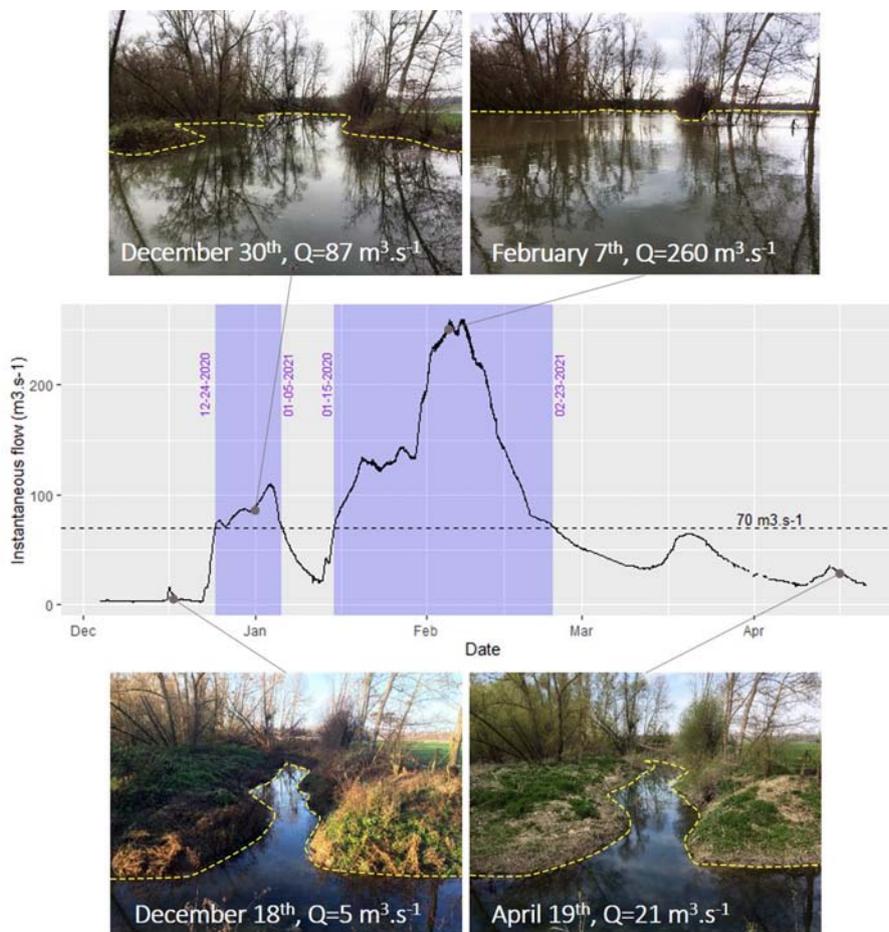


Figure 2. – Evolution of the waterflow between December 2020 and April 2021 (Photos of the restored Pignicourt spawning area taken before, during and after the floods. The water level rose considerably, flooding the spawning area and the surrounding fields in winter, before dropping again considerably from the end of February. The flow indicated was measured in Berry-au-Bac).

total cumulative distance swum downstream was 7.7% higher at the end of the study (18.8 km against 17.3 km).

The GLM shows that waterflow is positively linked to the difference in cumulative distance upstream to downstream (Fisher test,  $p$ -value =  $1.972e^{-7}$ ), but negatively linked to their difference in number (Fisher test,  $p$ -value <  $2.2e^{-16}$ ). Thus, as flow increased, the movements appeared more often directed downstream, but conversely the movements directed upstream were also of higher amplitude (Fig. S1).

The average width of a pre-flood “preferential zone” was estimated at  $\pm 632$  m of the midpoint. “Explorative” movements (outside of zones) happened significantly more often upstream than downstream (McNemar’s Chi-squared test,  $p$ -value =  $1.893e^{-11}$ ): 96.1% of the MDM<sub>i</sub> directed downstream happened within the limits of a preferential zone against 89.7% of the MDM<sub>i</sub> upstream.

Three principal behaviours were observed during and after the floods: some northern pikes, that we called “returned”, left their “original” zone and came back to it afterwards; some “departed” left but did not come back; and some others, “sedentary”, did not leave at all (Table II). Two fish could not be classified. One because its behaviour

did not fit in any of those categories, and another because it swam down the Berry-au-Bac dam during the second flood and therefore left the study zone without being able to come back. Two northern pikes died and were therefore kept out of the analysis. Five fish were not detected at all during the floods. One of them is however considered to have stayed in the Suipe stream, as it was detected there just before and after the flood and was not recorded at the confluence by the fixed antenna in-between. The lack of detection was mostly due to difficulties of access to the flooded affluent.

Of the 21 remaining fish which were effectively followed during the whole period, 9 belong to the “returned” group, 5 to the “departed” group and 7 to the “sedentary” group.

No behavioural difference appeared between males and females. However, fish in the “departed” group were significantly larger than those in the other groups: at a 5% threshold (Mann-Whitney,  $p$ -value = 0.030) for the “sedentary” group and at a 10% threshold (Mann-Whitney,  $p$ -value = 0.067) for the “returned” group (Fig. 3). All three behaviours are described below taking as example a model individual.

The individual no 155, a 58 cm-long female, showed a behaviour typical of the “explorer” group (Fig. 4): display-

Table I. – Identification and characteristics of each marked sample of northern pike and European catfish, in their order of capture. Ages are estimated from scalimetric analysis. Anaesthesia and awakening times are given in minutes.

| Species | Tag ID | Spaghetti number | Length (cm) | Weight (g) | Sex         | Age (year)  | Date of capture | Anaesthesia time |         | Awakening time |
|---------|--------|------------------|-------------|------------|-------------|-------------|-----------------|------------------|---------|----------------|
|         |        |                  |             |            |             |             |                 | Stabulation      | Surgery |                |
| Catfish | 22     | 9632             | 73          | 2214       | <i>n.a.</i> | <i>n.a.</i> | 21-sep          | 3                | 3       | 9              |
| Catfish | 55     | 9544             | 106         | 6090       | <i>n.a.</i> | <i>n.a.</i> | 22-sep          | 5                | 9       | 14             |
| Catfish | 94     | 9545             | 93          | 4920       | <i>n.a.</i> | <i>n.a.</i> | 22-sep          | 5                | 11      | 14             |
| Catfish | 112    | 9628             | 150         |            | <i>n.a.</i> | <i>n.a.</i> | 21-sep          | 7                | 15      | <i>n.a.</i>    |
| Catfish | 117    | 9534             | 155         |            | <i>n.a.</i> | <i>n.a.</i> | 22-sep          | 4                | 10      | 20             |
| Catfish | 133    | 9539             | 68          | 1745       | <i>n.a.</i> | <i>n.a.</i> | 22-sep          | 4                | 8       | 15             |
| Catfish | 161    | 9522             | 142         |            | <i>n.a.</i> | <i>n.a.</i> | 21-sep          | 4                | 10      | <i>n.a.</i>    |
| Pike    | 24     | 9634             | 53          | 1004       | ♀           | 2.8         | 21-sep          | 4                | 10      | 7              |
| Pike    | 40     | 9603             | 66          | 1630       | ♀           | 3.8         | 15-oct          | 3                | 6       | 10             |
| Pike    | 52     | 9537             | 63          | 1435       | ♀           | 2.8         | 22-sep          | 4                | 8       | 7              |
| Pike    | 53     | 9631             | 70          | 2090       | ♀           | <i>n.a.</i> | 21-sep          | 3                | 9       | 6              |
| Pike    | 63     | 9629             | 50          | 654        | ♀           | 2.8         | 21-sep          | 4                | 9       | 3              |
| Pike    | 64     | 9543             | 44          | 536        | ♂           | 2.8         | 22-sep          | 3                | 9       | 5              |
| Pike    | 73     | 9630             | 73          | 2584       | ♀           | 4.8         | 21-sep          | 5                | 7       | 5              |
| Pike    | 74     | 9542             | 52          | 850        | ♀           | 3.8         | 22-sep          | 4                | 9       | 5              |
| Pike    | 83     | 9535             | 74          | 2740       | ♀           | 4.8         | 22-sep          | 5                | 9       | 4              |
| Pike    | 89     | 9523             | 67          | 1672       | ♂           | 3.8         | 21-sep          | 4                | 12      | 4              |
| Pike    | 90     | 9525             | 70          | 2220       | ♀           | 4.8         | 21-sep          | 4                | 8       | 4              |
| Pike    | 93     | 9601             | 56          | 1065       | ♀           | 2.8         | 15-oct          | 2                | 4       | 5              |
| Pike    | 96     | 9551             | 72          | 2430       | ♀           | 4.8         | 15-oct          | 4                | 7       | 14             |
| Pike    | 101    | 9536             | 49          | 760        | ♂           | 2.8         | 22-sep          | 4                | 7       | 2              |
| Pike    | 111    | 9549             | 64          | 1860       | ♀           | 4.8         | 22-sep          | 4                | 8       | 10             |
| Pike    | 120    | 9524             | 47          | 660        | ♀           | 2.8         | 21-sep          | 4                | 8       | 4              |
| Pike    | 122    | 9626             | 53          | 1034       | ♂           | 3.8         | 21-sep          | 4                | 9       | 4              |
| Pike    | 135    | 9607             | 70          | 2120       | ♀           | 4.8         | 15-oct          | 5                | 8       | 15             |
| Pike    | 139    | 9548             | 57          | 1227       | ♀           | 2.8         | 22-sep          | 6                | 10      | 8              |
| Pike    | 150    | 9609             | 58          | 1075       | ♂           | 2.8         | 15-oct          | 5                | 7       | 20             |
| Pike    | 155    | 9541-9540        | 58          | 1125       | ♀           | 3.8         | 22-sep          | 5                | 10      | 4              |
| Pike    | 164    | 9627             | 75          | 2685       | ♀           | 5.8         | 21-sep          | 4                | 8       | 5              |
| Pike    | 166    | 9547-9546        | 75          | 2850       | ♀           | 4.8         | 22-sep          | 4                | 9       | <i>n.a.</i>    |
| Pike    | 179    | 9608             | 56          | 1081       | ♂           | 4.8         | 15-oct          | 3                | 7       | 12             |
| Pike    | 181    | 9605             | 82          | 3069       | ♀           | 5.8         | 15-oct          | 4                | 9       | 14             |
| Pike    | 188    | 9602             | 53          | 843        | ♀           | 2.8         | 15-oct          | 3                | 7       | 7              |
| Pike    | 200    | 9604             | 72          | 2396       | ♀           | <i>n.a.</i> | 15-oct          | 4                | 7       | 10             |
| Pike    | 202    | 9538             | 74          | 2558       | ♀           | 3.8         | 22-sep          | 4                | 10      | 6              |
| Pike    | 210    | 9550             | 56          | 1182       | ♀           | 2.8         | 22-sep          | 3                | 9       | 10             |
| Pike    | 212    | 9606             | 52          | 759        | ♀           | <i>n.a.</i> | 15-oct          | 3                | 7       | 7              |

Table II. – The three pike behaviours observed during both floods, their characteristics and the number of individuals belong in each.

| Behaviour                | During floods   | After floods               | N |
|--------------------------|---|----------------------------|---|
| Explorer                 | Research for new habitat ( $\geq 50\%$ fixes out of “zone”) | Return to original zone    | 9 |
| Departed                 | Research for new habitat ( $\geq 50\%$ fixes out of “zone”) | No return to original zone | 5 |
| Sedentary                | No research for new habitat ( $< 50\%$ fixes out of “zone”) | Stay on original zone      | 7 |
| Predated                 |   |                            | 2 |
| Disappeared before flood |   |                            | 1 |
| Insufficient data        |   |                            | 4 |
| Untypical behaviour      |   |                            | 2 |

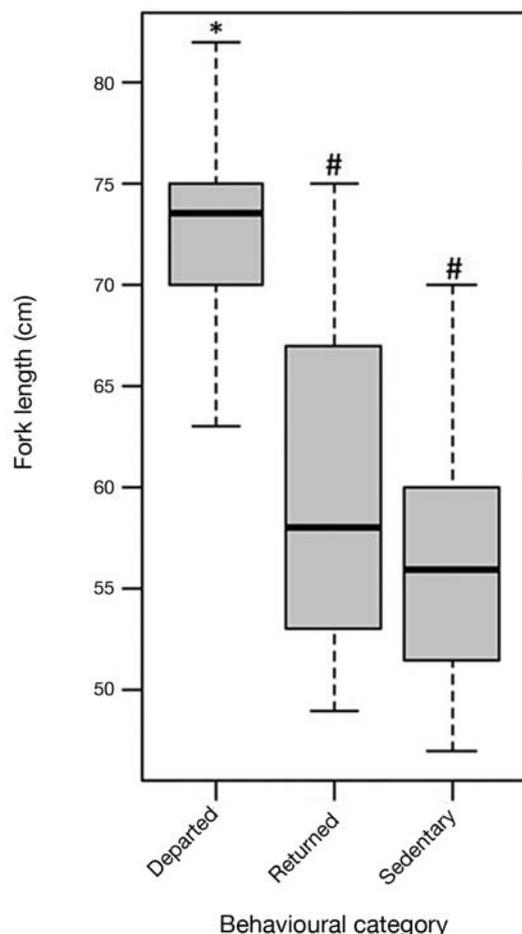


Figure 3. –Boxplot characterizing the sizes ranges per behavioural group of northern pikes

ing a relatively territorial comportment before the floods, it remained mainly in an area west of Guignicourt. The floods, especially the second one, seemed however to be the starting point for a new exploratory behaviour. The northern pike moved upstream until the Retourne stream, which it entered on the 1<sup>st</sup> of February, 2021. On the 8<sup>th</sup> of February, it was found in the flooded pastures in Neufchatel. It then came back to the main stream as waterflow lowered, where it was detected on the 16<sup>th</sup> of February near the Retourne stream. After a regular descent in the main river, it was detected again its pre-flood zone on the 17<sup>th</sup> of March and remained there.

The northern pike no. 83 is a 74 cm-long female that showed a behaviour typical of the “departed” group (Fig. 5): it also remained mainly west of Guignicourt before the flood. When waterflow started to increase, it swam upstream and was detected several times in the Pignicourt spawning area at the highest of the floods. It then swam upstream once again and reached the Retourne stream where it stayed, even after the water level went down.

Finally, the northern pike no. 111 is a 64 cm-long female

and presents a “sedentary” behaviour: after its release, it spent some time downriver before settling from October 22<sup>th</sup>, 2020 near the Guignicourt bridge. Its location stayed almost the same during and after the floods (Fig. 6). We were able to rule out the hypothesis of following dead or predated individuals thanks to the monitoring of fish for another 6 months after the end of this survey; seeing then that they resumed an activity.

#### Lateral movements

During the first flood, most of the northern pikes stayed in the minor riverbed. A few were detected in the restored Guignicourt spawning area, as well as in the confluence with the Suipe stream, where it was observed that the current speed was lower and the water less turbid. One fish also crossed the passage under the canal and swam upriver in the Suipe stream, and one was found in a flooded pasture about 20 m from the minor riverbed (Fig. 7).

During the second flood, a wider range of new habitats were flooded, and 13 northern pikes were recorded in those inundated areas, from 15 to about 300 m of the minor riverbed nearest point. Three northern pikes were recorded in the tributaries, one (no. 181) in the Suipe stream and two (no. 150 and no. 200) in the Retourne stream. The northern pike no. 155 was recorded at the confluence of the Retourne stream before probably leaving the minor bed to explore flooded pastures upstream (Fig. 4). The two others both crossed the tunnels under the canal, even though the water-flow coming from them at this time was consequent (Fig. 6). Those lateral movements and habitat utilization were observed in fish from all three groups mentioned above, and no difference could be observed between males and females.

After the floods, 24 northern pikes were retrieved alive in the riverbed despite the quick drop of the water level.

As an example (Fig. 8), the northern pike no 166 was detected in a flooded forest on 1<sup>st</sup> February. It was found in the minor riverbed after the water level decreased on the 23<sup>rd</sup>. Both locations are very near to each other; however, the river in this area was overflowing the field and the forest during the flood, making it hard to swim back to the river using the shortest perpendicular route.

Detections on the 26<sup>th</sup> of January and on the 6<sup>th</sup> of February 2021 at the confluence of the Suipe suggest that to reach this area and to leave it, the northern pike used the same easier path twice, following the dike, rather than swimming in the strong currents.

Four northern pikes were still missing at the end of the study (no. 73, 212, 139 and 135).

One of the northern pikes, a 52 cm female (no. 188), was found on February 19<sup>th</sup> in a flooded meadow that was no longer in contact with the river. On the next pass (25<sup>th</sup> February), the tag could not be detected despite a thorough search of the area. Many birds, in particular egrets, were present on

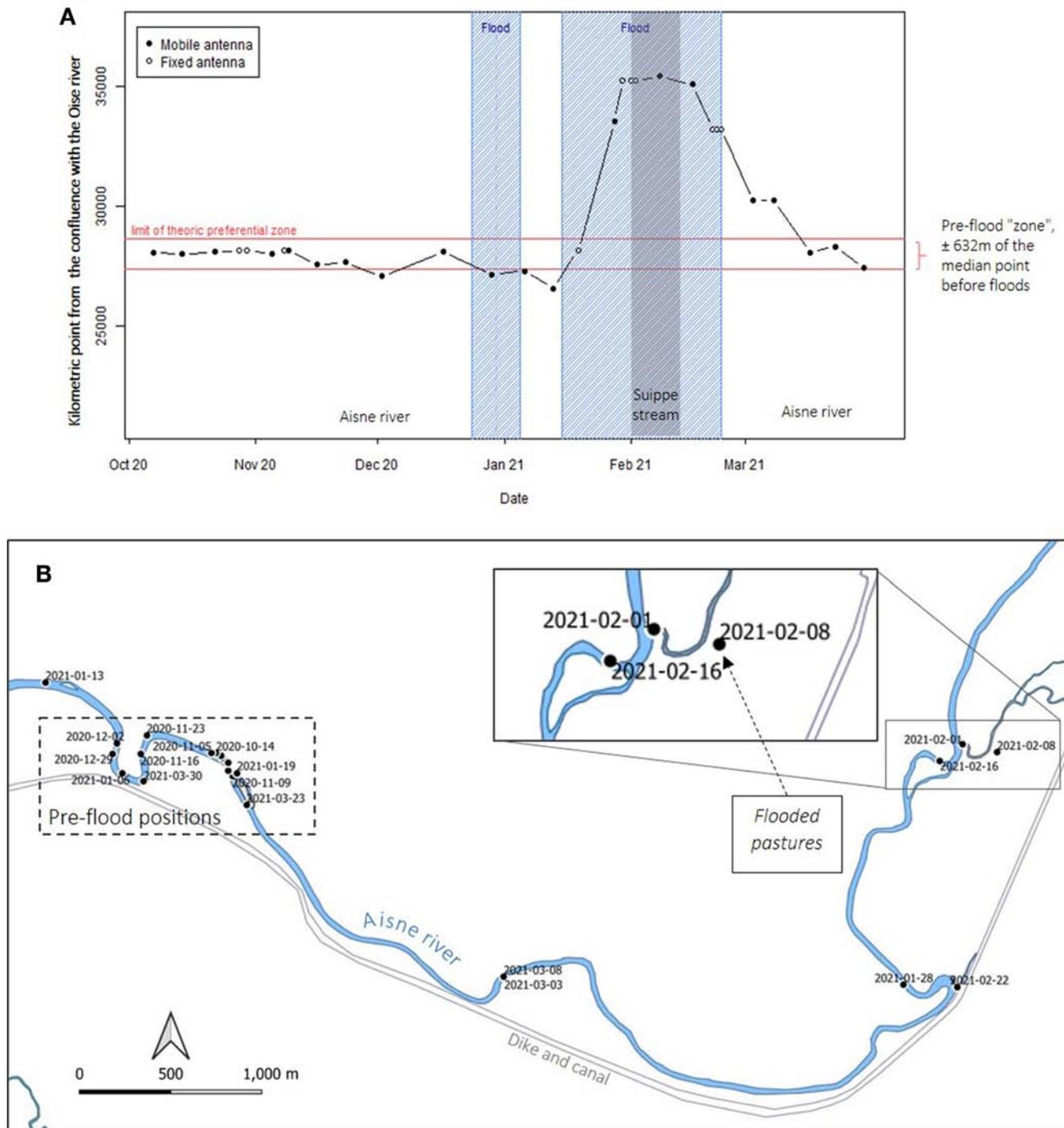


Figure 4. – Kilometric points recorded (A) and fixes (B) of the pike no 155 between October 2020 and March 2021.

the spot. The radio tag was then retrieved alone later under a bush near this area. Numerous droppings on the ground observed near to it suggest that this bush is used regularly as a perch for birds.

This could suggest predation by waterfowl on fish, including northern pikes, trapped by the recession.

**European catfish**

*Longitudinal movements*

The behaviour of the European catfish seemed to vary between individuals: five of them (ranging from 68 to 142 cm) were almost always detected in their preferential zone (Fig. 9). The two remaining (150 and 155 cm)

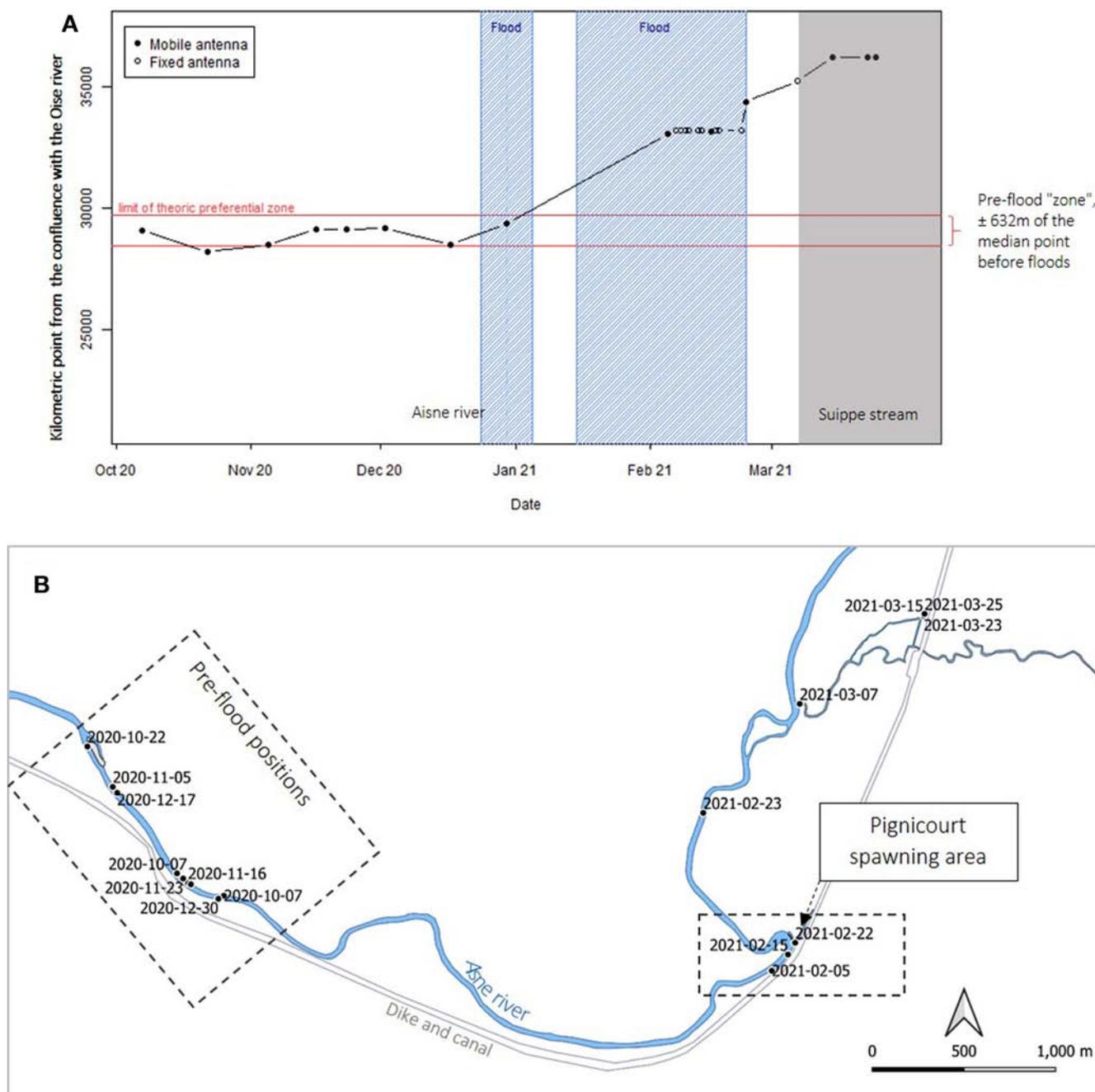


Figure 5. – Kilometric points recorded (A) and fixes (B) of the pike no 83 between October 2020 and March 2021.

seemed to explore a larger area. However, the number 117 was detected only once before the flood, and only by fixed antenna or in flooded land during floods, and could not be included in the following calculations.

The width of the preferential zone was estimated to be  $\pm 338$  m of the midpoint before the floods. All downstream movement happened inside this zone, whereas 9.9% of the upstream movements were recorded as “exploratory” (outside of the zones).

This pattern stayed remarkably steady during the floods: the preferential zone width was estimated at  $\pm 274$  m of the midpoint, with all downstream movements located inside zones against 10% of “exploratory” movements directed upstream.

In general, in terms of number as well as cumulated distance, the catfish seemed to favour upstream movements. Fifty-three movements were recorded upstream against 42 downstream, for a cumulated distance of 3.5 km and 2.9 km,

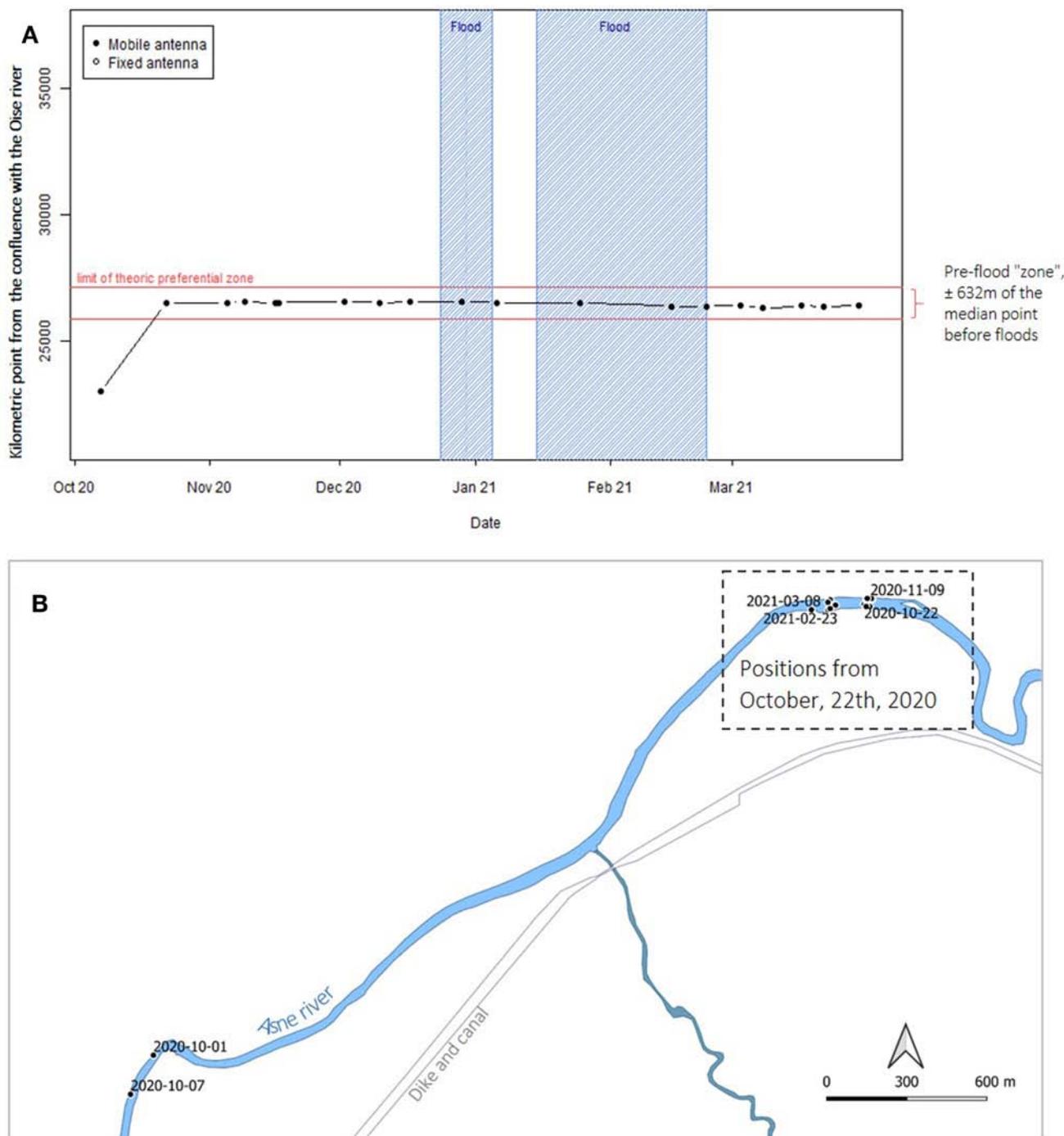


Figure 6. – Kilometric points recorded (A) and fixes (B) of the pike no 111 between October 2020 and March 2021.

respectively, *i.e.* a 17% difference.

Moreover, the GLM shows that response to waterflow was slightly different for European catfish and northern pikes. Increase in flow is negatively linked to the difference in cumulative distance upstream to downstream (Fisher test,  $p\text{-value} = 6.44e^{-5}$ ), but positively linked to their difference in number (Fisher test,  $p\text{-value} < 2.2e^{-16}$ ). Thus, as flow

increased, European catfish reacted by swimming more often upstream, but with lesser amplitudes (Fig. S2).

*Lateral movements*

All the European catfish, except the largest one (no. 117, 155 cm), were detected only in the minor riverbed during the floods. However, the individual no. 117 showed an important

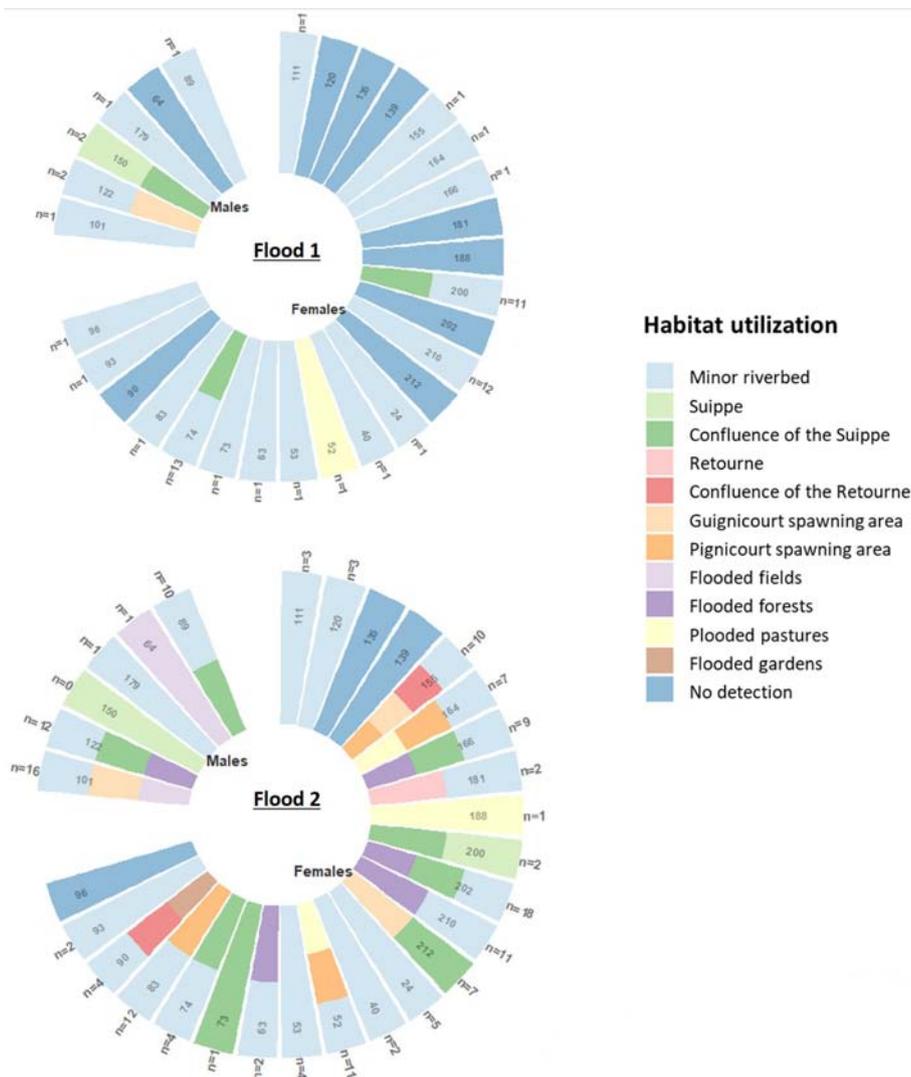


Figure 7. – Habitats used during the two floods by male and female northern pikes. One bar represents one pike, and the number of detections during the flood is indicated on top of each bar.

explorative behaviour: it was detected by the fixed antenna in the Guignicourt spawning area on the 2<sup>nd</sup> and 3<sup>rd</sup> of February, and one day later with the mobile antenna, in a flooded field about 375 m from the minor riverbed. The northern pike no. 64, 440 mm, which was lost during the first part of the second flood, was detected at the exact same times and places. The detection of the northern pike happened both time when the catfish was the nearest to the antenna, and it was no longer detected when the catfish was further. When floodwaters receded, the northern pike’s radiotag was retrieved alone in this field.

It is a strong evidence to suggest either predation or scavenging of the European catfish on the northern pike, which happened probably in the end of January. The European catfish was found back in the riverbed after the flood, near the place where the northern pike’s tag was retrieved (Fig. 10).

## DISCUSSION

Our survey, using a telemetric approach with radio tags and antennas, provided valuable data on the usage of new habitats by both northern pike and European catfish during winter floods. Behaviours of both species were then characterized.

### Northern pike behaviour

Of the 30 northern pikes caught, only one (no. 135) was not used in our dataset. We hypothesize that this one was probably angled at the beginning of November. Data from the 29 other specimens allowed us to better understand the species behaviour in the Aisne River during the winter floods.

Northern pike can leave the riverbed to explore new areas when waterflow reaches a certain level (Masters *et al.*, 2002;

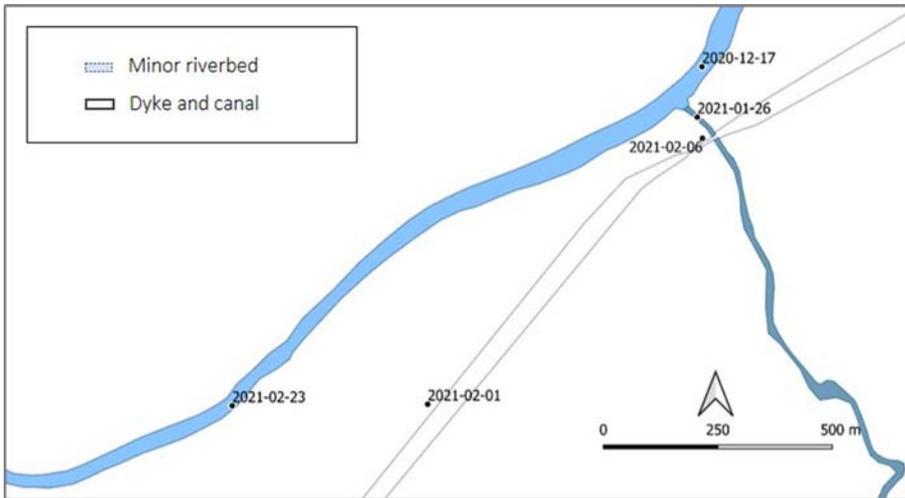


Figure 8. – Successive positions of the pike no. 166 during and after flood and supposed route that was followed.

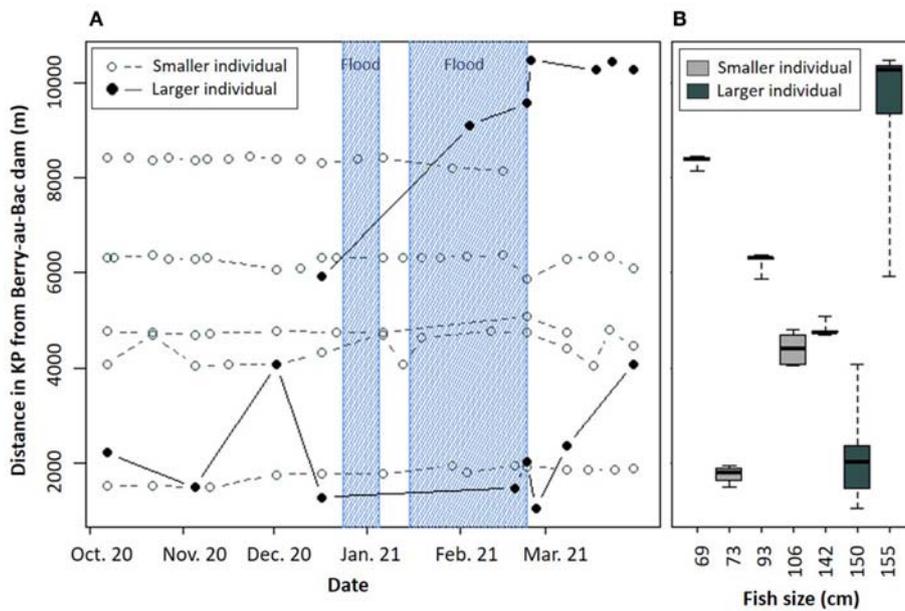


Figure 9. – Distance (in meters) from the Berry-au-Bac dam KP of the 5 smaller catfishes (light) and the two larger (dark) versus time (a) or size (b)

Kobler *et al.*, 2008; Pauwels *et al.*, 2017). Our results about *E. lucius* highlighted three types of behaviours: “sedentary”, “returned” and “departed”. Post-flood homing was observed in a large number of displaced individuals. This was already described by Langford (1981), who monitored the natural or experimental movement of individuals during floods in the regulated Thames, up to 1.5 km. In this study, northern pikes mainly homed to their pre-flood location afterwards.

In at least one observed case, northern pikes favoured paths with lesser currents during floods. Northern pikes tended to stay in slower-flowing glides, pools, backwaters and side channels (DosSantos, 1991; Lamouroux *et al.*, 1999; Masters *et al.*, 2002; Knight *et al.*, 2009; Skov *et al.*, 2018). Moreover, the current in the river channel during the flood (estimated from the instantaneous flow divided by the vertical section of the river at the time of the floods at Berry-

au-Bac) seems to have reached a speed of up to 1 m.s<sup>-1</sup>. If northern pikes show excellent burst swimming capabilities (Webb and Skadsen, 1980), they cannot sustain high performances for long, and a critical swimming speed (Ucrit) was estimated to be of about the body length.s<sup>-1</sup> (Jones *et al.*, 1974). It would have been in this regard highly improbable for northern pikes ranging from 44 to 82 cm in body lengths to swim directly against the strongest currents.

It also seems that larger fish tend to explore further and are more inclined to stay in new areas instead of returning to their “usual” territory after the floods. Conversely, the smaller individuals seem to stay closer to their pre-flood habitat despite the increase in waterflow. We suggest that experience and the decrease in the number of predators as they grow could allow bigger individuals to venture more easily and for a longer time outside their usual zones. This would be con-

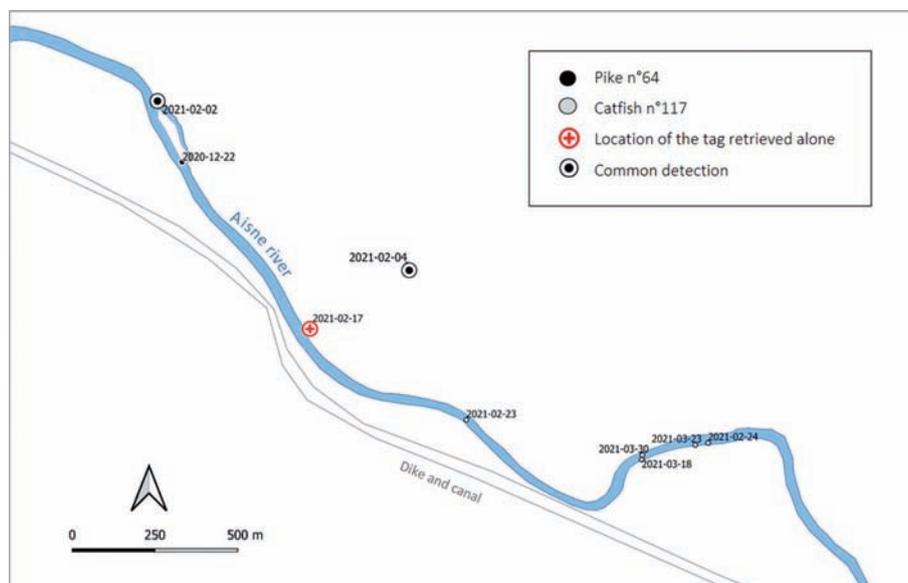


Figure 10. – Correspondence of the positions of the pike no 64 and the European catfish no. 117 on the 2<sup>nd</sup> and 4<sup>th</sup> or February. The cross corresponds to the place where the pike's tag was retrieved, on the 17<sup>th</sup> of February. The European catfish is seen alone in the river nearby on the 23<sup>rd</sup>.

sistent with the observations of Grimm and Klinge (1996) showing that northern pikes over 53 cm are less restricted to areas protected by vegetation than smaller ones. Chapman and Mackay (1984) even showed that the largest individuals (> 65 cm) were free to move from bank areas to more exposed extra-coastal zones.

Two hypotheses could explain the exploratory behaviour of northern pikes during floods (Masters *et al.*, 2002): (i) shelters- or food-seeking, (ii) cyprinids *sensu lato* move onto flooded lands to feed, either on other species of forage fish which also use these new habitats, or on terrestrial insects and worms, even if their calorie intake stays lower in winter than in summer (Diana, 1979).

The end of winter also coincides with the migration period, when northern pikes are known to often travel long distances (Koed *et al.*, 2006; Sandlund *et al.*, 2016). The movements of great amplitude observed in particular from February on could therefore also correspond to a research of suitable areas. Inventories and analyses on the fry would make it possible to date the start of spawning. This would indicate that individuals that do not “return” to their original zone (the “departed”) could be in the migratory stage and would maybe come back to it later. The “sedentary” and “returned” could then either have already carried out their reproduction, or on the contrary not be yet in their migratory stage.

It must nonetheless be noted that most of the centre of the flooded area was unreachable at the highest level of water, and thus detections at this time mostly reflect the behaviour of fish which were the closest to the shores. It is possible that some fish spent more time in the minor riverbed but were under-represented in our statistics due to the impossibility to reach them. As an example, the northern pike no. 179 was not detected at all during the floods but when water receded

was found again in the minor riverbed, very near to its last detection, suggesting that it might have just stayed on its original position. Several other fish were detected only a few times near the shores and could have spent more time in the riverbed without being effectively recorded there.

We also observed northern pikes in waters with low visibility. Northern pikes are known for mainly hunting and directing themselves visually (Craig and Babaluk, 1989; Craig, 2008). Thus, this result may challenge this idea and could suggest that northern pikes can use this environment as well, at least as a shelter. The idea that northern pikes can use other senses to hunt in turbid waters has also been developed by Andersen *et al.* (2008); they concluded that northern pikes could adapt to low visibility and turbid conditions by an increase in activity. Moreover, no differences were found by whether Jepsen *et al.* (2001) nor Andersen *et al.* (2008) when comparing the physical conditions of northern pikes living in lakes with different turbidities. It is therefore likely that a behavioural modification can compensate for these environmental variations.

### European catfish behaviour

*Silurus glanis* is not native in the wild Aisne and had not been observed before 2012 (Duntze, 2012). So the surveyed individuals belong to a young population benefiting favourable conditions and in particular a little-exploited ecological niche, allowing it to grow considerably (Proteau *et al.*, 2008).

The period we studied, October to March, usually corresponds to a drop in activity for *S. glanis* (Hilge, 1985; Proteau *et al.*, 2008; Copp *et al.*, 2009; Cucherousset *et al.*, 2018; Lenhardt *et al.*, 2021). Moreover, European catfish is often considered as a “flood quiescent” fish (Slavík and

Horký, 2012; Brevé *et al.*, 2014), displaying a high-site fidelity (Carol *et al.*, 2007; Capra *et al.*, 2014; Lenhardt *et al.*, 2021). A strong tendency to immobility was indeed observed for most of the European catfish in this study, and the width of the preferential zone was minimal during the December-February period. However, we were able to observe important differences in terms of movement amplitude during this particular time. This could suggest the ability of the species to keep a winter activity.

The two largest European catfish of the study (150 and 155 cm, respectively) were the most mobile, even though concomitantly a 142 cm-long individual was never detected outside of its preferential zone. It therefore seems that if size can be a factor explaining greater mobility in European catfish, an important individual variability also exists. In general, there does not seem to be any demonstrated difference in the movements of European catfish in relation to their size. For example, Slavík *et al.* (2007), in a telemetry study on 17 European catfish in Slovakia over two years, found no difference in terms of home range size relative to body length, although spatial segregation between juveniles (males under 83 cm and females under 86 cm) and adults was observed. It also seems that smallest European catfish are also able to move in winter: Daněk *et al.* (2014) found, with telemetry data, that juveniles could show high activity and displacement in winter as well, for example linked to oxygen deficiency. We therefore hypothesized that the differences we observed reflected distinguishable strategies adopted by European catfish during winter floods, for example a partial quiescence which would concern only a part of the individuals, in this case the smallest.

The autumn-winter period generally corresponds to a decrease in spatial resources, and the increase in flow leads to the dispersal of prey. Food availability and prey mobility are a factor influencing European catfish movements (Boujard, 1995; Bolliet *et al.*, 2001; Lenhardt *et al.*, 2021). It has also been shown that fish populations confronted to limited resources could divide themselves into two categories, the dominants and the sub-dominants, with different adopted behaviours (Fausch, 1984). Competition can in particular induce an increase in home range size and aggressiveness of dominant fish, and simultaneously a reduction in the spatial activity of the sub-dominants. The differences we observed could therefore correspond to this phenomenon, which would be consistent with the single observation of the European catfish no 117 outside the minor bed.

Likewise, cannibalism of larger European catfish on juveniles could result in some smaller individuals staying in restricted areas for safety. We have no data to estimate the importance of this behaviour in the region, and the subject has rarely been studied according to the literature. Yet, the size of the European catfish studied here makes it relatively unlikely that they will be eaten by other predators (perch,

pikeperch) (Keskinen and Marjomäki, 2004; Sandlund *et al.*, 2016) and, as European catfish fishing is still anecdotal in this part of the river, we can consider that the other catfish represent the most substantial danger in their direct environment, especially if other preys become scarcer. There are however different opinions on cannibalism in European catfish: if this behaviour is documented, some authors suggest that in colonization stages, cannibalism could be less common (Carol *et al.*, 2009; Vejřík *et al.*, 2017), inducing a greater recruitment and thus a positive dynamic of the population. Others consider that if European catfish diet tends to change slightly with age, it reflects the composition of available prey of suitable size and habitat use rather than a behavioural change (Omarov and Popova, 1985; Copp *et al.*, 2009).

Food intake and metabolic intensity of the European catfish have been shown to be strongly related to water temperature (Copp *et al.*, 2009), with a peak in spring and a minimum in winter (Mihálik, 1955). Similarly, according to a study lead in Germany, stomach contents increased significantly with temperature (Wysujack and Mehner, 2005). It was considered that *S. glanis* could not digest food when temperatures are below 10°C (Copp *et al.*, 2009). Nevertheless, recent studies showed that European catfish feeds during winter (De Santis and Volta, 2021; Vagnon *et al.*, 2022).

However, our data contradict those assertions, as the individual no. 117 was recorded moving during daytime and outside of the riverbed in February, even following the operator walking in the water with the mobile antenna. The consumption of a northern pike between January and February, and the subsequent excretion of the transmitter, also showed the fish ability to process food at this period. The fact that European catfish could move during daytime in winter has already been developed (Omarov and Popova, 1985; Slavík *et al.*, 2007). Moreover, Molnár and Tölg (1962) were able to estimate the duration of the gut transit for catfish in a 5°C-water, which in fact appeared relatively fast, in comparison to, for example, the northern pike (206 hours against 257).

Hence, this new observation supports the capacity of European catfish to maintain both swimming and feeding activities during winter floods. European catfish has shown a great capacity to develop new behavioural strategies, colonizing new areas and being very opportunistic, for example specializing in the catch of land birds in the Tarn River (Cucherousset *et al.*, 2012) or taking advantage of fish passes to predate migratory fish (Boulêtreau *et al.*, 2018, 2020; Guilleraut *et al.*, 2019). Using the major riverbed to catch or scavenge on preys exploring new environment emphasizes once again the high adaptability of this controverted predator.

Finally, literature said that exotic species are disadvantaged by floods for their establishment (Minckley and Meffe, 1987; Moyle, 1995; Vila-Gispert *et al.*, 2005) contrary to

native species that can be maintained through a combination of life-history strategies and physiological tolerances (Moyle *et al.*, 1986; Vila-Gispert *et al.*, 2005). Our results disagree with these assessments. Thus, life-history adaptations as well as aspects of the hydrological regime (duration and timing of floods) determine the response of the exotic species to flooding (King *et al.*, 2003).

### Ecological comparison of two top predators

Then according to our results, *E. lucius* and *S. glanis* have different behaviours during the winter floods, but also some characteristics in common.

Concerning trophic ecology, an individual of northern pike was predated by a specimen of European catfish. Predation of *S. glanis* on *E. lucius* is already documented by Didenko and Gurbyk (2016), while the reverse was recorded only on juvenile European catfish (Popova, 1978). That is why the northern pike is thus described as a mesopredator, while the European catfish is sometimes qualified as an apex predator even if some studies minimize its role by the low and selective predation on zooplanktivorous fish species (Adámek *et al.*, 1999; Wysujack and Mehner 2005; Copp *et al.*, 2009; Vejřík *et al.*, 2017). Thus, niches of northern pike and European catfish could overlap during flood events, rather to the detriment of northern pike. Whereas according to Vejřík *et al.* (2017), the interactions between these species seem to be limited. However, both species have comparable diets (Orlova and Popova, 1976; Popova, 1978; Omarov and Popova, 1985; Mehner *et al.*, 2000), and the pressure exerted on the stock of forage fish should be assessed and may thus enter in competition in a depleted environment (Didenko and Gurbyk, 2016). Moreover, if flood events become more common in the future, it is possible that such periods, where the behaviour of European catfish change, will become more frequent. The niches of the two species could therefore evolve towards a greater overlap, and we could wonder whether the proportion of northern pike in the diet of catfish will tend to increase. The dietary spectrum of *S. glanis* being greater than that of *E. lucius*, it might be able to exploit more resources in case of scarcity (Copp *et al.*, 2009).

Concerning their behaviour, both northern pike and European catfish explored the flooded fields near Guignicourt, where the water was particularly turbid due to the entrainment of suspended materials. However, both species show a preference for low flows, and could be impacted by significant changes during winter floods. Northern pike can seek out new habitats in this kind of situation (Masters *et al.*, 2002). European catfish, on the other hand, tend to be a rather quiescent predator when temperatures are low (Hilge, 1985; Slavík *et al.*, 2007; Alp *et al.*, 2011; Daněk *et al.*, 2014), even though this behaviour varies greatly from one European catfish to another (Slavík *et al.*, 2007; Slavík and Horký, 2012).

It appears that northern pike and European catfish modify the direction and the importance of their movements according to the flow. The northern pikes thus swam remarkable distances against the current during the floods. At the same time, European catfish also largely favoured upstream movements during these periods, although reducing the amplitude of their movements. Masters *et al.* (2005) similarly observed important upstream movements during winter flood in the River Frome (UK). Slavík *et al.* (2007) found that European catfish movements were inversely related to flow rate in the Berounka River (Slovakia), although the direction of those movements was not described. We have not found an explanation in the literature, but we believe that this could be linked to a better steering control against the current, as observed for boats for example.

It must also be noted that most of the fish of both species were able to find their way back into the river, even with the rapidly decreasing water. However, at least one of the northern pikes stayed trapped in a puddle, and the arrival of numerous birds in this formerly flooded area suggest that these episodes result in losses, especially in the Aisne department where the water levels change rapidly.

Nonetheless, it appears that the exploration of flooded area during hydraulic events is a part of the natural behaviour of the northern pike and, perhaps to a lesser extent, of the European catfish. Both species use then different fashions. European catfish can explore their environment and identify preys by their hydrodynamic traces with its barbels (Pohlmann *et al.*, 2001), whereas northern pike is known for mainly hunting and directing themselves visually (Craig and Babaluk, 1989; Craig, 2008) (but see above). This underlines the importance not only of the minor but also of the major riverbed.

### CONCLUSION

Our radio telemetric study on *E. lucius* and *S. glanis* during winter flood has allowed us to better understand their behaviours during these events which may be more frequent and stronger with climate change. Both northern pikes and European catfish explored or stayed in the riverbed and demonstrated an adaptability to various conditions. This study must be continued over longer periods of time and in other localities. Safeguarding unenclosed floodplains around riverbeds allows these exploratory behaviours to continue to take place and should therefore be considered in environmental policies.

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**On line Appendix. – Classification of the monitored pike according to their behaviour during floods.**

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Supplementary figures legends

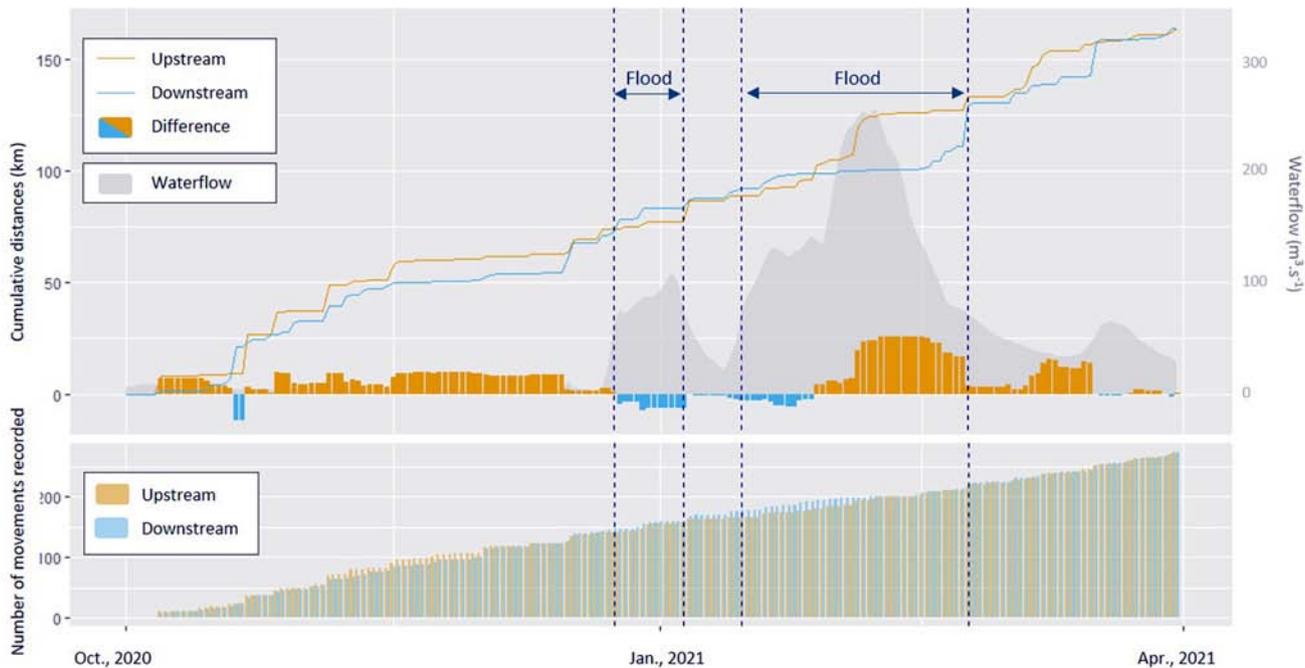


Figure S1. – Cumulative distance and number of recorded movements upstream and downstream versus waterflow between October 2020 and March 2021 for northern pikes.

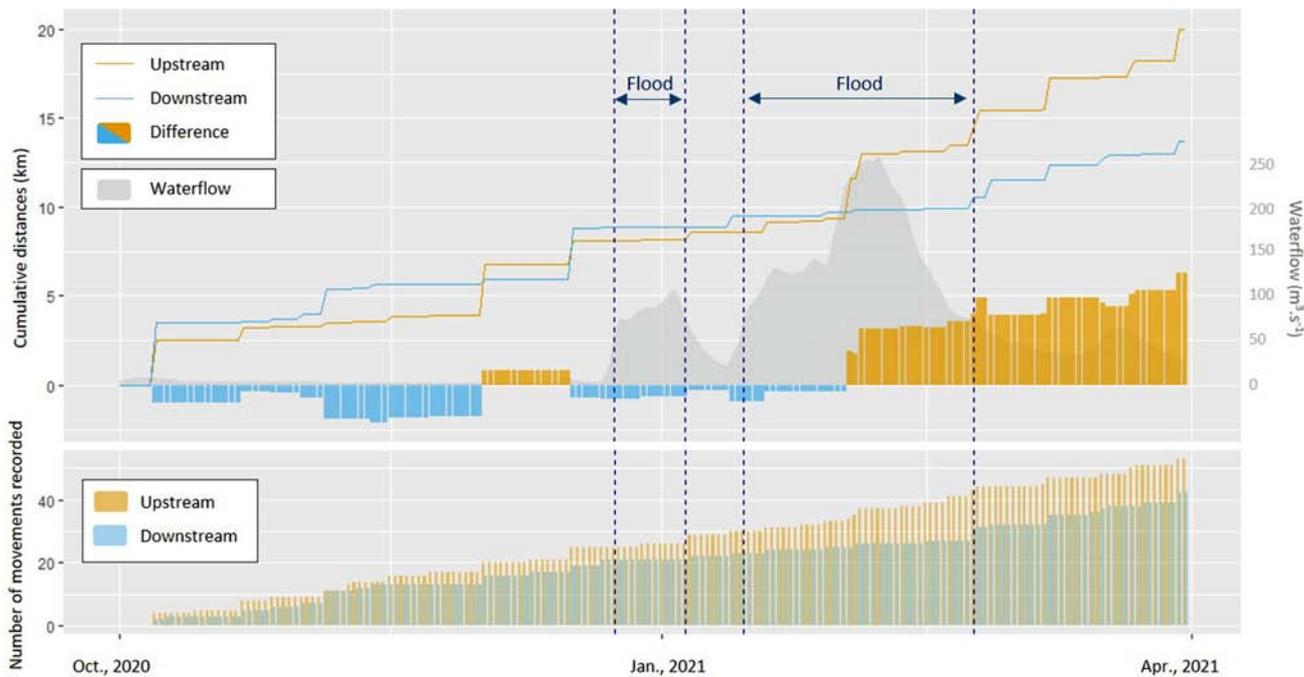


Figure S2. – Cumulative distance and number of recorded movements, upstream and downstream versus waterflow between October 2020 and March 2021 for European catfish.

