



Variability of the ecological niche of predatory fishes in lake ecosystems

Samuel Westrelin

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Université Fédérale



Toulouse Midi-Pyrénées

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Samuel WESTRELIN

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**Variabilité de la niche écologique chez des poissons prédateurs
lacustres**

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Préambule : cette thèse « Variabilité de la niche écologique chez des poissons prédateurs lacustres » est rédigée en anglais. Son résumé ainsi qu'une synthèse de chacun des cinq articles inclus dans ce travail sont également disponibles en français.

Foreword: this thesis "Variability of the ecological niche of predatory fishes in lake ecosystems" is written in English. Its main abstract and a synthesis of each of the five papers included in this work have been translated in French as well.

Résumé

Les écosystèmes d'eau douce et les lacs en particulier contribuent de façon importante à la biodiversité. Au sommet des réseaux trophiques, les prédateurs favorisent cette biodiversité et ont un rôle stabilisateur. Ils impactent directement et indirectement de nombreuses fonctions des écosystèmes et, par là même, de nombreux services écosystémiques. Maintenir la diversité des prédateurs est donc capital, et comprendre les mécanismes de leur coexistence une question clé en écologie.

La théorie des niches a identifié plusieurs mécanismes de coexistence. La niche est définie comme l'ensemble des conditions biotiques et abiotiques qui permettent l'existence d'une espèce. En ciblant la niche d'habitat et la niche trophique, deux composantes majeures de la niche écologique, nous avons cherché à montrer comment, dans la nature, les communautés de prédateurs se maintiennent en lacs. Les ectothermes étant particulièrement sensibles aux conditions abiotiques, nous visons également à évaluer comment les conditions environnementales affectent leur niche d'habitat. Des individus de brochet *Esox lucius* L., perche européenne *Perca fluviatilis* L., sandre *Sander lucioperca* (L.) et silure *Silurus glanis* L. ont été suivis et/ou échantillonnés dans un réservoir stratifié et un lac naturel peu profond. Nous avons estimé leur niche d'habitat en couplant leur positionnement par télémétrie acoustique à une cartographie de l'habitat. Leur niche trophique a été estimée par l'analyse des isotopes stables du carbone et de l'azote de tissus de nageoires.

Nos résultats mettent en évidence un partitionnement de l'habitat et de la niche trophique entre ces espèces, probablement comme moyen de limiter la compétition interspécifique, en accord avec la théorie. Cependant, les variations entre individus d'une même espèce sont souvent très importantes. Concernant la niche trophique, une plus forte abondance d'une espèce est en général corrélée à une plus forte variation intraspécifique, ce qui constituerait un autre mécanisme stabilisateur limitant la compétition intraspécifique. Le silure, quant à lui, ne semble pas élargir sa niche trophique lorsqu'il est plus abondant ; cela illustre son caractère généraliste au niveau individuel et pourrait en partie expliquer le succès de sa colonisation de nombreux écosystèmes. Les fluctuations environnementales témoignent d'un rôle moteur sur la niche de ces ectothermes, avec des impacts différents selon leur échelle temporelle et leur amplitude. Les changements saisonniers mettent en jeu un nombre limité de niches temporelles (saison froide/chaude) et modulent graduellement la niche d'habitat des espèces ; ils aboutissent à un moindre degré de partitionnement en saison de plus faible activité (automne, hiver). Dans

certaines conditions, les changements de niche d'habitat peuvent être extrêmes comme les agrégations hivernales de silures. Une sévère hypoxie de relativement courte durée a déclenché le regroupement de silures dans une zone refuge, probablement sans autre impact significatif sur l'espèce. Par contre, cet événement a probablement contribué à l'effondrement du stock de sandres juvéniles et, ainsi, considérablement modifié les interactions intra- et interspécifiques du guildes piscivore, comme montré sur la niche trophique.

Ces recherches donnent des clés aux gestionnaires de plans d'eau pour identifier les habitats ou ressources critiques à préserver, typiquement dans le cadre de la conservation d'espèces. Elles renseignent également sur l'intensité de la compétition interspécifique et peuvent éclairer sur le besoin ou non de réguler une espèce, ce qui peut être particulièrement utile lorsqu'une espèce exotique invasive pose question. Ainsi, ce type de recherche peut éclairer les plans de gestion à mettre en œuvre dans le contexte du changement climatique.

Abstract

Freshwater ecosystems, and lakes in particular, significantly contribute to biodiversity. At the top of the food web, predatory species promote biodiversity and stabilize ecosystems. They have direct and indirect cascading effects on numerous ecosystem functions as well as numerous services that these ecosystems provide to humans. Maintaining the diversity of these species is thus of utmost importance, and understanding the mechanisms of their coexistence is a crucial question in ecology.

Based on niche theory, there are several identified mechanisms of species' coexistence. Niche is defined as the range of environmental states, biotic and abiotic, specific to a species, which facilitate its existence. By focusing on habitat and trophic niches, two main components of the ecological niche, we aimed to highlight how wild predator communities are maintained in lacustrine ecosystems. Ectotherms being particularly sensitive to abiotic conditions, we also aimed to analyze how environmental conditions could affect their habitat niche. Individuals of pike *Esox lucius* L., perch *Perca fluviatilis* L., pikeperch *Sander lucioperca* (L.) and catfish *Silurus glanis* L. were tracked and/or sampled in a stratified reservoir and in a shallow natural lake. Their habitat niche was evaluated by coupling high resolution positioning acoustic telemetry with habitat mapping. The trophic niche was estimated by analyzing carbon and nitrogen stable isotope ratios of fin clips.

Our results provide evidence of habitat and trophic niche partitioning among these predatory species, probably as a way to limit interspecific competition and thus stabilize species coexistence, in accordance with ecological theory. Yet, in both these niche components, the variation among individuals is often very large. For the trophic niche, a greater abundance of species generally correlates to greater intraspecific variation, and is interpreted as another stabilizing mechanism that buffers intraspecific competition. However in catfish this does not appear to occur; its trophic niche does not widen when it is more abundant. This likely reflects its generalist behavior at the individual level and could partly explain its successful colonization of numerous ecosystems. Environmental fluctuations drive these ectotherms' niche, with different impacts depending on their timescale and their range. Seasonal environmental changes involve a limited number of temporal niches (cold/warm seasons) and gradually modulate species' habitat niche, leading to a lesser degree of partitioning in low activity seasons (autumn, winter). In some specific environmental conditions, habitat niche shifts can be extreme like for long-lasting aggregations of catfish in winter conditions. A severe short-term hypoxic event

triggered the grouping of catfish in a refuge area, probably without significant impact on this species. However, this event probably made the juvenile pikeperch abundance collapse, consequently affecting the juvenile piscivorous guild and intra- and interspecific trophic interactions, as shown for the trophic niche.

This research provides valuable insights for lake managers to identify potential critical habitats or resources to preserve for species conservation. It also gives useful information on the strength of competitive interactions among species and their sensitivity to environmental conditions. These results shed light on important questions like whether species need to be regulated. This is particularly important when lakes host invasive exotic species that raise concern. As such, this work provides insights for managing lake ecosystems in the context of climate change.

Le passé finit toujours par vous rattraper. Il y a de cela un peu moins de trois décennies, une thèse s'offrait à moi, d'abord en écologie terrestre, puis, quelques années plus tard, en météorologie. A chaque fois, j'ai mis ces opportunités de côté pour d'autres projets non moins passionnants ; une première fois, pour rejoindre Météo-France et devenir ingénieur météorologue, puis, une seconde fois, pour continuer à tracer ma route d'ingénieur dans le monde de la R&D dans des domaines super intéressants comme les modèles de prévision météorologique, la prévision cyclonique, et l'évaluation des risques hydro-météorologiques. Ne restait plus qu'à tirer le trait d'union entre l'hydro et l'écologie en étant accueilli au sein de l'équipe hydro-écologie de l'IRSTEA d'Aix-en-Provence. C'est toujours motivé par la compréhension des phénomènes naturels et émerveillé par le monde du vivant que je me suis mis à étudier l'écologie des brochet, perche, sandre et silure. Le projet décroché sur le silure a déclenché l'envie de m'investir dans ce travail de thèse.

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plomberie, merci pour la logistique impeccable de la manip. Dodo (Dorian Milesi), la force tranquille, merci pour ton dévouement sans failles et ta minutie dans la saisie des données. Julien (Dublon), le gai luron, (un peu ;)) pêcheur, (un peu) Mac Gyver, merci pour tout et en particulier le partage de ta passion des milieux aquatiques. Nine (Virginie Diouloufet), que dire ... je suis épuisé (mais ravi) rien qu'à l'idée de la longue énumération à faire ☺ ... toujours partante, merci pour ton dévouement et ton énergie hors norme dans toute tâche, ton art de mêler à la fois fougue et minutie. Ça a été un plaisir de bosser avec vous et j'espère bien que ça continuera.

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I.

Introduction

I. Introduction

A. Biodiversity in freshwater ecosystems

About 4.6 million km² of the Earth's continental "land" surface (>3%) is covered by freshwater. Water bodies largely dominate with 304 million natural lakes (4.2 million km² in area, mainly water bodies smaller than 1 km²) and, in addition, 800,000 impoundments covering approximately 0.5 million km² (Downing et al., 2006; Friedl & Wüest, 2009). In Europe, Kristensen & Hansen (1994) censused approximately 500,000 natural lakes with a minimum surface area of 0.01 km². These ecosystems provide a large set of services (water supply, water regulation, waste treatment, fish and other harvestable resources, cultural and recreational activities, support for biodiversity, etc...) that are key for humans (de Groot et al., 2012; Reynaud & Lanza, 2017; Dodds & Whiles, 2020) and are of high economic value (Costanza et al., 2014). Given the important variety of habitat types they offer, freshwater ecosystems host high biodiversity throughout the world with 73% of amphibian species (Vences & Köhler, 2008), 43% of fishes (Lévêque et al., 2008), more than 33% of invertebrates (mainly insects, Balian et al., 2008) and 1% of plants' species (Chambers et al., 2008). In particular, 13,000 strictly freshwater fish species live in lakes and rivers that cover only 1% of the Earth's surface, while the remaining 16,000 species live in salt water covering a full 70% (Lévêque et al., 2008).

Declining biodiversity generally alters ecosystem functions and reduces stability (Loreau et al., 2001; Cardinale et al., 2006) while higher diversity food webs could be more resilient to disturbance (Thébault & Loreau, 2005; Downing & Leibold, 2010; Dodds & Whiles, 2020), even if the relationship between biodiversity and stability can be much more complex (Pennekamp et al., 2018). In this context, biodiversity is traditionally considered as species richness (Dornelas et al., 2014), but it may be better understood by also considering functional diversity (Webb et al., 2002; Mori et al., 2013). Top-predators have been shown to play a key role in these stabilizing mechanisms (Rooney et al., 2006) and biodiversity is closely related to predator richness (Saleem et al., 2012).

Top-predators indeed play a key role in aquatic as well as terrestrial ecosystems (Hairston et al., 1960; Fretwell, 1987) and foster biodiversity by cascading effects on the whole trophic chain (Byrnes et al., 2006; Sergio et al., 2006; Myers et al., 2007; Estes et al., 2011). Multiple predators limit the competition among species on lower trophic levels (top-down control) (e.g. Rosenfeld, 2000; Baum & Worm, 2009). This enhances the growth of prey species, increases

complementarity and evenness among them (Saleem et al., 2012) and leads to a wider range of the available resources to be consumed (Loreau et al., 2001). Predators also stabilize complex ecosystems by foraging on prey over a large range of habitats, thus coupling different energy pathways (Rooney et al., 2006). The vast majority of ecosystems host numerous predators (Schoener, 1989b) whose variations in diversity and abundance have cascading consequences on food webs (Bruno & O'Connor, 2005; Rooney et al., 2006; Schmitz, 2007; Baum & Worm, 2009; Wasserman et al., 2016).

B. Ecological theory on species coexistence

How species from the same guild interact and coexist (Sommer, 1999; Matthews, 2012) is a keystone in understanding biodiversity and has motivated a century of research and the emergence of many theories (Grinnell & Swarth, 1913; Gause, 1934; Tilman, 1982; Chesson, 2000; Hubbell, 2001; Chase & Leibold, 2003; Chesson, 2018; Koffel et al., 2021). The coexistence of species is considered stable when their densities do not show any long-term trends (populations tend to not disappear), which does not oppose variations in time, and when they can recover from low densities (Chesson, 2000).

Early, Grinnell & Swarth (1913) introduced the “niche” concept that encompassed everything that conditioned the existence of a species at a given location, whereas Elton (1927) mainly defined the niche by the position in trophic chains (such as carnivore, herbivore, etc...). At this initial stage, niche was focused on the environment and closely linked to the competitive exclusion principle. This principle states that sympatric species can not have completely overlapping niches (Gause, 1934), which was later reinforced by Hutchinson (1957) and Hardin (1960). At the same time, the niche concept shifted to become an attribute of the species, not of the environment: the “fundamental” niche is defined as the range of environmental states, biotic and abiotic, specific to a species, which allowed its existence (Hutchinson, 1957; Begon et al., 2006).

The niche theories will be built on the concept of species resource utilization distribution (modern coexistence theory, Chesson, 2000), an operational declination of the theoretical niche concept (see Pocheville, 2015 for the history of the ecological niche concept). In this declination, the axes of the niche can be very diverse, including notably food and resources in general, space, and time (MacArthur & Levins, 1967; Schoener, 1974; Schoener, 1989a). In the theory of limiting similarity, some maximum level of similarity between species niche is

bearable (Abrams, 1983). Resources dynamics and competition for resources are dominant factors in the contemporary niche theory (Tilman, 1982), in which Chase & Leibold (2003) more intimately combined niche and competition as causes and consequences of diversity. They not only included the ecological factors in the niche, but also the impact of the organisms themselves on these factors (notably resources, predators and stresses) (figure I.B.1); the environment plays a central role by mediating the interactions between species, and, reciprocally, species can impact their environment (e.g. Odling-Smee et al., 2013) which, in turn, creates a feedback on these interactions.

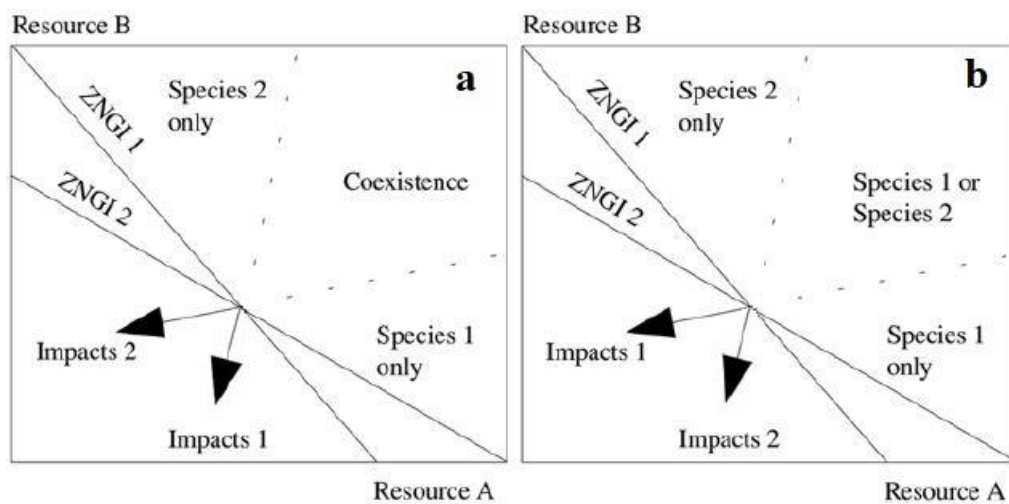


Fig I.B.1: This chart shows the responses and impacts of two species 1 and 2 from, and on, two substitutable resources A and B. “Arrows” represent vectors summarizing the impact of each species on resources A and B. “Lines” represent the zero net growth isoclines (ZNGI). In this example, the growth rate is negative under the ZNGI and positive above, the half-plane above the ZNGI hence represents the area of viability of the species. Last, the higher the intersection of a species’ ZNGI with a resource axis, the higher it needs of that resource. Panel a: 1 needs more B and depletes B the more, conversely 2 needs more A and depletes A the more; the direction of the impact vectors and the intersection point of the isoclines define an area of coexistence. Panel b: the vectors of impacts have been reversed: the zone of coexistence has evolved into an exclusion zone. The range of environmental values that species are experiencing depends on the species characteristics, but also on the intrinsic dynamics of the environment, such as the rate of resource renewal (Niche theory after Chase & Leibold, 2003).

The differential use of resources, or resource partitioning, is one of the important mechanisms allowing the coexistence of species in niche theories (Chesson, 2000; Chase & Leibold, 2003;

Levine & HilleRisLambers, 2009; Kalmykov & Kalmykov, 2014). Two types of coexistence mechanisms have been identified: equalizing mechanisms, which lower fitness differences between species, and stabilizing mechanisms, which promote coexistence by concentrating intraspecific competition relative to interspecific competition (Chesson, 2000). Stabilizing mechanisms are essential for species coexistence and resource partitioning is one them. Pathogens and predators (natural enemies) can also have a stabilizing effect (the most abundant species suffers the most). In the modern coexistence theory, these stabilizing mechanisms are categorized as niche differences, whereas equalizing mechanisms relate to average fitness differences, ie how species differ in their degree of adaptedness to their common environment (Chu et al., 2017; Letten et al., 2017). Among equalizing mechanisms, we can cite tradeoffs as for example the tradeoff between competitive ability and susceptibility to predation: species can differentiate their niche via a competition-predation trade-off if one species is a better competitor when predators are absent, and the other is better when predators are present (Chesson & Huntly, 1997). In the absence of stabilizing mechanisms, these average fitness differences predict competitive exclusion (Chesson, 2000).

The neutral theory of diversity considerably challenged the niche theories (Hubbell, 2001). Indeed, in this theory, species have the same niche and individuals the same fitness regardless of the species (figure I.B.2). Paradoxically, this theory can predict most basic patterns of biodiversity (Chave, 2004; Munoz & Huneman, 2016) and is actually not incompatible with the niche theories (Leibold & McPeck, 2006). Although equivalent fitness among individuals is a very strong hypothesis, obviously not supported in the wild, the weaker assumption of equivalence of average fitness at the species level often holds in stable communities. These low average fitness differences are satisfied in modern coexistence theory, and explain why both theories converge in numerous cases (Chave, 2004). The neutral model is actually a special case of coexistence theory where stabilizing mechanisms are absent and species have equivalent fitness (Adler et al., 2007).

Whereas individuals from the same species have long been treated as equivalent (Schoener, 1986b), more recently, approaches based on individuals have increasingly gained momentum (Dall et al., 2012; Sih et al., 2012). Indeed, intraspecific richness and variation have substantial effects on ecological dynamics and is an integral part of species niche (Toscano et al., 2016; Raffard et al., 2019). Intraspecific variability represents a large proportion of trait variability (e.g. Siefert et al., 2015; Luiz et al., 2022): out of 15 freshwater species, Luiz et al. (2022) found it contributed 31 % of the total trait variability in average and up to 70 % for one species.

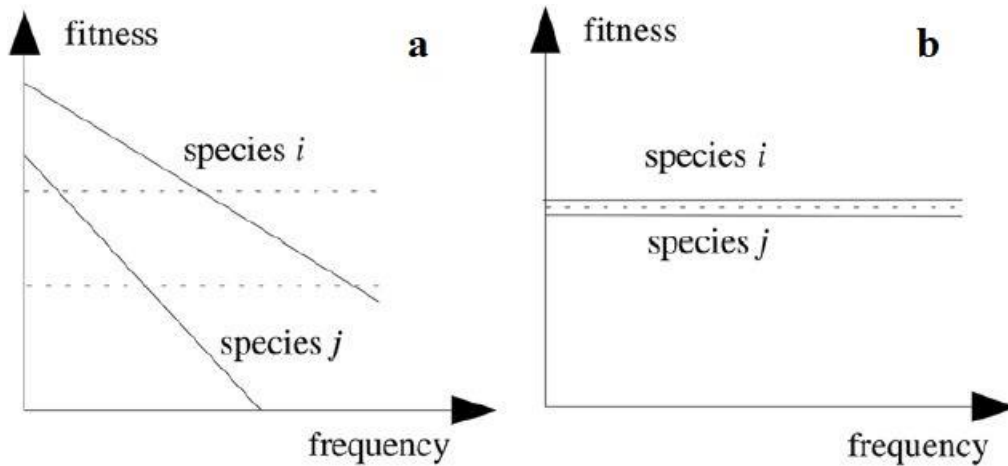


Fig I.B.2: Diagram illustrating the typical assumptions of the niche theory (panel a) and the neutral theory (panel b). Panel a: species have different average fitness (dotted lines), but each undergoes a negative frequency-dependence (solid line) which stabilizes coexistence (the slope of the line represents the intensity of stabilization). Panel b: species show no frequency-dependence, but have equal average fitness (After Adler et al., 2007).

This intraspecific variability plays on intraspecific competition and, by cascading effect, on species coexistence: “Variation among individuals within populations allows species to differ in their distributions of responses to the environment, despite the fact that the populations to which they belong do not differ, on average” (Clark, 2010). It is a major stabilizing mechanism.

Although general, the framework of coexistence theory remains focused on negative interactions (competition, predation, parasitism). Yet, positive interactions also occur in nature such as facilitation (e.g. Eklöv & VanKooten, 2001; Collins et al., 2017), mutualism (e.g. Hay et al., 2004) and commensalism (e.g. Lee et al., 2009) (for a review in freshwaters, see Silknetter et al., 2020). Very recently, Koffel et al. (2021) presented a unified theory encompassing the modern coexistence theory and positive interactions.

C. Environmental variation and species coexistence

Environmental variation is an important equalizing mechanism following the intermediate disturbance hypothesis: species can reach an equilibrium state and exclude other competing species under reduced environmental fluctuations, whereas increased fluctuations prevent species from reaching equilibrium, because species respond differently, and therefore prevent competing species from excluding others (Connell, 1978; Chesson & Huntly, 1997).

Environmental variation occurs across different timescales and can be regular and deterministic or stochastic (Chesson, 2000). It can promote species coexistence by minimizing average fitness differences (equalizing mechanism) or by creating different temporal niches (stabilizing mechanism) (Chesson, 2000; Chesson, 2008; Liu et al., 2021). Periodic seasonal variation involves a limited number of temporal niches (e.g. cold or warm season) in comparison to stochastic environmental variation that can potentially create more diversified temporal niches (e.g. sudden warming or cooling, periods of flood and drought, strong winds, bottom anoxia, severe hypoxia). As such, stochastic temporal environmental variation stabilizes a system of competing species and increases the persistence time of diverse assemblages (Chesson & Warner, 1981; Dean & Shnerb, 2020; Meyer et al., 2022), while long-term environmental variation promotes competitive exclusion (Liu et al., 2021) like climate change for example (e.g. McCormick et al., 2013; Van Zuiden et al., 2016). Stochastic fluctuations are common in nature and can have a significant effect on the ecological and evolutionary dynamics of populations (Cai, 2022).

D. My questions

The diversity of top-predators plays a crucial role within ecosystems and impacts trophic interactions throughout food webs (Schmitz, 2007; Wasserman et al., 2016). By exerting predatory pressure on lower trophic levels, predators limit competition among species within the same guild and promote biodiversity (e.g. Wallach et al., 2015). Most importantly, their ecological roles are not limited to food web dynamics though most studies focus on this aspect. Predators are connected to numerous other ecosystem functions and socioecological services via both direct and indirect pathways (Ripple et al., 2014; on aquatic predators, Hammerschlag et al., 2019). Understanding the mechanisms that underlie the coexistence of these competing species, that maintain their diversity, is thus a crucial question in ecology (Schmitz, 2007).

In relatively closed systems such as lakes, wherein resources tend to be limited (Essington & Carpenter, 2000; Craig et al., 2015), the mechanisms of coexistence developed in the niche theory can be particularly pronounced. Moreover, ectotherms are directly impacted by abiotic conditions. Environmental conditions, such as vertical gradients of temperature and oxygen in stratified lakes that segregate the physical habitat and vary between seasons, affect the spatial distribution of fish (Magnuson et al., 1979; Imbrock et al., 1996; Muška et al., 2018). They could thus impact habitat partitioning, as species fulfill different physiological requirements

regarding temperature and oxygen. Trophic variables in lakes vary with environmental conditions too (Mehner et al., 2005), what can induce shifts in the flow of energy and thus, relocation of biomass and changes in species trophic interactions (Sentis et al., 2017; Su et al., 2021). This could also play an important role in trophic partitioning.

In freshwater ecosystems, top-predators in the food web are piscivorous species. Whereas multiple piscivores very often coexist (Schoener, 1989b), few studies examined the co-occurrence of predators at the top of the food web in freshwater ecosystems, except Guzzo et al. (2016) and Hodgson et al. (1997). By focusing on habitat and trophic niches, two main components of the ecological niche, I aimed to determine which mechanisms are involved in driving stability in wild predator communities in lacustrine ecosystems. In particular, I investigated whether habitat partitioning and trophic niche partitioning between species were at play and also evaluated within-species variability by sampling of individuals over extended periods (> 1 year). I paid particular attention to get time integrated results to evaluate seasonal and diel variations as well as the stability of patterns across years. Moreover, by zooming on individuals in populations, I explored how variable and harsh environmental conditions could influence species habitat niche.

I hypothesized coexisting predatory species partitioned their habitat, but with variation across seasons, when the lake was stratified and the physical habitat became very constraining. I also expected some diel variation associated with the circadian rhythm of each species. I hypothesized this habitat partitioning would correlate with a trophic partitioning. Regarding habitat, I expected that environmental variations would impact species habitat niche, but with consequences very depending on the timescale and the strength of these variations.

To answer these questions, I built my thesis on five scientific articles that either have been published (3 of them), either are being revised (1) or are in preparation (1 close to submission). A synthesis of each article is given before the core paper itself. They are fully provided according to the following outline developed after this introduction and a preliminary section (II.) that briefly presents the technologies and biological models used. A general discussion and the perspectives of this thesis are proposed in a final section.

III Inter- and intraspecific variability of the ecological niche in a freshwater predator community

A. Habitat partitioning among three predatory fish in a temperate reservoir

- B. Interannual variability of the trophic niche of young-of-the-year of four piscivorous fish species coexisting in a natural lake

IV Influence of variable or harsh environmental conditions on the habitat niche of a population of freshwater predators

- A. Habitat-use and preference of adult perch (*Perca fluviatilis* L.) in a deep reservoir: variations with seasons, water levels and individuals.
- B. Overwintering aggregation patterns of a freshwater giant
- C. European catfish *Silurus glanis* behaviour in response to a strong summer hypoxic event in a shallow lake.

II.

Technologies and biological models
used

II. Technologies and biological models used

The technologies as well as the biological models used are largely exposed in the scientific articles that form the backbone of this thesis. Nevertheless, I briefly introduce them below.

A. Technologies deployed

1. *Acoustic telemetry*

Habitat niche has been estimated by quantifying availability and use of the different habitat types accessible to the fish. For this purpose, reality mining and high-throughput movement ecology technologies have been implemented (Hussey et al., 2015; Nathan et al., 2022). The reality mining technology was based on using high resolution acoustic telemetry: an underwater network of omnidirectional acoustic receivers permanently listens to ultrasonic emissions from tags surgically implanted in fish body cavity. These receivers, deployed at known locations, are associated with synchronization tags that allow for the correction of the receiver internal clock drift and record the exact time of each fish detection. The reference tags, also deployed at known locations but different from those of the receivers, are spread all over the lake to detect potential anomalies in the network (Figures II.A.1 and II.A.2). Fish detections are run on triangulation algorithms that calculate individual positions (Baktoft et al., 2015; Baktoft et al., 2017). This generates a big dataset of positions (2D or 3D-positioning) at high temporal and spatial resolution (\sim every 1'30'' to 5' and a few meters horizontally in our case) over up to several years (Nathan et al., 2022). In relating these positions to environmental conditions and habitat features, space-use and habitat preferences can be estimated (Manly et al., 2002; Aarts et al., 2008; Nathan et al., 2022). Interestingly, when the studied lakes are of reasonable size, as in our case (\sim 100 ha), telemetry can cover the entire ecosystem (Lennox et al., 2021), as in the both experimental setups used in this study (Figures II.A.1 and II.A.2).

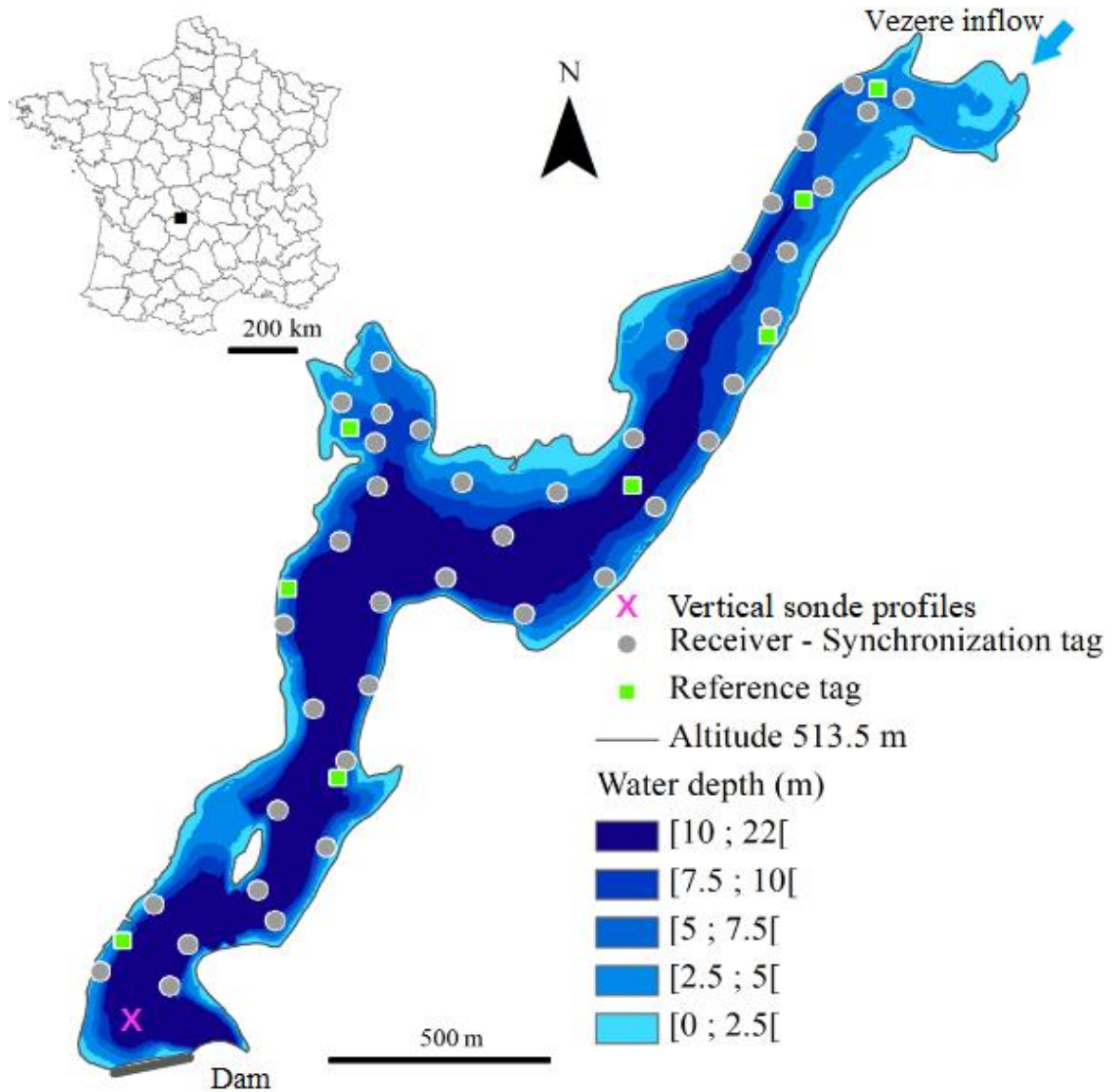


Fig II.A.1 Bathymetric map of the Bariousses reservoir (black square over France map with department boundaries) at the high-water level with the acoustic telemetry set up. Acoustic receivers and their associated synchronizing tags are represented by grey dots. Reference tags are symbolized by green squares. The pink cross locates the hourly temperature profiles made at the deepest point in the lake. The Vézère river flows into the lake at its northeast extremity.

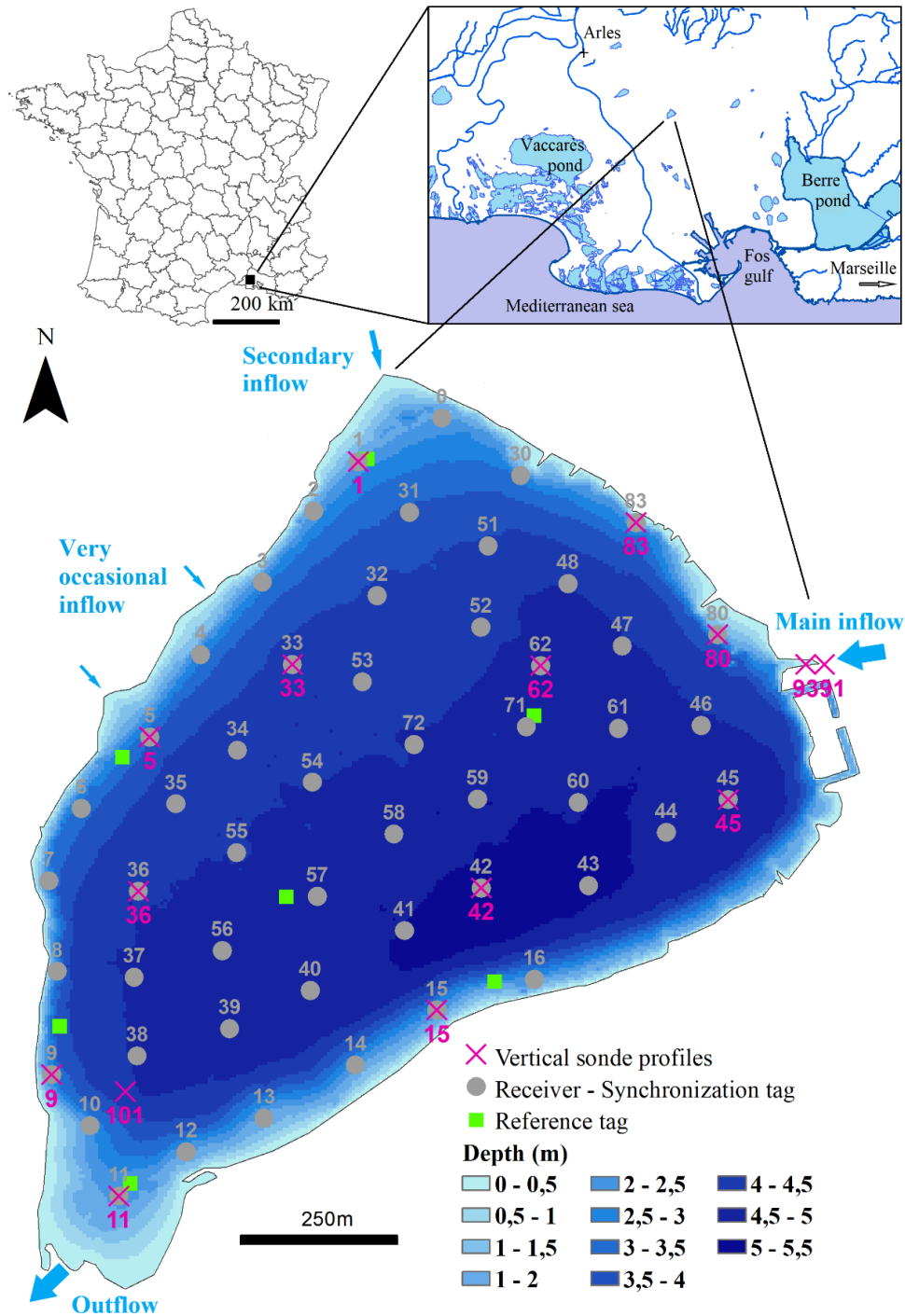


Fig II.A.2 Bathymetric map of “Etang des Aulnes” at the water level of 11.14 m above sea level and experimental setup. Acoustic receivers and their associated synchronizing tags are represented by grey dots. Reference tags are symbolized by green squares. Pink crosses locate the temperature and dissolved oxygen profiles (monthly everywhere and hourly at the deepest point 42). The primary canal flows into the lake on the eastern bank at location 91 and a secondary canal on the northern bank close to location 0. The lake outflows in a canal at its southwest extremity.

2. *Stable isotope analysis*

The trophic niche was estimated by using the stable isotope analysis. The stable isotopes of tissues have been shown to cycle across the food web in a predictable relationship between a consumer and its prey (Fry, 2006; Grey, 2006). As the isotopic turnover rate of tissues takes time (e.g. ~3 month for muscle, Busst & Britton, 2018), this method provides long-term diet patterns contrary to gut content analysis which only gives a snapshot of the diet (e.g. Rybczynski et al., 2008; Vander Zanden et al., 2015; Davidsen et al., 2017); it also analyses what is assimilated and not only what is ingested (Phillips et al., 2014). Nitrogen and carbon stable isotopes (^{15}N and ^{13}C , and more precisely the ratios of their abundance to that of their lighter stable isotope, ^{14}N and ^{12}C) are widely used. Nitrogen ratios exhibit stepwise enrichment with trophic transfers and are used for estimating the trophic positions, which describe the ecological role of an organism in food webs (Post, 2002). Carbon ratios can be used for determining the energy sources of a consumer (Post, 2002). Nitrogen and carbon ratios represent an organism's trophic niche and give access to other metrics for characterizing the trophic structure of communities (Layman et al., 2007; Jackson et al., 2011; Quezada-Romegialli et al., 2018).

B. Biological models used and datasets collected

1. *Biological models and their ecology*

Northern pike *Esox lucius* Linnaeus, 1758, perch *Perca fluviatilis* Linnaeus, 1758, pikeperch *Sander lucioperca* (Linnaeus, 1758) and catfish *Silurus glanis* Linnaeus, 1758, are four widespread predatory fishes in European lakes where they often coexist (Figure II.B.1).

Pike is a diurnal predator, mainly littoral, which prefers vegetated areas (Chapman & Mackay, 1984a; Craig, 1996; Jepsen et al., 2001) and ambushes prey (Raatt, 1988; Eklöv, 1997). Perch is also a visual predator that can hunt in schools (Zamora & Moreno-Amich, 2002); in summer, it frequents the pelagic zone during daytime and moves to the littoral during the night (Imbrock et al., 1996; Pekcan-Hekim et al., 2005). Pikeperch hunts in the twilight in open waters (Craig, 2000). Perch and pikeperch occupy deeper waters in winter (Vehanen & Lahti, 2003; Huuskonen et al., 2019). Catfish is nocturnal and can follow prey by detecting hydrodynamic and chemical cues (Pohlmann et al., 2001); it prefers still waters where it is found in the lower third of the water column or in benthic habitats (Copp et al., 2009; Cucherousset et al., 2018).

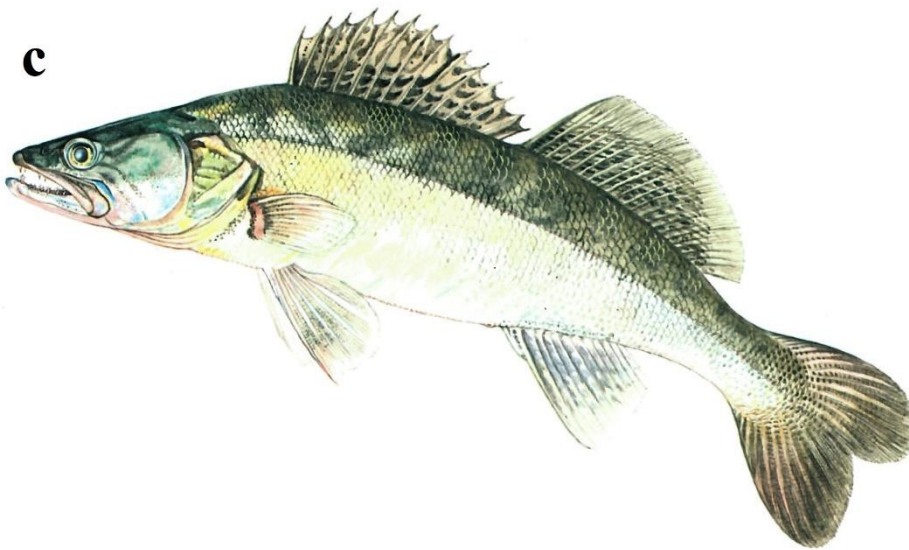
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b



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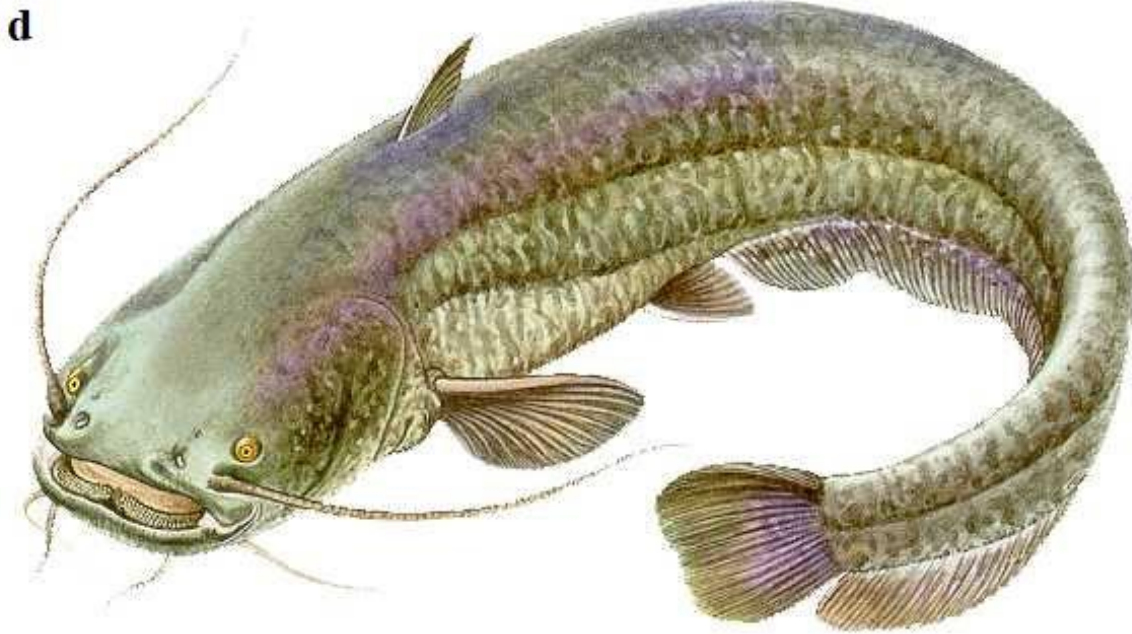


Fig II.B.1 Realistic representation (not to scale) of the four predatory species studied in this thesis (from Hisek Kvetoslav in Pivnicka & Cerny, 1987). Panel a: northern pike *Esox lucius* Linnaeus, 1758; maximum total length 150 cm, common length 40 cm for male and 55 cm for female, mean length at maturity 39.9 cm, maximum age 30 years. Panel b: European perch *Perca fluviatilis* Linnaeus, 1758; maximum total length 60 cm, common length 25 cm, mean length at maturity 16.3 cm, maximum age 22 years. Panel c: pikeperch *Sander lucioperca* (Linnaeus, 1758); maximum total length 100 cm, common length 50 cm, mean length at maturity 37.2 cm, maximum age 17 years. Panel d: catfish *Silurus glanis* Linnaeus, 1758; maximum total length 273 cm, mean length at maturity 87.5 cm, maximum age several decades. Data from Beverton & Holt (1959); Kottelat & Freyhof (2007); Boulêtreau & Santoul (2016); Froese & Pauly (2022).

Concerning juvenile stages, pike is dependent on vegetation and prefers complex structured habitats in the littoral zone (Craig, 2008). Through its first year of life, perch occupies different habitats according to its two ontogenetic diet shifts and, as soon as it can swim, migrates inshore where it grows and forms large shoals before migrating into deeper waters when the temperatures fall in autumn (Coles, 1981; Treasurer, 1988; Kjellman et al., 1996). Young pikeperch prefer pelagic and open areas with low light intensity (Lehtonen et al., 1996; Luchiar

et al., 2006). Juvenile catfish movements show minor differences with adults and at least no striking agonistic behavior suggesting they use sheltered areas in benthic habitats (Slavík et al., 2007; Slavík et al., 2012; Daněk et al., 2016).

In general, pikeperch, a piscivorous specialist (Kangur & Kangur, 1998; Huuskonen et al., 2019), occupies the highest position in the trophic web (Pérez-Bote & Roso, 2012). Pike is mainly piscivorous but more plastic (Craig, 2008), and catfish is opportunistic (Kopp et al., 2009; Syväranta et al., 2010; Vejřík et al., 2017; Vagnon et al., 2022). Perch can be classified as a trophic generalist that can switch between piscivorous, zooplanktivorous and macroinvertebrate feeding (Dörner et al., 2003; Schulze et al., 2012; Herlevi et al., 2018). Pike and pikeperch feed on zooplankton and other invertebrates when juveniles but usually become piscivorous at substantially smaller lengths than perch (Matěna, 1998; Mittelbach & Persson, 1998; Vašek et al., 2018; Yazıcıoğlu et al., 2018; Jacobson et al., 2019). Catfish, more recently introduced in western and southern Europe (Cucherousset et al., 2018), is an opportunistic, omnivorous forager whose diet reflects the prey available in its habitat (Copp et al., 2009) and which has a broad dietary spectrum (Vejřík et al., 2017). Juvenile catfish diet is composed of crustaceans, molluscs and fish (Rossi et al., 1991; Syväranta et al., 2010).

2. Experimental setup

My research is based on data collected from two experimental setups.

The first setup was located in the western central part of France in a deep reservoir (Bariousses reservoir, 86.6 ha, mean depth 7.1 m, oligotrophic, see Figure 1). The thermal regime of this reservoir is monomictic with four distinct temperature regimes. In spring, the water temperature rapidly increased and stratification occurred. In summer, water was warmer and a thermocline at about 4.5 m depth was observed. In autumn, water temperatures decreased rapidly when water mixing occurred and, in winter, water was mixed and homogeneously cold (Fig II.B.1). The summer thermocline was associated with an oxycline that separated saturated surface waters from unsaturated deep waters. In this reservoir, habitat use and preferences (used for evaluating habitat niche) of the predator community were followed. Pike, perch and pikeperch individuals, all adults, were tagged with ultrasonic tags and tracked over two years (2012-2013). This study was designed and led by a PhD student (Roy, 2014) and I participated in the last field campaigns (from June 2013), in particular including the high-resolution mapping of the different littoral habitat types all around the lake, the receivers' downloading and the tagging

of a few fish. Then, I benefited from the raw fish positions. I screened these raw data, designed, coded and ran all the analyses hereafter exposed in which I processed roughly 2 million positions.

The second site was located in southeast France in a shallow natural lake “Etang des Aulnes” lake, 104 ha, mean depth 3.8 m, eutrophic, see Figure II.A.2). In this lake, temperatures showed that waters were mixed from October to March. The stratification process started in spring when waters were warming up and stratification was maximum in summer when surface temperatures could reach up to 30 °C. During the stratification period, waters were however regularly mixed by strong northern winds typical from this area. Then, temperatures decreased and water mixing occurred (Fig II.B.2). Waters were in general well oxygenated, except some regular bottom anoxic events from the heart of summer till the start of autumn (Fig II.B.3). We first aimed to investigate the trophic niche of the young-of-the year predator community composed of pike, perch, pikeperch and catfish, and also focused on movements and habitat-use (habitat niche) of the catfish population. We tracked catfish individuals (total length > 700 mm) with acoustic telemetry for four years (2018-2021). Each autumn, concomitantly with tagging campaigns, we sampled the whole food web for stable isotope analysis. I entirely designed, conducted and led this study from the search of funding, administrative and financial monitoring of the project to the most technical and scientific aspects. I took part to all field sampling campaigns. After raw data screening, roughly 5 million positions and 1,500 isotope data had been processed.

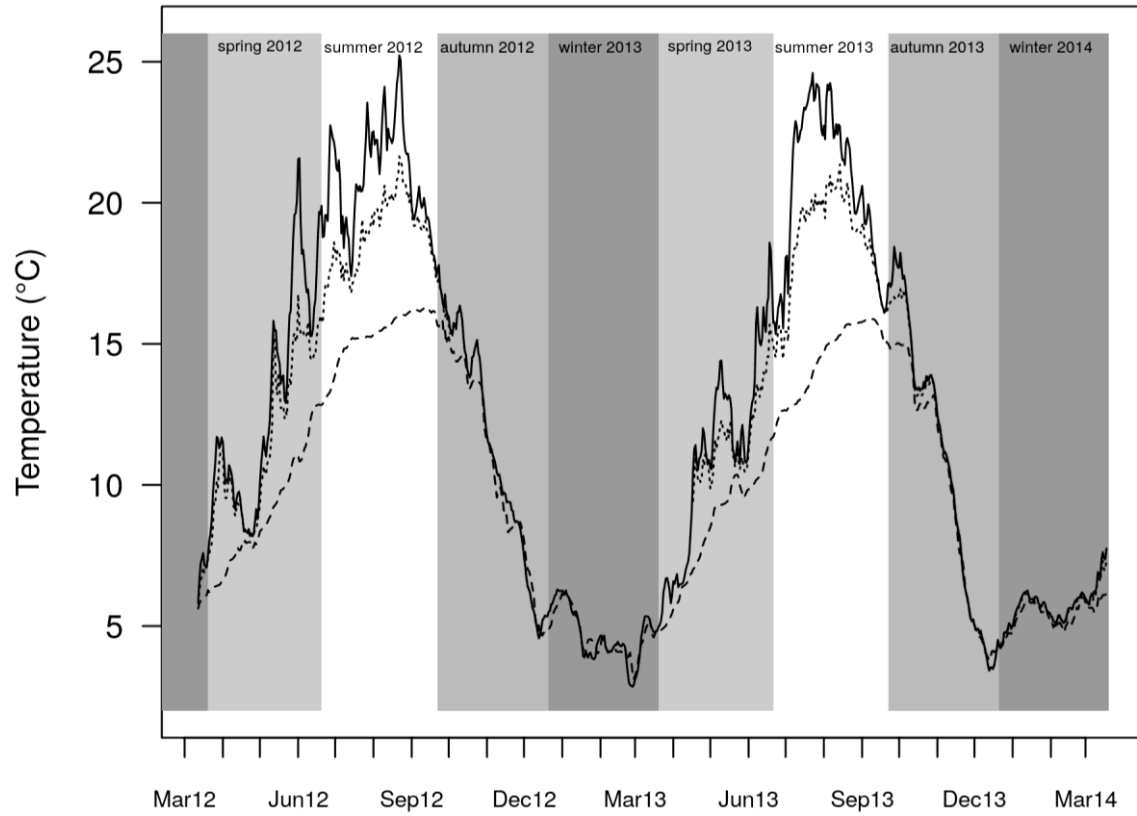


Fig II.B.1 Temperature variations in the Bariousses reservoir over the study period March 2012-March 2014. Mean daily temperature (°C) measured at three different depths (solid, dotted and dashed lines for 0.5, 3.5 and 18.5 m, respectively) at the deepest point of the Bariousses reservoir (see Fig II.A.1). The shading of periods in deep dark grey, dark grey, light grey and white represents winter (mixed water), autumn (mixing occurring), spring (stratified water) and summer (stratified water), respectively.

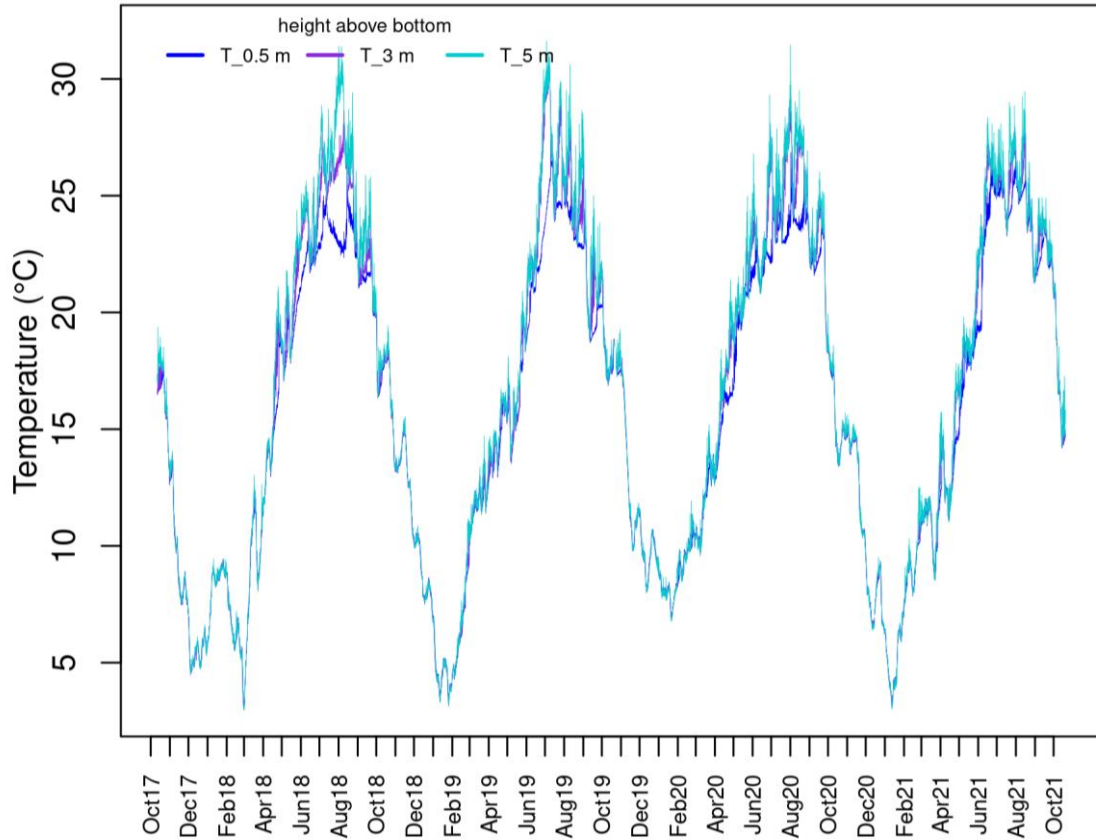


Fig II.B.2 Temperature variations in “Etang des Aulnes” over October 2017-October 2021. Hourly temperature (°C) measured at three different depths (dark blue, violet and cyan lines for 0.5, 3 and 5 m above the bottom, respectively) at the deepest point of “Etang des Aulnes” (6 m-deep, point 42 on Fig II.A.2).

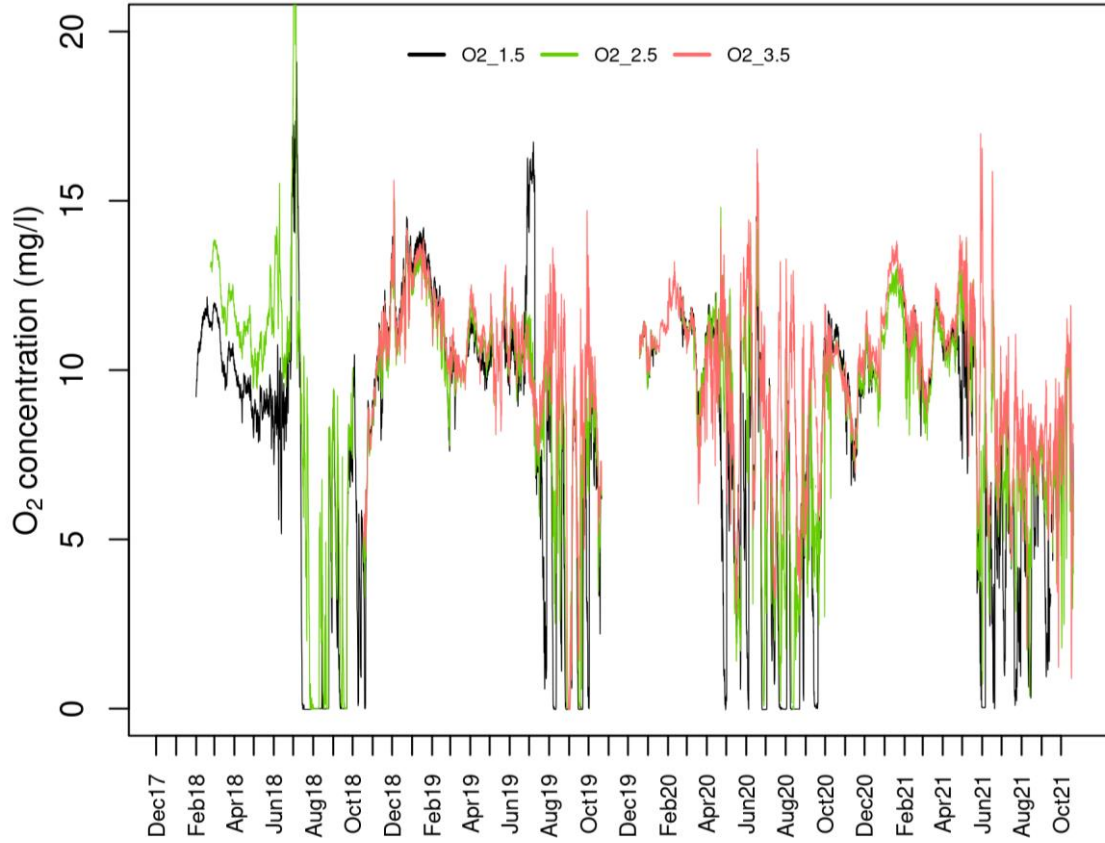


Fig II.B.3 Dissolved oxygen variations in “Etang des Aulnes” over October 2017-October 2021. Smoothed hourly dissolved oxygen concentration (mg/L) measured at three different depths (black, dark green and red lines for 1.5, 2.5 and 3.5 m above the bottom, respectively) at the deepest point of “Etang des Aulnes” (6 m-deep, point 42 on Fig II.A.2).

III.A

Variability of the habitat niche of a
freshwater predator community

III. Inter- and intraspecific variability of the ecological niche of a freshwater predator community

A. Habitat partitioning among three predatory fish in a temperate reservoir

1. *Synthesis (English)*

Pike, perch and pikeperch are three widespread predatory species in European lakes, where they often coexist. As potential competitors, we hypothesized that habitat partitioning is determinant for their coexistence. Though we suspected it could vary between seasons, due to a physical segregation of the habitat by the stratification/homogenization processes, and with the circadian rhythm specific to each species. In the Bariousses reservoir, adult individuals (9 pike, 22 perch and 26 pikeperch) were tracked with high-resolution positioning acoustic telemetry for up to two years. A pressure sensor contained in their tag provided their depth. Their 2D-positioning provided the water depth of their position. Selection ratios were used to quantify fish preferences of water depth, which provided information on their littoral-pelagic preference. Mean species selection ratios were calculated for each habitat type (water depth classes) as well as a confidence interval that took into account the within-species variability and quantified the intraspecific variability. The range of mean selection ratios among species quantified the interspecific variability. From littoral to pelagic waters pike is first found, then perch and finally pikeperch. Pike was the closest to the surface while pikeperch was the deepest. However, this general pattern was variable across seasons. In summer, during the reservoir stratification, the three species mainly used the upper layer and were likely physiologically constrained by a hypoxic hypolimnion. In summer, perch more intensively used the pelagic zone during daytime, whereas pike and pikeperch, respectively diurnal and nocturnal, did not exhibit any habitat shifts between periods of the day. When water was mixing and fish activity was decreasing (autumn, winter), individuals were more evenly distributed along the littoral-pelagic axis and closer to the bottom. Perch had a more variable habitat niche that could help to minimize interactions with pike and pikeperch. Our results highlighted that species coexistence is associated with habitat partitioning among these three predators, with intraspecific differences that could be as large as interspecific ones, in agreement with the coexistence theory.

2. *Synthesis (French)*

Partitionnement de l'habitat entre trois espèces de poissons prédatrices dans un réservoir des latitudes tempérées.

Le brochet, la perche et le sandre sont trois espèces de poissons prédatrices très répandues dans les lacs d'Europe dans lesquels elles coexistent souvent. Potentiellement en compétition, nous avons fait l'hypothèse que leur coexistence reposait sur un partitionnement de l'habitat, qui pouvait varier avec les saisons, en lien avec la ségrégation physique de l'habitat au cours des processus de stratification et d'homogénéisation des eaux en lac, ainsi qu'avec le cycle diurne spécifique à chaque espèce. Dans le réservoir des Bariousses, les mouvements d'individus adultes de ces trois espèces (9 brochets, 22 perches et 26 sandres au total) ont été suivis à haute résolution par télémétrie acoustique sur deux années. Un capteur de pression contenu dans l'émetteur acoustique implanté dans leur cavité abdominale permettait de restituer leur profondeur. Reliée à la bathymétrie, leur position 2D fournissait la profondeur de la colonne d'eau à leur emplacement. Les ratios de sélection ont été utilisés pour identifier les hauteurs d'eau qu'ils préféraient, et ainsi renseigner leur préférence littorale versus pélagique. Pour chaque classe de hauteur d'eau, les ratios de sélection moyens par espèce ainsi qu'un intervalle de confiance quantifiant la variabilité inter-individuelle ont été calculés. L'étendue des variations des ratios moyens spécifiques quantifiait la variabilité interspécifique. De la zone littorale à la zone pélagique, se trouvait d'abord le brochet, puis la perche et enfin le sandre. Le brochet était le plus proche de la surface et le sandre le plus profond. Ce schéma général variait cependant au cours des saisons. En été, lorsque les eaux étaient stratifiées, les trois espèces utilisaient principalement l'épilimnion, probablement contraintes physiologiquement par un hypolimnion offrant des conditions d'oxygénation moins favorables. En été, la perche utilisait plus intensément la zone pélagique durant la journée alors que le brochet et le sandre, respectivement diurne et nocturne, ne montraient aucun changement d'habitat avec les différentes phases du jour. Quand les eaux étaient mélangées et que l'activité des poissons diminuait (automne, hiver), les individus étaient plus régulièrement répartis le long de l'axe littoral-pélagique et plus proches du fond. La perche occupait une gamme d'habitats plus large, ce qui pourrait minimiser les interactions avec le brochet et le sandre. Nos résultats ont mis en évidence que la coexistence de ces trois espèces était associée à un partitionnement de l'habitat, avec cependant des différences intraspécifiques qui pouvaient être aussi importantes que les variations interspécifiques, en accord avec la théorie de la coexistence des espèces.

3. Core paper

Samuel Westrelin, Julien Cucherousset, Romain Roy, Laurence Tissot, Frédéric Santoul & Christine Argillier, 2021. Habitat partitioning among three predatory fish in a temperate reservoir. *Ecology of Freshwater Fish* 31:129-142 doi:<https://doi.org/10.1111/eff.12619>

Abstract

The diversity of predatory species plays a key role in ecosystem functioning but our understanding of the mechanisms underlying their coexistence is limited, particularly in freshwater ecosystems. Northern pike *Esox lucius*, European perch *Perca fluviatilis* and pikeperch *Sander lucioperca* are three widespread predatory species in European lakes, where they often coexist. As potential competitors, we hypothesized that partitioning habitat is a determinant of species coexistence. This was tested by quantifying the variability of their habitat use in tracking adult individuals in the Barriousses reservoir (France, 86.6 ha, mean depth 7.1 m). Specifically, we investigated their distribution along the littoral - pelagic and depth axes along the daily cycle and across seasons. From littoral to pelagic waters were first found pike, then perch and finally pikeperch. Pike was the closest to the surface while pikeperch was the deepest. This general pattern was, however, variable across seasons with the three species located in the upper layer in summer during reservoir stratification. Individuals were more evenly distributed along the littoral-pelagic axis and closer to the bottom when water was mixing (autumn, winter). In summer, perch used more intensively the pelagic zone during daytime. Other species did not show any diel change of habitats. Our results highlighted that species coexistence is associated with habitat partitioning among these three predators, with perch showing a more variable behavior regarding habitat characteristics. Now more than ever, in the context of global change which modifies habitats, it is of crucial importance to understand coexistence mechanisms of species that shape ecosystems.

Keywords: *Esox lucius*; *Perca fluviatilis*; *Sander lucioperca*; littoral - pelagic habitat use; vertical habitat use; diel and seasonal habitat use

Introduction

Top predators play a key role in ecosystem functioning (Hairston et al., 1960; Fretwell, 1987) and more specifically their diversity is of the utmost importance (Sinclair et al., 2003). Understanding how these competing species can coexist (Sommer, 1999) is a crucial question in ecology (Schmitz, 2007). The differential use of resources among species (i.e. resource partitioning) is a key mechanism allowing species coexistence (Schoener, 1986a; Chesson, 2000). In fish, niche segregation was shown to be primarily driven by partitioning of food resources and habitat (Ross, 1986). The coexistence of fish can also occur through more complex mechanisms such as spatial segregation with diet overlap linked to different feeding strategies or foraging sites (e.g. Sala & Ballesteros, 1997; Liedke et al., 2017; Pothoven, 2018; Raby et al., 2019). Competition can lead to shift of habitat use and diet (e.g. Brodersen et al., 2012). To date, however, our understanding of the coexistence of top predators in lakes is overall limited (but see Guzzo et al., 2016).

Northern pike (*Esox lucius*, hereafter pike), European perch (*Perca fluviatilis*, hereafter perch) and pikeperch (*Sander lucioperca*) are three common predatory species in European lakes (Kottelat & Freyhof, 2007) that are primarily piscivorous when adults, although variability in their diet has commonly been reported (Campbell, 1992; Craig, 2008). Pike is a diurnal predator that ambushes prey (Raatt, 1988; Eklöv, 1997); perch can hunt in schools during daytime in pelagic zone (Eklov, 1992; Craig, 2000) and pikeperch hunts in the twilight in open waters (Craig, 2000). These different feeding strategies could favor a trophic segregation, with competition affecting the trophic niche of perch (Schulze et al., 2012). In ectotherms, environment may influence resource partitioning to fulfill physiological requirements as optimal temperature and oxygen conditions vary among species, especially in the case of stratified lakes where vertical gradients of temperature and oxygen segregate the physical habitat, depending on the season. This affects the spatial distribution of fish (Magnuson et al., 1979) and habitat partitioning could then be more pronounced in stratified lakes (Guzzo et al., 2016). These three species have different physiological requirements for temperature and oxygen that could contribute to their coexistence (Helland et al., 2008; Verberk et al., 2012) along environmental gradients. The optimum temperatures increase from pike to perch and pikeperch, 10-24°C, 16-27°C and 27-30°C, respectively (Souchon & Tissot, 2012). Perch is able to cope with hypoxic conditions down to 1.1-2 mg/L (Jones, 1964) while pike avoids zones with less than 3-4 mg/L of dissolved oxygen (Casselman & Lewis, 1996) and pikeperch appears as the most demanding in oxygen (> 4mg/L at 5°C and > 7 mg/L at 20°C, Dolinin, 1974). Pike

is mainly littoral and present in shallow waters (Chapman & Mackay, 1984a; Craig, 1996). In summer, piscivorous perch frequents the pelagic zone during daytime and moves to the littoral, laying on the bottom, during the night (Imbrock et al., 1996; Pekcan-Hekim et al., 2005), while it migrates to deeper waters in winter (Thorpe, 1977). Pikeperch prefers open waters and occupies deeper waters in winter compared to summer (Vehanen & Lahti, 2003). In a manipulative experiment, Schulze et al. (2006) showed that the introduction of pikeperch in a lake where pike and perch were residential led to a shift of perch habitat use towards the littoral over spring and summer. While these studies suggest that habitat segregation might occur among the three species when they coexist, quantification of their habitat use, including the vertical dimension and daily cycle, is lacking.

In the present study, we quantified the habitat use of coexisting pike, perch and pikeperch in a deep reservoir in France. Adults of each species were tracked over two years and their spatial distribution (littoral - pelagic and vertical) analyzed over the different stratification periods and over the daily cycle. We predicted that species coexistence was associated with habitat partitioning, pike mainly using the littoral zone, pikeperch deeper waters and perch the pelagic zone. We expected these main patterns to vary across seasons, when the lake was stratified and the physical habitat became very constraining. We also expected some diel variation associated with the circadian rhythm of each species.

Materials and methods

Study site

The study was conducted in the Bariousses reservoir (45.33°N, 1.49°E) in the western central part of France (Figure III.A.1). At the mean water level, which was hourly measured by Electricité de France (EDF), its area covered 86.6 ha, mean depth was 7.1 m and maximum depth was 19.4 m. Main annual features emerge in the water regulation scheme of this reservoir whose levels varied between 507.1 m and 513.5 m above sea level over the study period (March 2012 – March 2014). High water levels (> 511.9 m, quantile 66%) are from far the most frequent in spring whereas the low ones (< 511.3 m, quantile 33%) are the most frequent in autumn because, at the beginning of this season, the water level is lowered in order to collect rainwater. In winter, water levels are more evenly distributed over their whole range. In summer, the water level is kept stable around its mean value ([511.3; 511.9 m]) to sustain recreational activities concentrated between the shore and the island (Figure III.A.1). The thermal regime of this reservoir was monomictic with four distinct temperature regimes. In

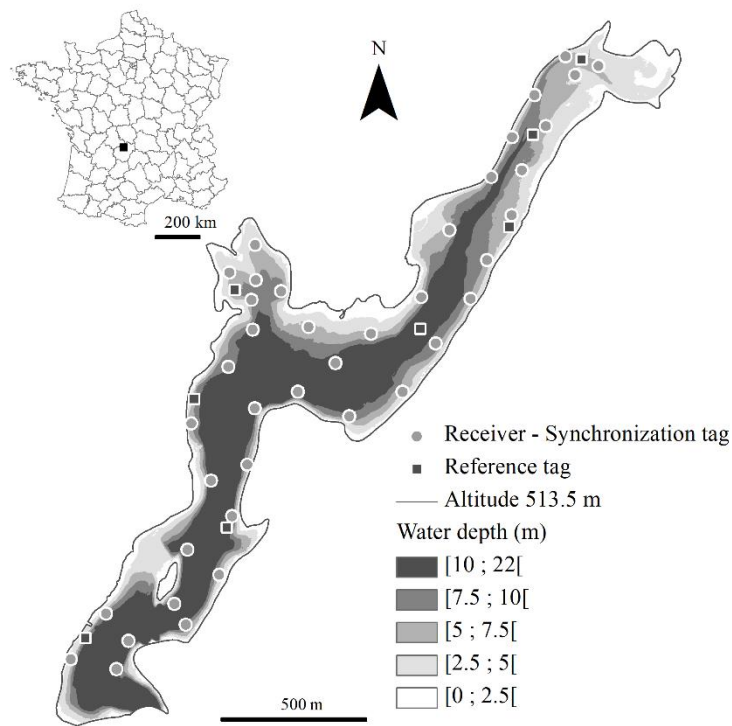


Fig. III.A.1 Location of the study site (black square over France map with department boundaries) and bathymetric map of the Bariousses reservoir at the high water level with the location of the receivers and synchronizing tags (adapted from Westrelin et al., 2018).

spring (April to June), the water temperature rapidly increased and stratification occurred. In summer (July to September), water was warmer and a thermocline at about 4.5 m depth was observed. In autumn (October to December), water temperatures decreased rapidly when water mixing occurred and, in winter (January to March), water was mixed and homogeneously cold (Figure III.A.2). The summer thermocline was associated with an oxycline that separated saturated surface waters from unsaturated deep waters; the hypolimnion had an oxygen saturation rate ranging from approximately 40% (4 mg/L) at its top to 15% (1.5 mg/L) at its basis. During the other seasons and over all depths, the dissolved oxygen concentration was 6 mg/L at the lowest. Representative oxygen profiles based on measurements made in 2011 are given in Suppl. Mat. III.A.1. The Secchi transparency depth varied between 1.3 and 2.5 m. In 2010, measurements made for the European Water Framework Directive monitoring program (WFD2000/60/EC, 2000) gave concentrations of 0.73 mg/L and <0.01 mg/L for total nitrogen

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and total phosphorus in the euphotic zone, respectively. This corresponds to an oligotrophic reservoir. The fish assemblage of the reservoir was determined with a standardized procedure using a multi-mesh gillnet fishing protocol in 2010 (CEN, 2005) and included 11 species. It was dominated by Cyprinidae and Percidae, as commonly observed in lowland reservoirs (Irz et al., 2002). In terms of catch per unit effort (cpue, number per net in 12 hours), the dominant species were roach (*Rutilus rutilus*, cpue 0.37, biomass per unit effort -bpue in g per net in 12 hours, 15.3), ruffe (*Gymnocephalus cernua*, cpue 0.14, bpue 2.1), perch (cpue 0.06, bpue 3.6), pikeperch (cpue 0.02, bpue 4.0) and common bream (*Abramis brama*, cpue 0.01, bpue 3.7). In terms of bpue, the dominant species were roach, carp (*Cyprinus carpio*, bpue 10.7, cpue <0.01), tench (*Tinca tinca*, bpue 8.3, cpue <0.01), chub (*Squalius cephalus*, bpue 4.8, cpue <0.01), pikeperch and common bream.

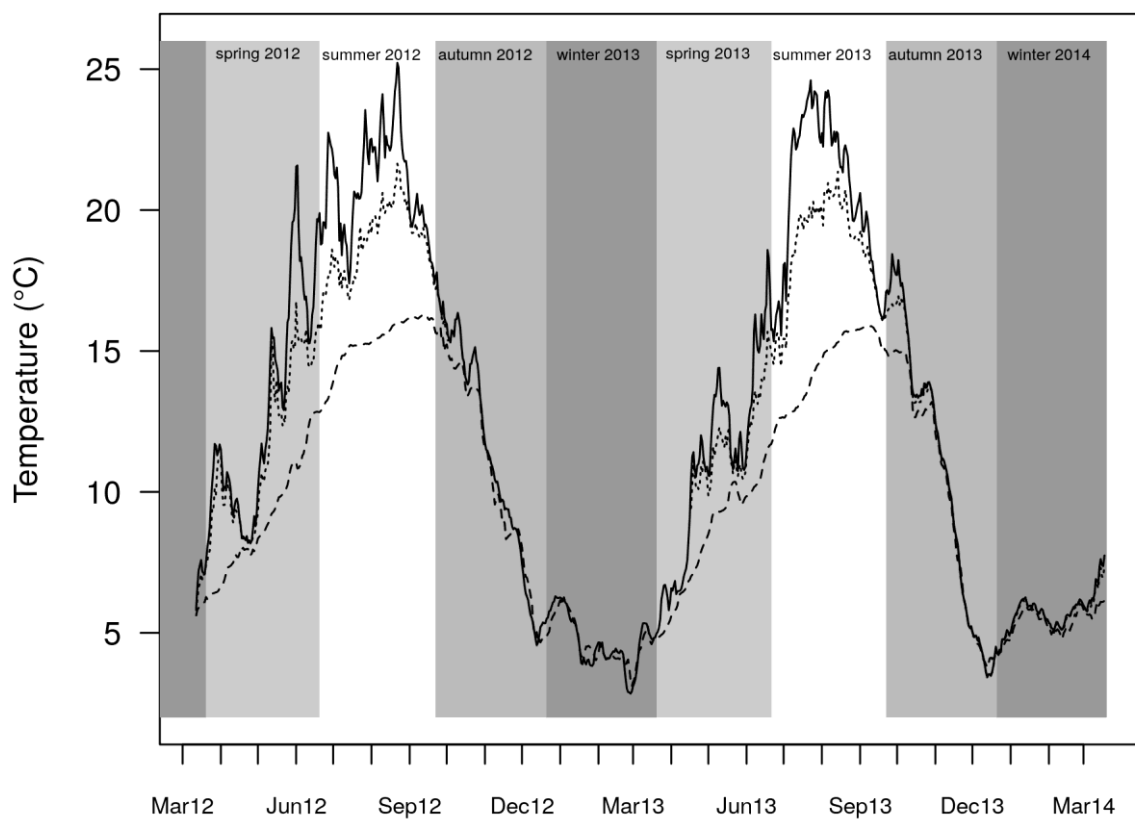


Fig. III.A.2 Mean daily temperature (°C) measured at three different depths (solid, dotted and dashed lines for 0.5, 3.5 and 18.5 m, respectively) at the deepest point of the lake. The shading of periods in deep dark grey, dark grey, light grey and white represents winter (mixed water), autumn (mixing occurring), spring (stratified water) and summer (stratified water), respectively.

Fish tagging

The surgical procedure is detailed in Westrelin et al. (2018) as advocated by Thiem et al. (2011). Specifically, a total of 17 pike, 29 perch and 25 pikeperch, all adults, were caught by fishing in the whole reservoir or with nets set up at dawn, during daytime and at dusk for a maximum of 2 hours over four sampling campaigns (winter, summer and autumn 2012 and spring 2013). Fyke nets were used in shallow areas (< 3 m depth), whereas in deeper areas, pelagic gillnets fishing from 2 m above the bottom and benthic gillnets fishing up to 2m above the bottom were set. Twelve pikeperch originating from a fish farm completed this sample. Fish mean total length was 498 mm, 395 mm and 485 mm, and mean weight 788 g, 958 g and 1059 g for pike, perch and pikeperch, respectively. Vemco V9P-2L (47 mm long, 6.3 g in the air, 90 s mean burst interval, mean battery life 385 days, pressure sensor that gave the fish depth) and V8-4L (20.5 mm long, 2 g in the air, 90 s mean burst interval, mean battery life 163 days, no pressure sensor) acoustic transmitters were used. Twelve pike, 22 perch and the 37 pikeperch had a tag with a pressure sensor. The transmitter weight in the air did not exceed 2% of the fish body weight in accordance with literature recommendations (Winter, 1996; Snobl et al., 2015). Great attention was paid to fish welfare during fish handling and surgery, and all protocols were accepted by the veterinary authority.

Fish tracking

An array of 40 underwater VR2W 69kHz omnidirectional acoustic receivers (Vemco) with their associated synchronization tag (V13-1L) plus eight reference tags were anchored at the bottom (between 0.65 and 1.5 m above the bottom), and throughout the reservoir between January 2012 and March 2014 (Figure III.A.1, for details see Roy et al., 2014; Westrelin et al., 2018). The synchronization tags, deployed at known locations, allowed for the correction of the receiver internal clock drift and thus indicated the exact time of each detection (Smith, 2013). The reference tags, also deployed at known locations but different from those of the receivers, were spread all over the reservoir to detect potential anomalies in the network. Vemco Positioning System was used to calculate 2D fish positions that were filtered according to Roy et al. (2014) recommendations; the mean position error was 3.3 m throughout the reservoir. Fish depth was assessed using pressure sensors (accuracy of 0.5 m and resolution of 0.075m in our environmental conditions). Only the positions recorded after a minimum of 2 days after release were included in the analyses to limit potential effects of surgery (Bridger & Booth, 2003; Vehanen & Lahti, 2003). At the end of the study, 16 stationary individuals (3 pike, 3 perch, 8

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pikeperch) were considered to be dead or to have lost their tag rapidly after release and 18 individuals (5 pike, 4 perch, 3 pikeperch) were rarely located (less than 5 days in a season). These 34 individuals were removed from the analyses. Hence, 9 pike, 22 perch and 26 pikeperch (8 from farm), corresponding to 5-8 pike, 12-20 perch, 14-23 pikeperch individuals depending on the season, were subsequently used in the analyses (Table III.A.1). The time series of their positions used in this study are represented on Suppl. Mat. III.A.2, III.A.3 and III.A.4 for pike, perch and pikeperch, respectively.

Table III.A.1 Number of individuals (n) tracked by season for each species with the total number of positions (Npos). The total length (TL, mm, mean and range) and weight (W, g, mean and range) are given at the time of tagging.

		Spring	Summer	Autumn	Winter
Pike	n	5	8	5	5
	Npos	22,244	32,996	44,729	54,359
	TL	553 425-629	535 425-629	515 425-596	553 425-629
	W	1072 398-1513	978 398-1513	861 398-1221	1072 398-1513
Perch	n	13	20	16	12
	Npos	170,032	214,035	194,037	263,292
	TL	412 320-486	404 320-486	415 320-486	409 320-486
	W	1033 383-1800	964 383-1800	1071 383-1800	990 383-1800
Pikeperch	n	14	23	17	18
	Npos	70,650	185,519	282,974	269,500
	TL	464 360-596	507 360-695	502 360-695	477 360-695
	W	931 354-1914	1223 354-3000	1221 354-3000	1038 354-3000

Data analysis

Timescales

Analyses were conducted according to season and daily cycle. The four seasons (Table III.A.1) corresponded to the thermal regimes (Figure III.A.2). As water temperature regimes were very similar over the 2-year study period (Figure III.A.2, Suppl. Mat. III.A.5), data from the same seasons were pooled as in Westrelin et al. (2018). The daily cycle was defined at an hourly resolution. Dawn was defined as the period including the hour preceding the sunrise hour, the sunrise hour itself and the following hour. Dusk was defined as the period including the hour preceding the sunset hour, the sunset hour itself and the following hour. These two periods of the day lasted three hours each. Daytime was the period following dawn and preceding dusk; night was the period following dusk and preceding dawn.

Water depth

The lake was discretized in a 10 m × 10 m grid. In each grid cell, the mean water depth, deduced from bathymetry and hourly water level, was computed (5 classes: [0; 2.5[- littoral zone, [2.5; 5[- sublittoral zone, [5; 7.5[, [7.5; 10[and [10; 22[m). The deepest class had a broader range to avoid very small numbers of positions. Each fish position was associated to a grid cell. For each individual, the use of a water depth was calculated as the proportion of positions observed in the corresponding class (see Westrelin et al., 2018 for methodological details). It was then averaged across individuals and by species. The selection is the process by which an animal chooses a habitat (Johnson, 1980), in our case the water depth, and the species mean selection ratios quantify it by estimating the use of a water depth regarding its availability (Manly et al., 2002). They were calculated for each combination of season and day periods, and also for each season. The mean selection ratio pools observations from all fish of the same species in the sample, but the confidence interval accounts for the variation in water depth selection across individuals (Manly et al., 2002). When a selection ratio and confidence interval are higher or lower than 1.0 for a water depth, respectively, the preference or avoidance for this water depth is significant (Manly et al., 2002; Rogers & White, 2007).

Fish depth and bottom ratio

The fish depth in the water column was used to calculate the bottom ratio, defined as the ratio of the distance of the fish to the bottom over the water depth, varying between 0 (close to the

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bottom) and 1 (close to the surface). Mean individual bottom ratios were calculated over seasons and periods of the day. These individual ratios were averaged by species and their standard deviations were calculated. The effects of species, season, period of the day and water depth on individual bottom ratios were tested using beta regressions (Ferrari & Cribari-Neto, 2004). Fish identity was considered as a random effect to explicitly account for individual variability and repeated measurements on the same individual. The full model could be written as follows:

$$\text{logit}(\overline{\text{BR}}_{\text{ind}}) = \alpha + \text{SPECIES} * \text{WATER DEPTH} * \text{SEASON} * \text{DAY PERIOD} + s(\text{ind}) + \varepsilon$$

where $\overline{\text{BR}}_{\text{ind}}$ is the expected mean individual bottom ratio in]0,1[, α is the overall intercept, day period is the period of the day, $s(\text{ind})$ is a smoothing function modelling the individual effects (Wood, 2008) having the advantage of getting a significance test of these effects and an evaluation of the explained variance of the model, and ε is the error term following a normal distribution with zero mean. The most parsimonious simple model was selected by running a forward stepwise-based procedure (Venables & Ripley, 2002). Following the recommendations of Richards (2008), all models having an AIC value within a range of 6 from the lowest AIC value were initially selected and, among them, the more complex models that did not have an AIC value lower than all the simpler models within which they were nested were removed. The model fitting was assessed with regards to the homogeneity and normality of the residuals (Zuur et al., 2009) and to the percentage of explained variance (Hastie & Tibshirani, 1990). Significant interactions involving species were further analyzed by Tukey comparisons of pairwise estimated marginal means of the different factor levels of predictors (Lenth, 2016). The thermocline depth was calculated from vertical temperature profiles with R 3.0.1 (R Core Team, 2013) and rLakeAnalyzer package (Winslow et al., 2018). Selection ratios were generated by using adehabitatHS package (Calenge, 2006). The selection is the process by which an animal chooses a habitat (Johnson, 1980) and selection ratios quantify it by estimating the use of a habitat regarding its availability (Manly et al., 2002). Beta regressions were performed in the mgcv package (Wood, 2006) and pairwise comparisons of estimated marginal means in the emmeans package (Lenth, 2016).

Importantly, as there were no significant differences in habitat use (selection and bottom ratios) between farmed and wild pikeperch (Suppl. Mat. III.A.6 - III.A.9), individuals from both origins were pooled in the analyses.

Results

No significant diel pattern was observed in the selection ratio of water depth between species, seasons, and day periods (Suppl. Mat. III.A.10), except in one case. Specifically, perch in summer preferred the littoral and sublittoral zones during dawn, dusk and night but shifted to the sublittoral and [5;7.5[m water depths during daytime (Figure III.A.3). The bottom ratio was significantly impacted by the combination of species, season and water depth but the period of the day was not involved in any significant interaction with species (Table III.A.2). This means that the season and water depth impacted the vertical distribution of species whereas the period of the day did not (Suppl. Mat. III.A.11). In the following, only seasonal scale is considered.

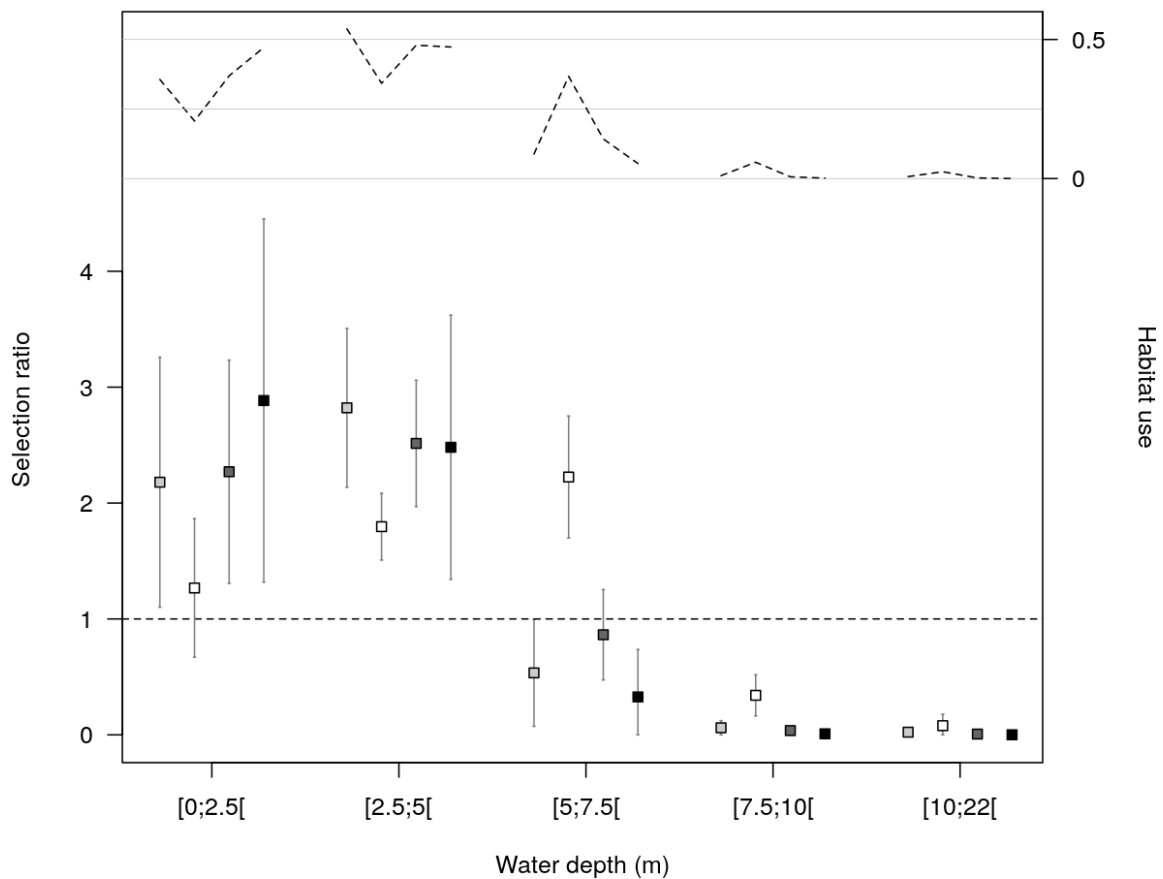


Fig. III.A.3 Selection ratio of water depth (Mean \pm 95% Bonferroni confidence interval) for perch ($n = 20$) in summer for each period of the day (light grey, white, dark grey and black squares for dawn, daytime, dusk and night, respectively) on the left axis. A selection ratio of 1 indicates “no preference” and is represented by a horizontal dashed line. Habitat use (used proportion of each water depth) is represented on the right axis with a dashed line.

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Table III.A.2 Numeric results from the Beta regression that tested the fixed effects of season, water depth, species, period of the day and their interactions, on individual bottom ratios. Fish identity was used as a random effect.

ALL SPECIES	Bottom ratio		
	d.f.	Chi-sq	p-value
Season	3	87.953	< 0.001
Water depth	4	84.081	< 0.001
Species	2	4.794	0.091
Day period	3	6.732	0.081
Season: Water depth	12	42.866	< 0.001
Season: Species	6	32.393	< 0.001
Water depth: Species	8	52.708	< 0.001
Water depth: Day period	12	48.498	< 0.001
Season: Water depth: Species	24	133.768	< 0.001
Individual	51	1220	< 0.001
	Fixed effects	Fixed and random effects	
Explained variance (%)	42.7	57.7	

Regarding littoral - pelagic seasonal partitioning, during all seasons, pike was the species that used the littoral zone the most. This corresponded to 65.5 % of the time in spring and 58.4 % in summer when this zone was preferred (Figures III.A.4a and III.A.4b). In autumn and in winter, it lowered to 31.2 % and 32.1 %, respectively (Figures III.A.4c and III.A.4d). The sublittoral zone was the second most used zone by pike all year long (range 17.9 % - 31.2 %), preferred in summer and autumn (Figures III.A.4b and III.A.4c). Its intense use of the littoral zone in spring and summer was associated with an avoidance of zones deeper than 5 m. These deeper zones became more frequented by this species in autumn and winter. Perch was the species that used the sublittoral zone the most, range 40.0 % - 42.4 % over all seasons, and also preferred it except in winter (Figures III.A.4a to III.A.4d). In spring and summer, perch also preferred the littoral zone which was its second most used zone (Figures III.A.4a and III.A.4b). In summer, perch also used the [5; 7.5[m zone (20.9 %), zone that progressively became its second most used in autumn (Figure III.A.4c), and evenly frequented the [7.5; 10[m zone in

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winter (Figures III.A.4d). Pikeperch did not show any strong consistent pattern across the seasons. In spring, it preferred the [5; 7.5[m zone which was its most used (41.8 %) and also used [2.5; 5[and [7.5; 10[m zones (20.1 % and 17.2 %, respectively) (Figure III.A.4a). In summer, its littoral use raised up to 29.1 % while it used all other zones relatively homogeneously without any preference (Figure III.A.4b). In autumn, it left the littoral (Figure III.A.4c) and, in winter, used the deepest parts (40.5 %) followed by the [7.5; 10[(29.9 %) and [5; 7.5[m (16.8 %) ones (Figure III.A.4d).

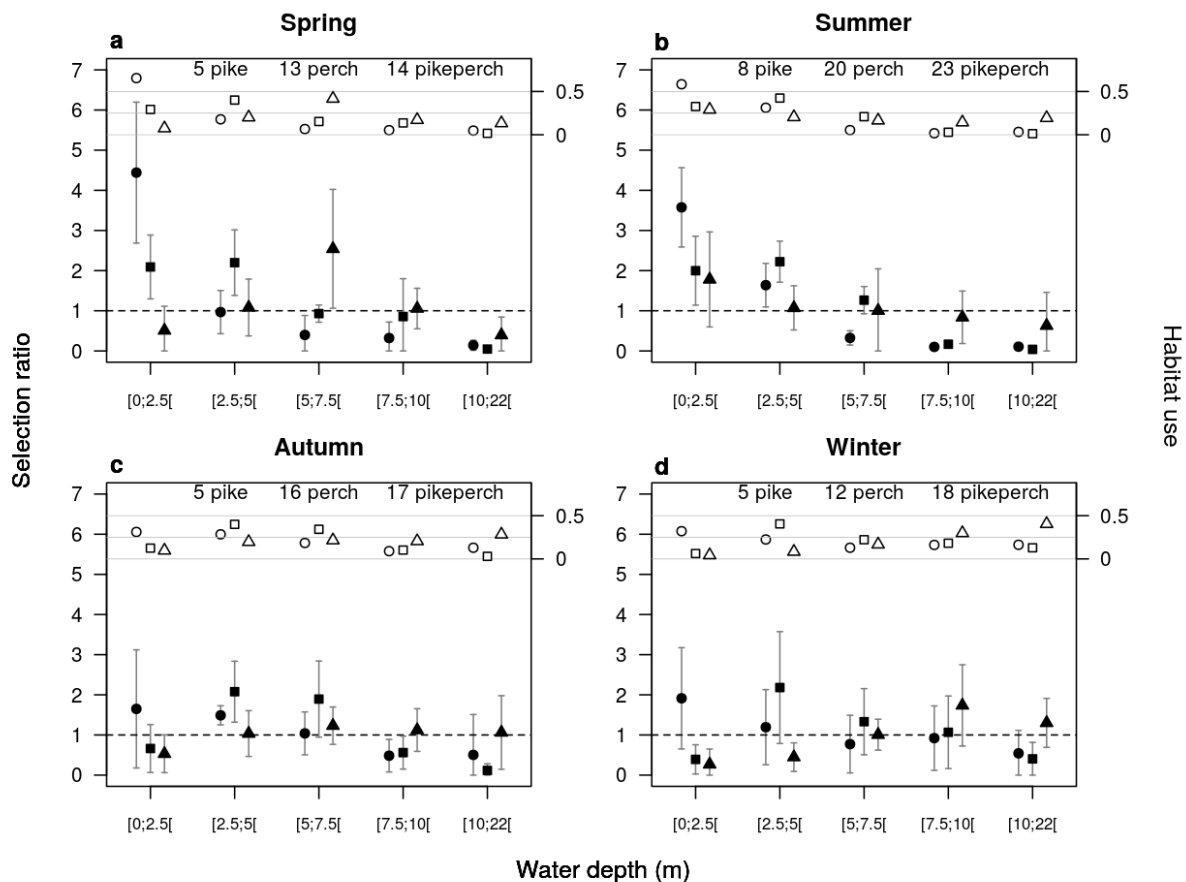


Fig. III.A.4 Selection ratio of water depth (Mean \pm 95% Bonferroni confidence interval) in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) and for each species (black dots, black squares and black triangles for pike, perch and pikeperch, respectively) on the left axis. A selection ratio of 1 indicates “no preference” and is represented by a horizontal dashed line. Habitat use (used proportion of each water depth) is represented on the right axis (circles, white squares and white triangles for pike, perch and pikeperch, respectively). In each season, the number of pike, perch and pikeperch taken into account is provided.

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Regarding vertical seasonal partitioning, in spring, perch and pikeperch were very close to the bottom down to 10 m depths (Figure III.A.5a). On the other hand, pike was very close to the bottom in the littoral zone but in the third quarter above perch and pikeperch in the sublittoral zone (Figure III.A.5a). When it visited zones deeper than 5 m, pike was much above the thermocline albeit with a very high variability (Figures III.A.5a and III.A.6a), again less deep than perch and pikeperch. Generally all species were closer to the surface in summer compared to spring; the between-individual variability appeared quite high though (Figures III.A.5b and III.A.6b). Pike was found around the third deepest quarter of the water column when in its preferred littoral and sublittoral zones, above perch and pikeperch (Figure III.A.5b). In autumn,

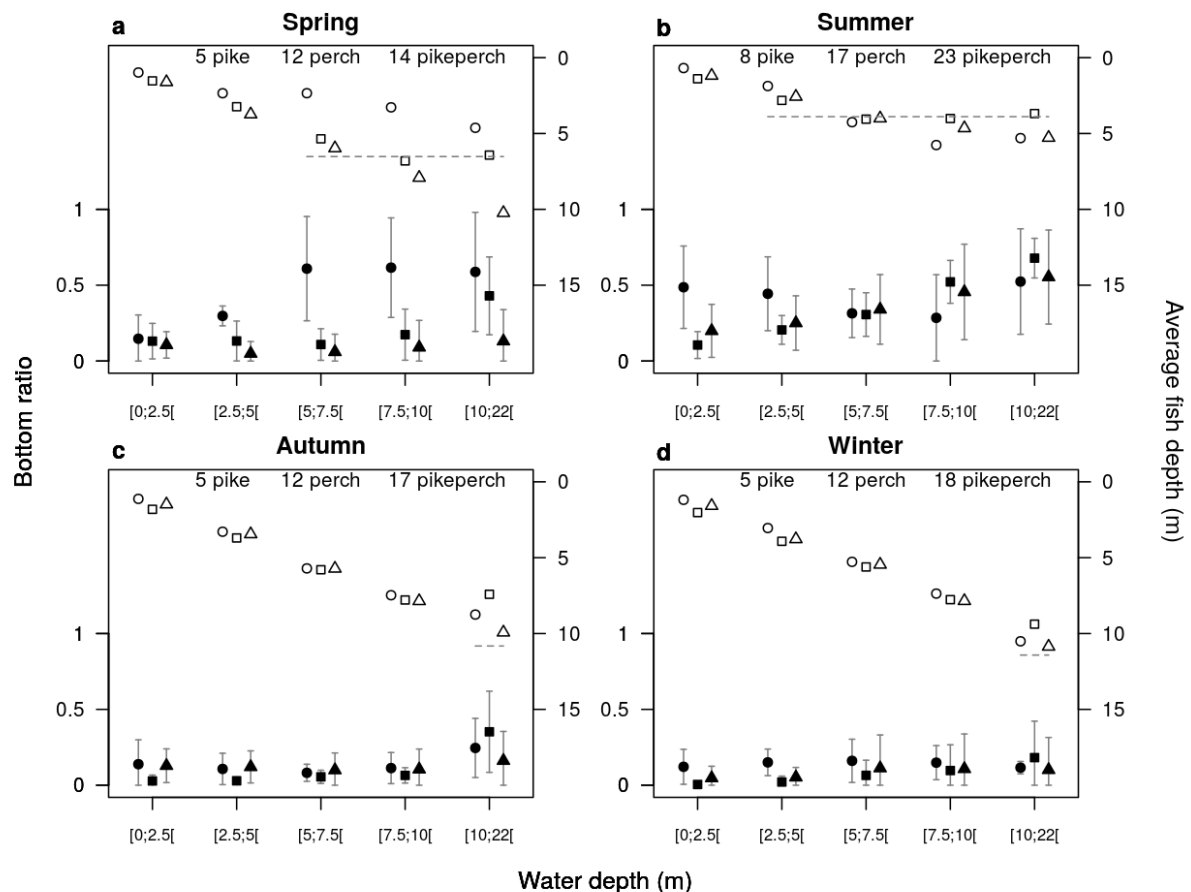


Fig. III.A.5 Bottom ratio (Mean \pm SD) in each season (a) spring, b) summer, c) autumn and d) winter) for each species (black dots, black squares and black triangles for pike, perch and pikeperch, respectively) on the left axis. The average depth of species (circles, white squares and white triangles for pike, perch and pikeperch, respectively) and of the thermocline (grey dashed line) are represented on the right axis. In each season, the number of pike, perch and pikeperch taken into account is provided.

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while migrating towards deeper waters, species were getting much closer to the bottom (Figures III.A.5c and III.A.6c), this being pronounced in the deepest zone in winter (Figures III.A.5d and III.A.6d). Statistical background of these analyses is provided in Suppl. Mat. III.A.12.

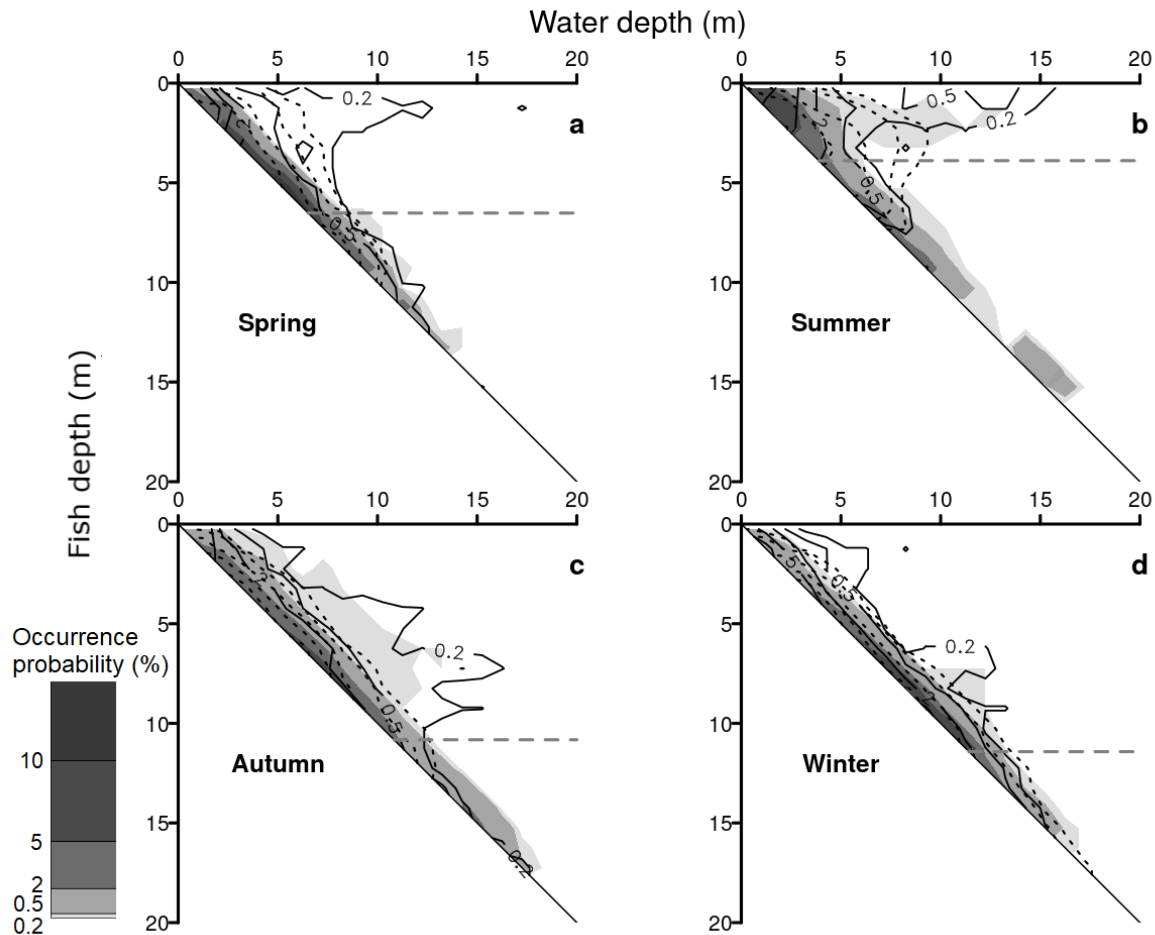


Fig. III.A.6 Occurrence probability (%) of each species (black solid, black dashed and grey-filled contours for pike, perch and pikeperch, respectively) along the littoral-pelagic and depth axes in each season (a) spring, b) summer, c) autumn and d) winter). The occurrence probability at one point of the space defined by the water depth and the fish depth is the proportion of positions (%) at this point. It has been calculated over 1 m-sided cells. The thermocline mean depth is represented by the horizontal grey dashed line.

Littoral - pelagic and vertical seasonal partitionings of species are synthesized in Figure III.A.6. The general pattern of the species distribution along the littoral - pelagic axis was the following:

pike, perch and pikeperch. Pike was closer to the surface than both other species. Pikeperch was often found deeper than the other two species. This general pattern was modulated by the season, species becoming more evenly distributed from littoral to pelagic, but closer to the bottom when the lake water was mixed in autumn and winter. All species appeared more concentrated in the 0-7.5 m zone in spring and summer, and closer to the surface in summer, following the thermocline and avoiding the deoxygenated hypolimnion.

Discussion

The present study demonstrated that habitat partitioning occurred along both the littoral - pelagic axis and the depth axis when the three species coexisted. The main driver was seasonal and contrary to our expectation, no diel vertical migration was observed. The only significant diel pattern was the more intensive use of the pelagic zone by perch during daytime in summer.

Seasonal movement patterns

As expected, fish movement patterns were influenced by the season, in all likelihood, to avoid unfavorable physical conditions and to satisfy different physiological and biological requirements. We could observe that more than half of the fish, including some of the smallest ones, were mature. By considering the size of the remaining ones, we could reasonably suppose most of them as also being mature. Spring corresponds to the reproduction period of pike, perch and pikeperch (Kottelat & Freyhof, 2007), when perch and pikeperch also move closer to the littoral to find spawning habitats (Craig, 2000). In summer, the deoxygenated and colder deep hypolimnetic waters could explain the concentration of the three species closer to the surface to reach satisfying oxygenation conditions and/or to remain the closest to their optimum temperature range (Kubečka & Wittingerova, 1998; Čech & Kubečka, 2002; Nordahl et al., 2020), following the rising of the thermocline which was very closely linked to the reservoir's hydrological management.

Pike

Pike was mainly in the littoral zone with rare incursions into the pelagic zone. Its littoral position and migrations between the littoral and central parts of the lake confirmed results of some previous studies (Chapman & Mackay, 1984a; Chapman & Mackay, 1984b; Cook & Bergersen, 1988). The deepest movements of pike were observed in autumn and winter, when temperature

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was lower and when dissolved oxygen concentration in the deeper zones was not limiting. Pierce et al. (2013) also observed that depth selection by pike was constrained by low dissolved oxygen concentration in some seasons. In the present study, the limited number of pike should make us cautious about findings even if these individuals were tracked over long periods.

Pikeperch

Pikeperch used different parts of the reservoir according to the season and spent a lot of time in shallow areas in summer, which is similar to what was found in Jepsen et al. (1999), Vehanen & Lahti (2003) and (Huuskonen et al., 2019). With the exception of summer when the lake was well stratified and the deepest areas less favorable in terms of oxygen, pikeperch was generally located in the deepest decile of the water column, probably seeking darkness (Craig, 1987) or prey (Huuskonen et al., 2019). This was in complete agreement with what Gorman et al. (2019) found on the walleye (*Sander vitreus*), a Northern American fish close relative of the European pikeperch (Craig, 2000).

Perch

Perch frequented deep waters in winter and moved inshore in spring. This was likely associated with spawning, as observed elsewhere (Eckmann & Imbrock, 1996). Perch remained in the littoral or epilimnetic waters until the autumn and then returned to deep waters for overwintering. Our results confirmed previous results showing that this species was more homogeneously distributed in winter than in summer (Eckmann & Imbrock, 1996; Imbrock et al., 1996).

The seasonal variations of habitat partitioning seemed to be mainly linked to the life history traits of species. Even if water level was shown not to influence the habitat use of perch in this reservoir, the highest diversity of littoral habitats in spring and intermediate in summer, due to the water regulation scheme (Westrelin et al., 2018), could make this littoral zone even more attractive for these predatory species in these seasons. On the other hand, the lower structural complexity of littoral habitat in autumn and to a lesser extent in winter could contribute to its lower use.

Diel movement patterns

Whereas seasonal patterns of habitat use seem to be essentially associated with avoiding unfavorable physical conditions (Lucas & Baras, 2001) and with finding favorable spawning

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sites (Eckmann & Imbrock, 1996) or prey (Huuskonen et al., 2019), diel movements are generally interpreted as a trade-off between foraging and predator avoidance behavior (Lucas & Baras, 2001). In general, small prey fishes in lakes escape predators by finding refuge in littoral shelters during daytime and moving offshore at night (Kubečka, 1993; Říha et al., 2015), which also seemed to be the case in the Bariousses reservoir (Goulon et al., 2018). We could have expected that these prey migrations would drive movements of piscivorous pike and perch. They are visual predators (Jepsen et al., 2001; Zamora & Moreno-Amich, 2002) and could then be particularly attracted by the littoral zone during daytime and less at night. Pikeperch, active in twilight (Jepsen et al., 1999; Poulet et al., 2005), could have performed diel vertical migrations from the bottom to forage pelagic prey during dawn and dusk as it has been reported to forage in the pelagic zone (Craig, 1987; Huuskonen et al., 2019).

Pike

Although pike shows a diel activity pattern, being active during daytime and at rest during the night (Craig, 1996; Baktoft et al., 2012), no corresponding diel pattern emerged in habitat use in our study, as pike was in the littoral zone all day long. Cook & Bergersen (1988) described pike that were positioned deeper, and in deeper waters at night, whereas Říha et al. (2015) found higher littoral densities at night.

Pikeperch

No diel vertical migration was observed for pikeperch in our study. Horký et al. (2008) found a predominant nocturnal or crepuscular activity of pikeperch which they linked to foraging and which was associated with diel migrations: resting in shallow areas at night and in deeper zones during the daytime. Jepsen et al. (1999) did not find clear diel activity rhythm, with the exception of certain periods in the late summer, when activity was predominantly nocturnal. Gorman et al. (2019) found weak evidence of diel vertical migration for walleye.

Perch

Perch movement from littoral to pelagic waters during daytime in summer was the only diel pattern highlighted by our study, which was the opposite way to the diel migration of prey. This diel pattern has already been described but seemed dependent on the trophic status of the lake (Imbrock et al., 1996; Jarvalt et al., 2005; Jacobsen et al., 2015; Nakayama et al., 2018). Imbrock et al. (1996) reported that, in summer and at night, perch rested on the littoral bottom.

In our case, perch was close to the bottom all day long, in its preferred zones, except in summer when it was constrained by the physical habitat partitioning to stay close to the thermocline.

Farmed versus wild pikeperch

Interestingly farmed and wild pikeperch used the littoral-pelagic and vertical habitats similarly. The stress of establishing themselves in a novel environment could however lead to behavioral changes. Farmed fish are capable of adopting dispersion behavior similar to wild individuals (e.g. Solem et al., 2013; Zimmermann et al., 2013) but they need to explore more their new environment (e.g. Uglem et al., 2008; Dempster et al., 2010). This could lead to a habitat use different from wild conspecifics. Eel-tailed catfish *Tandanus tandanus* translocated from a reservoir to a river selected habitats that were more common in their original environment and different from the riverine individuals (Carpenter-Bundhoo et al., 2020). In a translocation experiment of wild large-bodied pike and European catfish *Silurus glanis*, translocated individuals showed persistent larger activity space-sizes than residents but no difference in activity (Monk et al., 2020). In our case, farmed fish exploited the most favorable habitats as wild residents did which could mean that the carrying capacity of the reservoir was not reached. This could prevent stocked fish from being displaced from favorable habitats through prior-residence effects (Deverill et al., 1999). Moreover, our farmed pikeperch came from an extensive pond farm which had possibly got them used to conditions close to wild ones and could have helped them to well establish in the reservoir.

Habitat partitioning

The main movements of potential preys did not seem to strongly drive the habitat use of the adults of the studied piscivorous species. Our results suggest that other factors played a role, such as temperature (Nakayama et al. 2018), competition and/or intraguild predation. All tagged fishes had not reached a refuge size and the smallest could be preyed upon by the biggest piscivorous individuals present in the reservoir. It has been shown that cannibalism and intraguild predation were enhanced in low productive systems in which other prey fishes are lacking (Mehner et al., 1996). Typically, the smallest perch could avoid the littoral zone during daytime to escape large pike.

Although the three species have marked circadian rhythms of activity, very little evidence of diel variations of habitat partitioning existed. Pike and pikeperch stayed in their preferred habitats, littoral and deep waters, respectively. Only perch performed diel movements between

the littoral and pelagic zones. The plastic nature of perch regarding the environment (Craig, 2000) probably played a role in the habitat partitioning between the three species. In a manipulative experiment that consisted of introducing pikeperch in a lake already inhabited by perch and pike, perch shifted its habitat use towards the littoral while pike was hardly affected (Schulze et al., 2006). In this case, large perch were exclusively pelagic during daytime before pikeperch introduction, and became half pelagic half littoral after (Hölker et al., 2007). Perch would then modify its habitat niche to minimize interaction with pike and pikeperch. The plasticity in habitat use of perch is associated with a generalist diet (Craig, 1978; Craig, 2000) that enables the species to coexist with more specialist species like pike and pikeperch (Schulze et al., 2012), mainly piscivorous (Kangur & Kangur, 1998). This resource partitioning was probably enhanced by the oligotrophic nature of the Bariousses reservoir (Kobler et al., 2009; Guzzo et al., 2016) which did not offer abundant preys, forcing species to specialize in order to reduce interspecific competition (Araújo et al., 2011). Large variations of selection ratios and bottom ratios in some cases stressed that a high within-species individual variability could also be important and could correspond to the coexistence of different behavioral types using separated habitats, as already observed with pike (Kobler et al., 2009) and perch (Marklund et al., 2019). This could aim at reducing the intraspecific competition (Kobler et al., 2009).

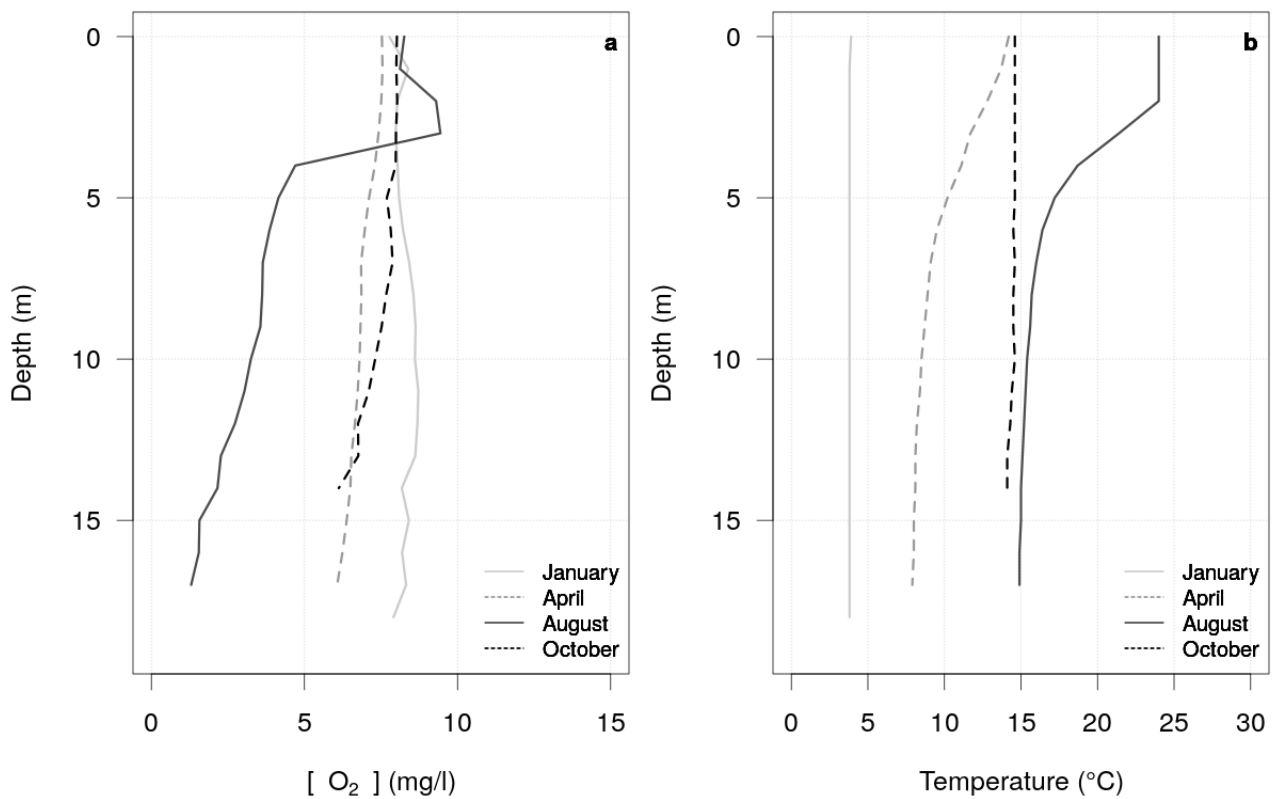
Conclusions

More knowledge is needed to fully understand how predatory species coexist. Leading a similar study with different assemblages of predators (e.g. any combination from one species alone to all three together, as in our case), along with a trophic component, would allow us to validate our hypotheses regarding the underlying mechanisms of habitat partitioning. In conclusion, this study revealed the existence of seasonal habitat partitioning among these three predatory species both in the littoral - pelagic and vertical dimensions. Our results highlighted that habitat partitioning is associated with the coexistence of predatory fish species in a reservoir. This mechanism, supported by the plasticity of perch in its habitat use, could explain how pike, perch and pikeperch coexist in numerous European lakes. In the context of global change that modifies habitats and their availability, understanding coexistence mechanisms of predatory species that shape ecosystems is more than ever of crucial importance.

Acknowledgements

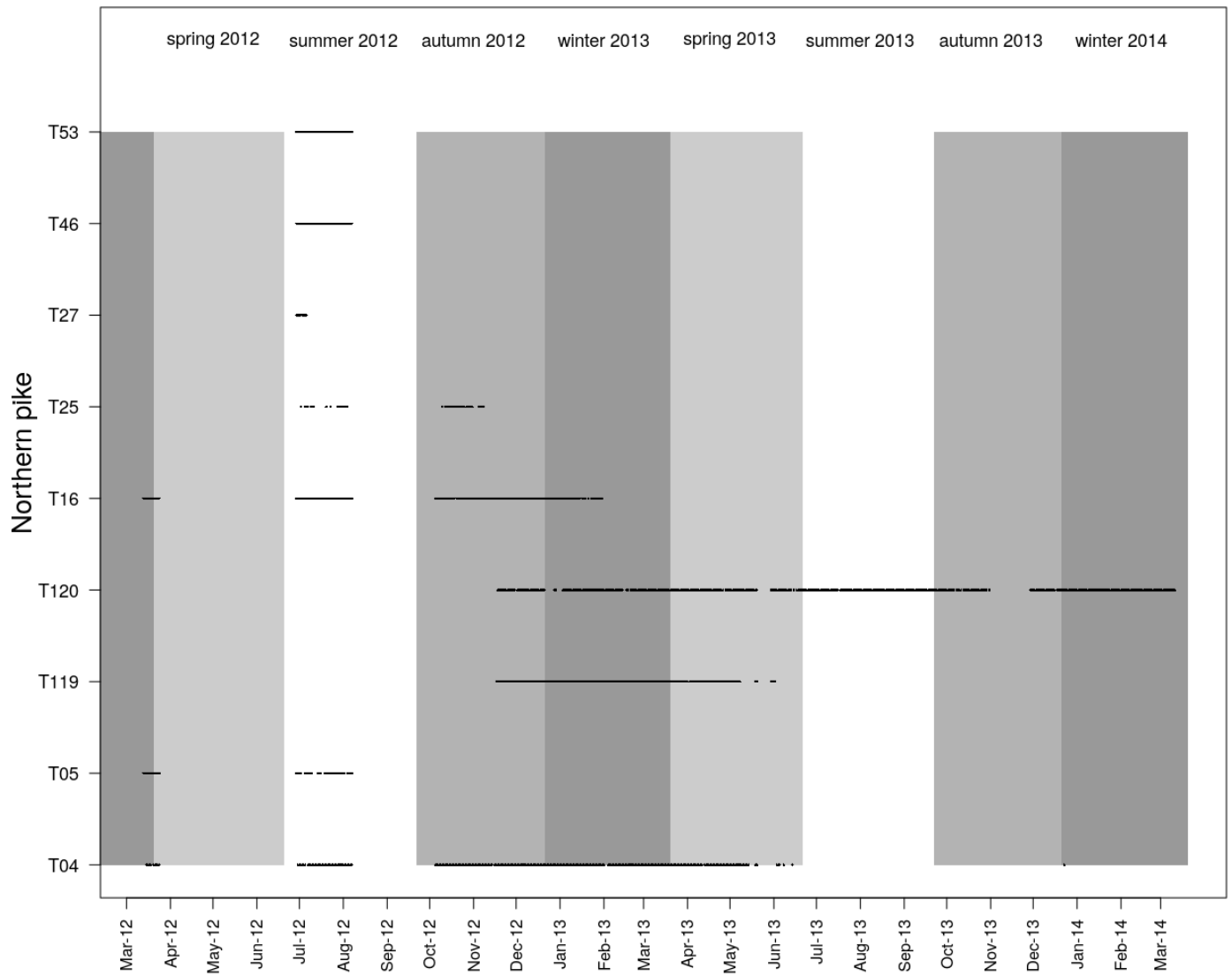
We would like to thank Tiphaine Peroux, Julien Dublon, Virginie Diouloufet, Mario Lepage and Charles Roqueplo for their field work, Yann Le Coarer for dGPS treatments, Maxime Logez for suggestion of some useful R packages, Nathalie Reynaud for GIS treatments and Coralie Garron and Justine Haas for English correction. We also thank numerous other people who occasionally helped in the field. We are grateful to the two anonymous reviewers for their careful reading and constructive remarks that significantly improved the finished document.

4. Supplementary materials



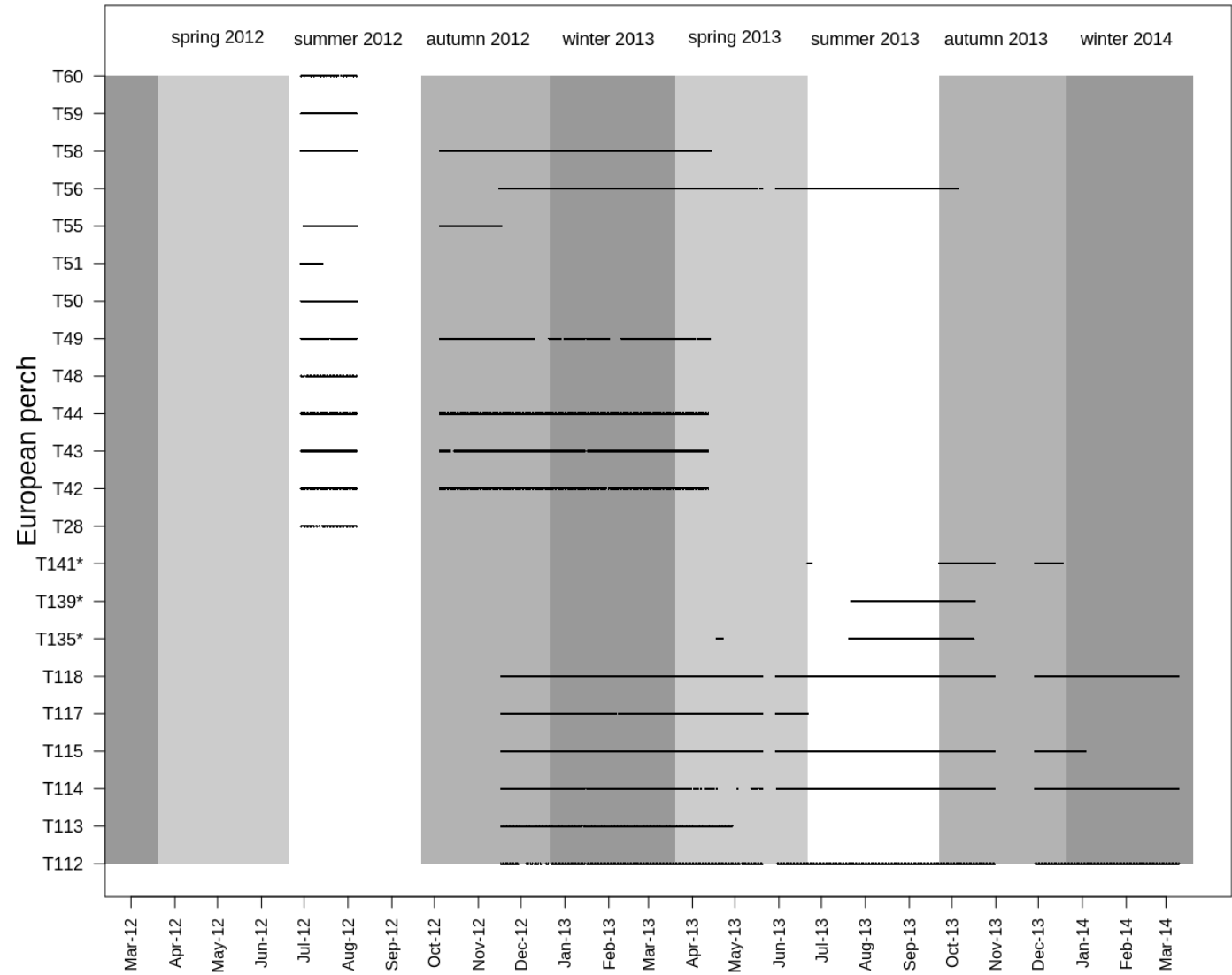
Suppl. Mat. III.A.1 Seasonal oxygen and temperature vertical profiles in 2011 (panels a and b, respectively). The profiles in solid grey, dashed grey, solid black and dashed black lines were measured on 20th January, 21st April, 23rd August and 19th October 2011, respectively, close to the dam in the southern part of the Bariousses reservoir.

III.A Variability of the habitat niche of a freshwater predator community



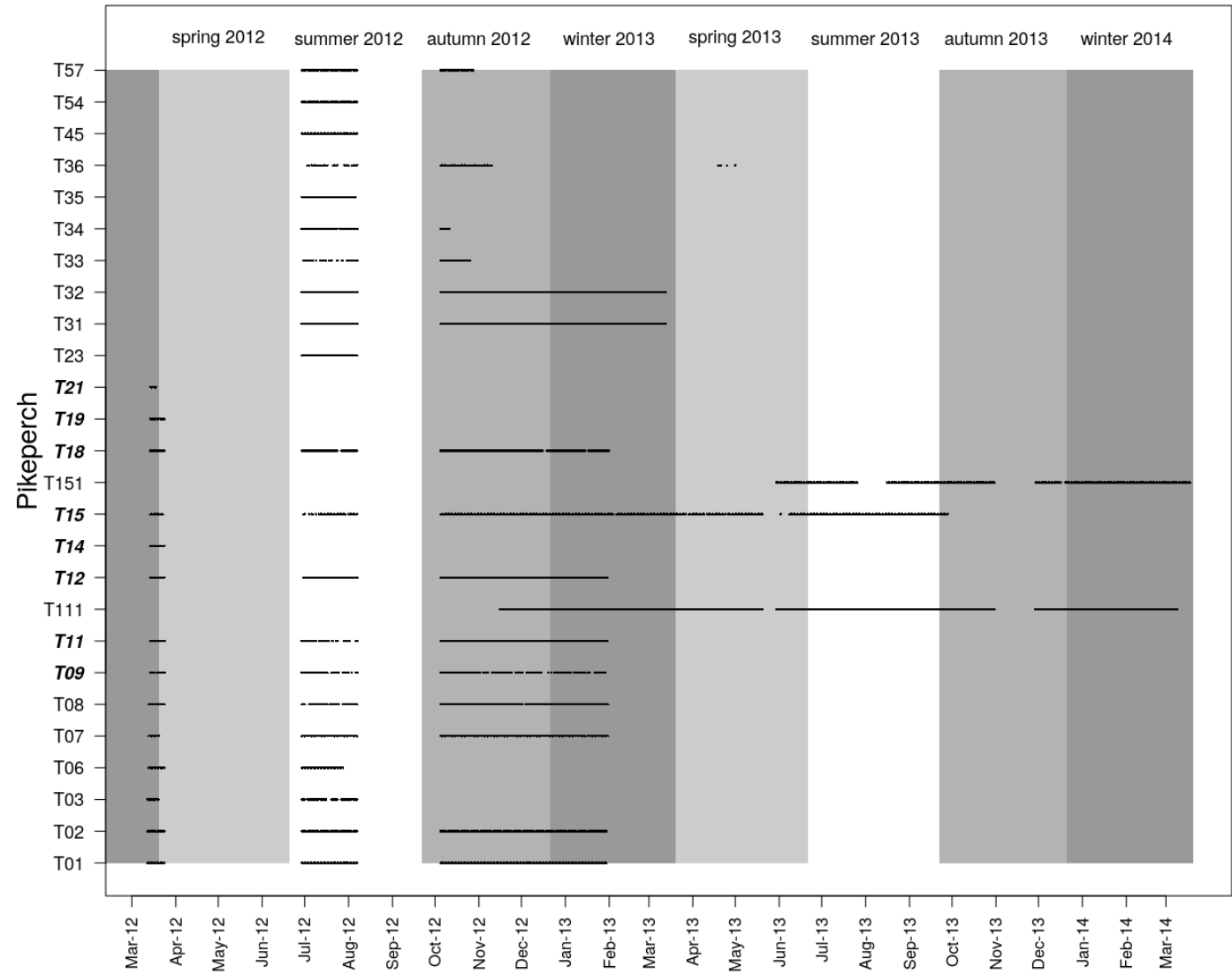
Suppl. Mat. III.A.2 Time series of the positions of pike, *Esox lucius* (black dots). The shading of periods in dark grey, grey, light grey and no shading are representative of winter, autumn, spring and summer, respectively.

III.A Variability of the habitat niche of a freshwater predator community



Suppl. Mat. III.A.3 Time series of the positions of perch, *Perca fluviatilis* (black dots). * indicates tags without pressure sensor. The shading of periods in dark grey, grey, light grey and no shading are representative of winter, autumn, spring and summer, respectively.

III.A Variability of the habitat niche of a freshwater predator community



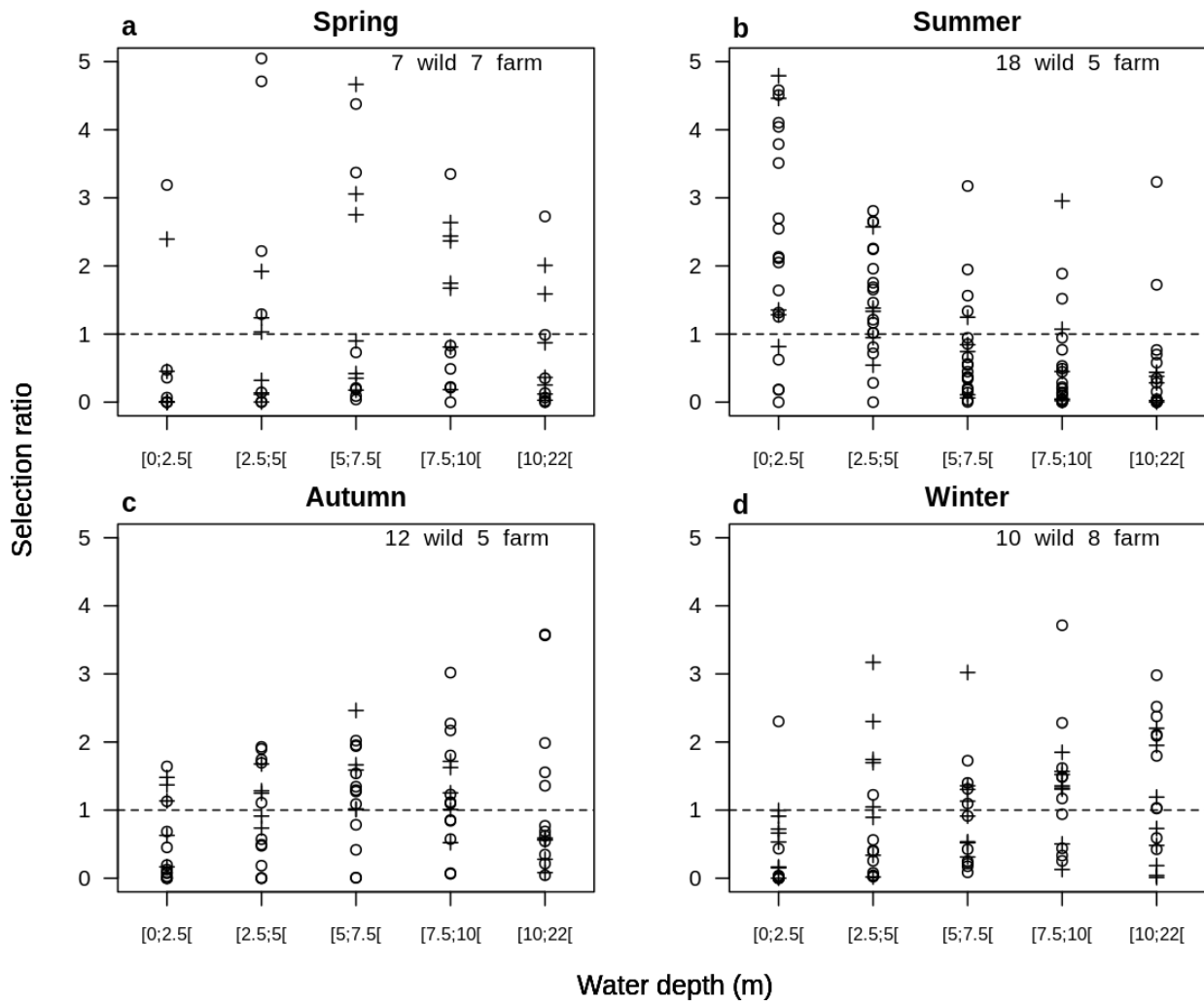
Suppl. Mat. III.A.4 Time series of the positions of pikeperch, *Sander lucioperca* (black dots). Italic bold ID indicates farmed pikeperch. The shading of periods in dark grey, grey, light grey and no shading are representative of winter, autumn, spring and summer, respectively.

Suppl. Mat. III.A.5 Comparison of seasonal mean daily temperature profiles between the different years (from spring 2012 to winter 2014). The distributions of mean daily temperatures at three depths (0.5, 3.5 and 18.5 m corresponding to Figure III.A.2) were compared between the same seasons of the different years with a Kruskal-Wallis test. When temperatures are different, both means are given; when they are not different, the global mean is given. P-values are given in italics. In spring, temperatures between 2012 and 2013 were not different at 3.5 and 18.5 m but at 0.5 m, the mean temperature was warmer in 2012 than in 2013 (13.0 °C and 11.1 °C, respectively). In summer, temperatures between 2012 and 2013 were not different at 0.5 and 3.5 m; at 18.5 m, the mean temperature was warmer in 2012 than in 2013 by 0.8 °C. In autumn, temperatures between 2012 and 2013 were not different at 0.5 and 18.5 m. The comparison was not made at 3.5 m but, except in early fall, temperature was very homogeneous all along the vertical profile in autumn (see Figure III.A.2). The winter was colder in 2013 compared to 2014 by about 1 °C in average. Yet temperatures during both winters were much cooler than in any other season and characteristic of this season. In general, temperature differences between years ranged between a 1 °C interval, the biggest difference appearing in spring when the surface layer was warmer in 2012 compared to 2013 by about 2 °C. Aside these values, each season clearly kept its main features whatever the year with rapidly increasing temperatures in spring, water stratification all along the summer when the temperatures were the highest, fast decreasing temperatures in autumn and cool and relatively stable temperatures in winter (see Figure III.A.2). This led us to pool data from the same seasons over the two-year study.

III.A Variability of the habitat niche of a freshwater predator community

	Spring	Summer	Autumn	Winter
0.5 m depth	$\overline{T}_{2012} = 13.0$	$\overline{T} = 20.7$	$\overline{T} = 10.9$	$\overline{T}_{2013} = 4.7$
	$\overline{T}_{2013} = 11.1$			$\overline{T}_{2014} = 5.8$
	<i>0.009</i>	<i>0.99</i>	<i>0.29</i>	<i>< 0.001</i>
3.5 m depth	$\overline{T} = 11.7$	$\overline{T} = 18.7$	(1)	No data in 2013
	<i>0.31</i>	<i>0.83</i>		
18.5 m depth	$\overline{T} = 8.7$	$\overline{T}_{2012} = 15.3$	$\overline{T} = 10.3$	$\overline{T}_{2013} = 4.1$
		$\overline{T}_{2013} = 14.5$		$\overline{T}_{2014} = 5.1$
	<i>0.11</i>	<i>< 0.001</i>	<i>0.15</i>	<i>< 0.001</i>

⁽¹⁾ As only the first 10 days of autumn are available in 2012 at 3.5 m depth, the comparison was not made with the full time series in 2013 (90 days).



Suppl. Mat. III.A.6 Mean individual selection ratio of water depth in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) for pikeperch (crosses for farmed individuals and white dots for wild individuals). In each season, the numbers of farmed and wild pikeperch are provided.

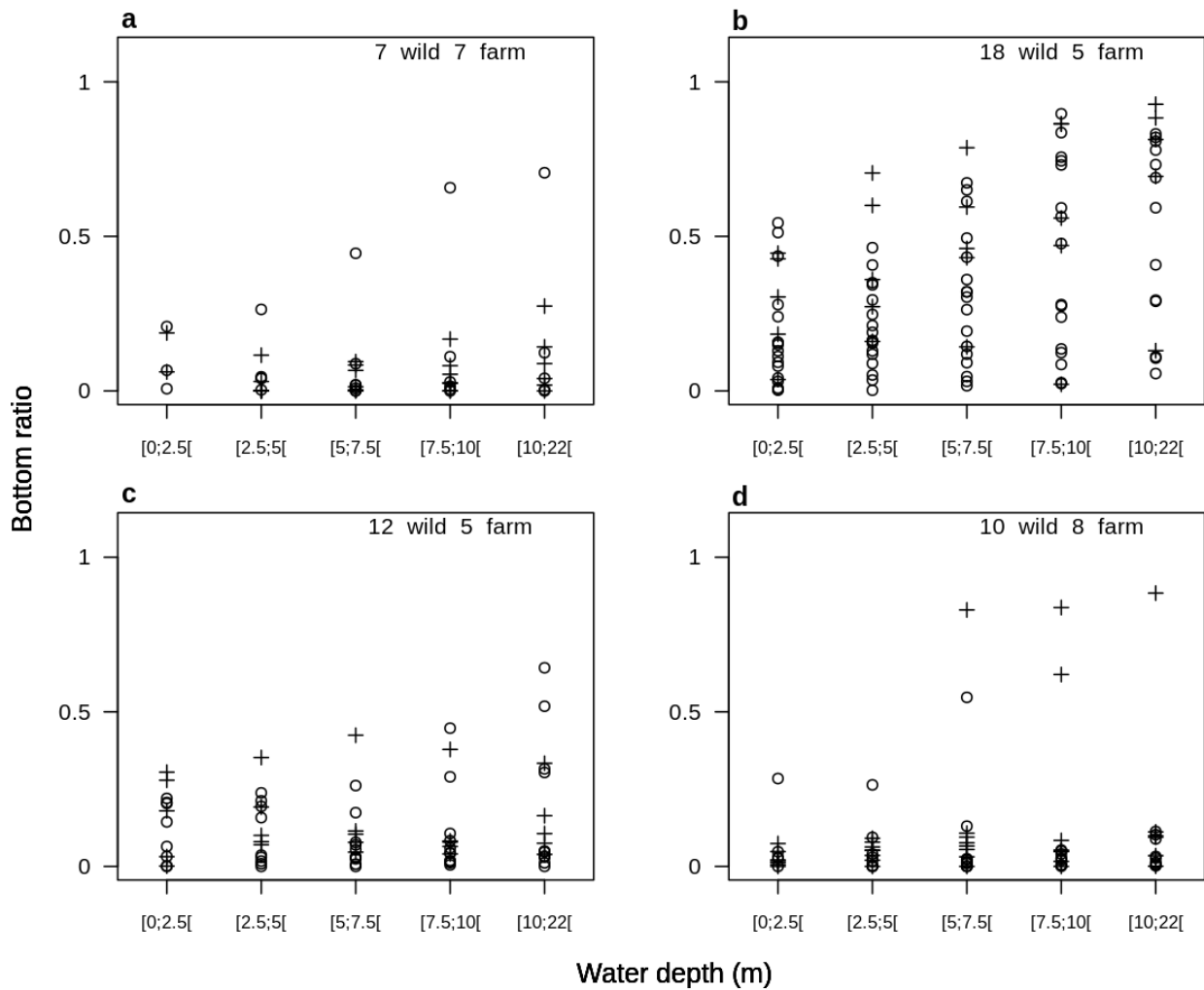
III.A Variability of the habitat niche of a freshwater predator community

Suppl. Mat. III.A.7 Results of the following generalized additive mixed-effects model

$$\log(\overline{SR_{ind}}) = \alpha + \text{WATER DEPTH} * \text{SEASON} + \text{WATER DEPTH} * \text{ORIGIN} + s(ind) + \varepsilon$$

where $\overline{SR_{ind}}$ is the expected mean individual selection ratio of pikeperch, strictly positive; α is the overall intercept; origin discriminates wild from farmed pikeperch, $s(ind)$ is a smoothing function modelling the individual effects (Wood, 2008) and ε is the error term following a normal distribution with zero mean. To take into account the skewed distribution of individual selection ratios towards zero, a Tweedie family function with a log-link was used (Gilman et al., 2012). This model tested the fixed effects of water depth, season, pikeperch origin and some of their interactions, as well as the individual effects, on selection ratios. The percentage of explained variance quantified the data variability represented by this model. Results demonstrated that there was no effect of pikeperch origin.

Pikeperch	Selection ratio		
	d.f.	F	p-value
Water depth	4	3.008	0.018
Season	3	14.297	<0.001
Origin	1	1.396	0.238
Water depth: Season	12	6.327	<0.001
Water depth: Origin	4	1.786	0.131
Individual	24	0	1
All effects			
Explained variance (%)	17.1		



Suppl. Mat. III.A.8 Mean individual bottom ratio in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) for pikeperch (crosses for farmed pikeperch and white dots for wild ones). In each season, the numbers of farmed and wild pikeperch are provided.

III.A Variability of the habitat niche of a freshwater predator community

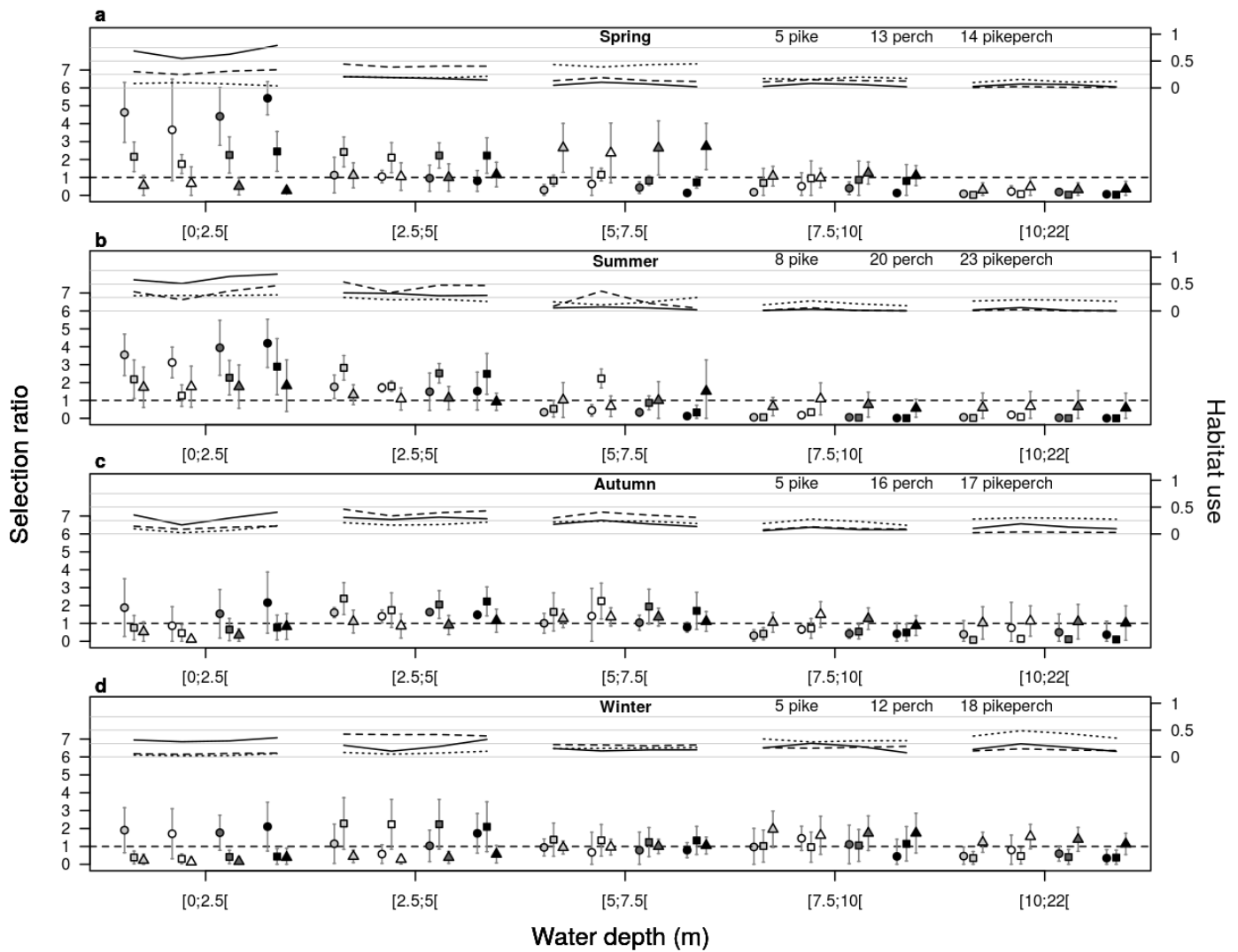
Suppl. Mat. III.A.9 Results of the following Beta regression

$$\text{logit}(\overline{\text{BR}}_{\text{ind}}) = \alpha + \text{WATER DEPTH} * \text{SEASON} + \text{WATER DEPTH} * \text{ORIGIN} + s(\text{ind}) + \varepsilon$$

where $\overline{\text{BR}}_{\text{ind}}$ is the expected mean individual bottom ratio in $]0,1[$, α is the overall intercept, origin discriminates wild from farmed pikeperch, $s(\text{ind})$ is a smoothing function modelling the individual effects (Wood, 2008) and ε is the error term following a normal distribution with zero mean. This model tested the fixed effects of water depth, season, pikeperch origin and some of their interactions, as well as the individual effects, on bottom ratios. The percentage of explained variance quantified the data variability represented by this model. Results demonstrated that there was no effect of pikeperch origin.

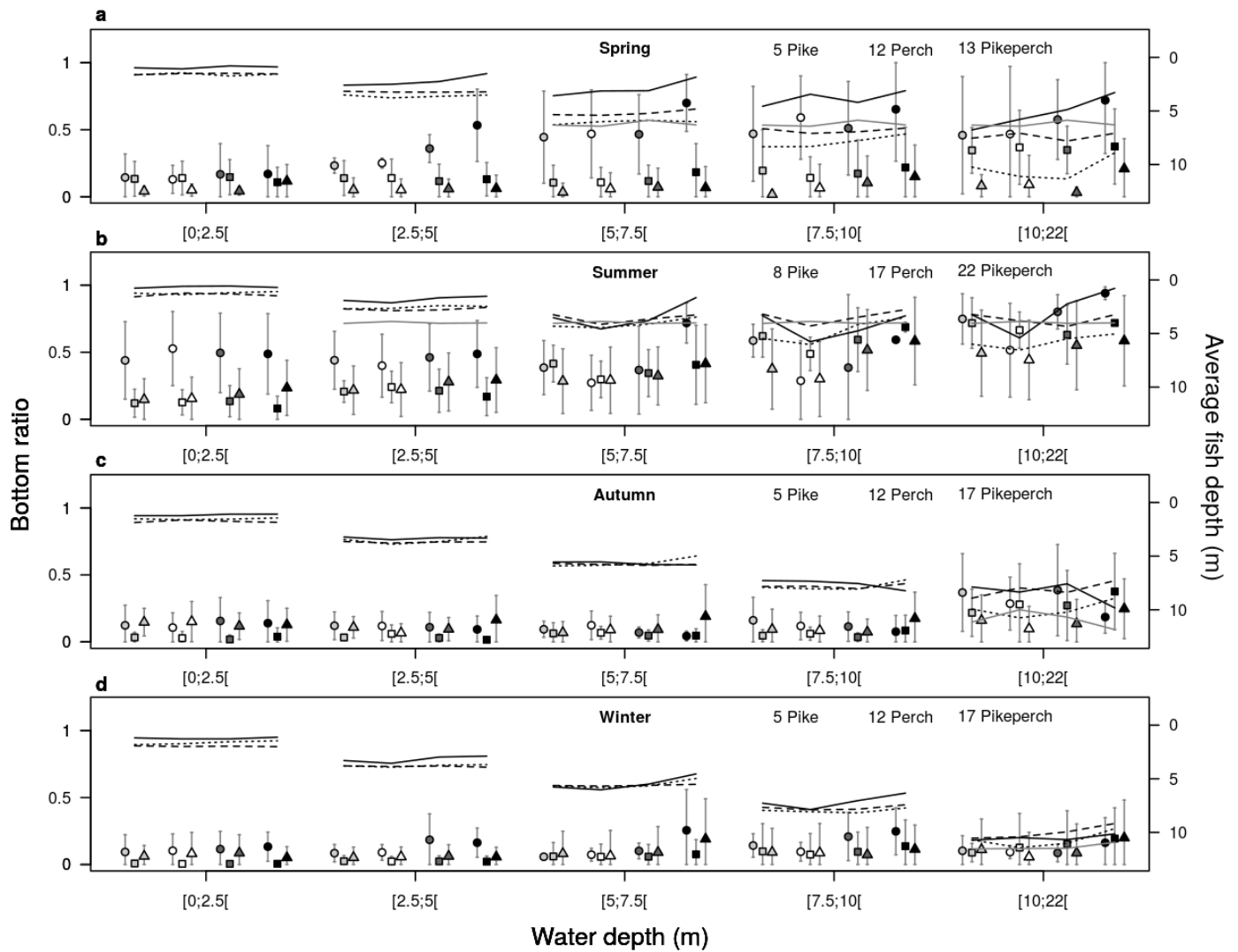
Pikeperch	Bottom ratio		
	d.f.	Chi-sq	p-value
Water depth	4	21.820	<0.001
Season	3	53.694	<0.001
Origin	1	3.527	0.060
Water depth: Season	12	43.790	<0.001
Water depth: Origin	4	0.737	0.947
Individual	24	177.6	<0.001
All effects			
Explained variance (%)	50.7		

III.A Variability of the habitat niche of a freshwater predator community



Suppl. Mat. III.A.10 Selection ratio of water depth (mean \pm 95% Bonferroni Confidence Interval) for each species (dots, squares and triangles for pike, perch and pikeperch, respectively) and each period of the day (dawn, daytime, dusk and night displayed in light grey, white, dark grey and black symbols, respectively) in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) on the left axis. A selection ratio of 1 indicates “no preference” and is represented by a horizontal dashed line. Habitat use (used proportion of each water depth) is represented on the right axis (solid, dashed and dotted line for pike, perch and pikeperch, respectively). In each season, the number of pike, perch and pikeperch is provided.

III.A Variability of the habitat niche of a freshwater predator community



Suppl. Mat. III.A.11 Bottom ratio (mean \pm SD) for each species (dots, squares and triangles for pike, perch and pikeperch, respectively) and each period of the day (dawn, daytime, dusk and night displayed in light grey, white, dark grey and black symbols, respectively) in each season (spring, summer, autumn and winter in panels a, b, c and d, respectively) on the left axis. The average depth of species (solid, dashed and dotted line for pike, perch and pikeperch, respectively) and of the thermocline (grey solid line) are represented on the right axis. In each season, the number of pike, perch and pikeperch is provided.

III.A Variability of the habitat niche of a freshwater predator community

Suppl. Mat. III.A.12 Estimated marginal means of bottom ratio for the different species, season and water depth combinations. In each season/water depth category, estimated bottom ratios that are significantly different between species (based on Tukey comparisons of pairwise estimated marginal means at the 95% level of the beta regression) are labelled with different letters (a, b, c).

	Spring				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.09 ^a	0.18 ^a	0.37 ^a	0.44 ^a	0.60 ^a
Perch	0.04 ^b	0.08 ^b	0.11 ^b	0.13 ^b	0.30 ^b
Pikeperch	0.04 ^b	0.02 ^c	0.04 ^c	0.07 ^c	0.07 ^c
	Summer				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.37 ^a	0.40 ^a	0.40 ^a	0.67 ^a	0.60 ^{a,b}
Perch	0.11 ^b	0.23 ^b	0.41 ^b	0.60 ^a	0.72 ^a
Pikeperch	0.09 ^b	0.25 ^b	0.31 ^a	0.37 ^b	0.51 ^b
	Autumn				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.05 ^a	0.08 ^a	0.09 ^a	0.13 ^a	0.22 ^a
Perch	0.02 ^b	0.06 ^a	0.10 ^a	0.10 ^a	0.31 ^a
Pikeperch	0.02 ^b	0.07 ^a	0.07 ^a	0.10 ^a	0.11 ^b
	Winter				
	[0;2.5[[2.5;5[[5;7.5[[7.5;10[[10;22[
Pike	0.10 ^a	0.09 ^a	0.08 ^a	0.14 ^a	0.13 ^{a,b}
Perch	0.01 ^b	0.03 ^b	0.08 ^a	0.12 ^a	0.15 ^a
Pikeperch	0.01 ^b	0.03 ^b	0.06 ^a	0.07 ^b	0.09 ^b

III.B

Variability of the trophic niche of a
freshwater predator community

B. Interannual variability of the trophic niche of young-of-the-year of four piscivorous fish species coexisting in a natural lake

1. *Synthesis (English)*

In the predatory community of the Bariousses reservoir, habitat partitioning among species has been highlighted, probably as a way to decrease interspecific competition and, as such, would contribute to species maintenance, in agreement with coexistence theory. As a follow-up, this raises the question whether or not this habitat partitioning coincides with a trophic partitioning, another main component of the ecological niche. Unfortunately, isotopic sampling had not been performed on individuals in this reservoir. Moreover, in the second site “Etang des Aulnes”, very few perch and pikeperch adults were caught, making an isotopic analysis on adult stages statistically irrelevant, whereas juvenile stages were abundant. In order to tackle this question, we thus analyzed isotopic data collected over three years in the young-of-the-year (YOY) predatory community in the “Etang des Aulnes”.

With pike, perch and pikeperch, catfish is another fish-eating species, that was more recently introduced in western Europe, raising concerns about its impact on recipient ecosystems due to its very large size and its invasive reputation. As such, these four species can exist in sympatry in some freshwater ecosystems, which is the case in “Etang des Aulnes” where all four species have coexisted for roughly forty years now. The juvenile community of these species is usually abundant in this shallow eutrophic lake and we wondered how they shared resources as the growth of these vulnerable stages is key to recruitment. For this, we focused on the trophic niche of YOY which we estimated with carbon and nitrogen stable isotopes of fin tissues sampled in three consecutive autumns, thus integrating their diet over the summer, their main growth period. We investigated the variations of trophic interactions, niche segregation versus niche overlap, across years. We found that the hierarchy in trophic position between species was consistent across years and similar to what is known about adults, but with large variations around a general pattern: pike and pikeperch tended to occupy the highest trophic positions while perch occupied the lowest, and catfish had highly variable positions. Furthermore, species partitioned their niches, probably to decrease interspecific competition. Species abundance largely fluctuated across years, leading to niche enlargement of densely populated species except for catfish, interpreted as a way to limit intraspecific competition. The tight niche of catfish, even when the cohort was abundant, could be an expression of its generalist diet at the individual level: individuals are not specialized on specific items, but instead have a diversified

III.B Variability of the trophic niche of a freshwater predator community

diet that, in average, gives a similar isotopic signature for each individual. This could be due to resources that are not limiting in this eutrophic lake. All of these mechanisms contributed to preserving YOY body conditions that did not significantly vary between years. In accordance with the habitat partitioning of adults, these results highlighted that the coexistence of these four YOY predators is associated with trophic niche partitioning, with marked intraspecific variation of the niche area, in agreement with the coexistence theory.

2. *Synthesis (French)*

Variabilité interannuelle de la niche trophique de juvéniles de l'année de quatre espèces de poissons piscivores coexistant dans un lac naturel.

Au sein de la communauté prédatrice adulte du réservoir des Bariousses, le partitionnement d'habitat mis en évidence permet probablement de limiter la compétition interspécifique et contribuerait ainsi au maintien des populations correspondantes, en accord avec la théorie de coexistence des espèces. Cela soulève naturellement la question de savoir si ce partitionnement d'habitat s'accompagne d'un partitionnement trophique, une autre composante importante de la niche écologique. Malheureusement, l'expérimentation menée sur les Bariousses ne comportait pas de prélèvements isotopiques. Par ailleurs, dans l'étang des Aulnes, très peu de perches et sandres adultes ont été capturés, rendant les analyses isotopiques sur ces stades statistiquement non représentatives, alors que les stades juvéniles abondaient. Pour apporter des éléments de réponse à cette question, nous avons alors analysé des données isotopiques collectées pendant trois années durant sur les juvéniles de l'année de la communauté de prédateurs de l'étang des Aulnes.

Avec le brochet, la perche et le sandre, le silure est une autre espèce piscivore, plus récemment introduite en Europe de l'ouest, et qui suscite des interrogations quant à son impact sur les écosystèmes à cause de sa très grande taille et de son caractère invasif. Ces quatre espèces peuvent ainsi se côtoyer dans certains écosystèmes, comme c'est le cas dans l'étang des Aulnes depuis une quarantaine d'années maintenant. La communauté de juvéniles de ces espèces est en général abondante dans ce lac eutrophe peu profond, ce qui suscite des interrogations quant au partage des ressources entre ces stades particulièrement vulnérables dont la croissance est un facteur clé du recrutement. En vue d'y répondre, nous avons analysé la niche trophique des juvéniles de l'année, estimée à partir des ratios d'isotopes stables du carbone et de l'azote, estimés sur des bouts de nageoires prélevés durant trois automnes consécutifs. Cela couvrirait donc leur régime alimentaire de l'été, correspondant à leur principale période de croissance. Nous nous sommes alors intéressés aux variations des interactions trophiques, ségrégation de niche versus chevauchement de niche, au fil des années. La hiérarchie des positions trophiques des espèces s'est avérée relativement stable au fil des années et similaire à ce qui est connu sur les adultes, avec cependant une variabilité assez forte autour d'un patron général : le brochet et le sandre tendaient à occuper les positions les plus élevées alors que la perche occupait les plus

basses et que la position du silure était versatile. Par ailleurs, le partitionnement de niche était présent, très probablement pour limiter la compétition interspécifique. Les abondances des cohortes fluctuaient beaucoup entre les années, les fortes cohortes s'accompagnant d'une expansion de niche, excepté pour le silure, interprétée comme moyen de limiter la compétition intraspécifique. La niche étroite du silure, y compris lorsque la cohorte était très abondante, peut être une signature de son régime alimentaire généraliste : les individus ne sont pas spécialisés sur un type de ressources particulier mais ont un régime diversifié qui donne en moyenne une signature isotopique relativement similaire entre les individus. Cela pourrait être lié à des ressources qui ne sont pas limitantes dans ce lac eutrophe. L'ensemble des mécanismes mis en évidence contribuait à préserver la condition physique de ces juvéniles qui ne différait pas entre les années. Conformément au partitionnement d'habitat mis en évidence sur des adultes, et en accord avec la théorie de la coexistence des espèces, ces résultats montrent que la coexistence de ces quatre prédateurs, au stade juvénile, s'accompagne d'un partitionnement de niche trophique entre les populations, avec des variations spécifiques marquées de la taille de niche.

3. Core paper

Samuel Westrelin, Paride Balzani, Phillip Joschka Haubrock & Frédéric Santoul. Interannual variability of the trophic niche of young-of-the-year of four piscivorous fish species coexisting in a natural lake. In revision.

Abstract

1. Predatory fish species play a key role in aquatic ecosystems by exerting top-down control on the food web. Also, their intra-guild trophic interactions (i.e. competition) are crucial for the stability of the community. Yet, most studies focus on adult stages, while juveniles remain poorly studied, although their recruitment is the basis for the maintenance of predator populations.
2. We analyzed carbon and nitrogen stable isotopes ratios of the young-of-the-year of four coexisting widespread predatory fish species (Northern pike *Esox lucius*, European perch *Perca fluviatilis*, pikeperch *Sander lucioperca*, and European catfish *Silurus glanis*), sampled over three years in a shallow natural lake.
3. We found that the hierarchy in trophic position between species was consistent across years and similar to what is known about adults, but with large variations around a general pattern: pike and pikeperch tended to occupy the highest trophic positions while perch occupied the lowest, and catfish had very varying positions.
4. Furthermore, species partitioned their niches to decrease interspecific competition, but with some occasional overlaps, contributing to preserving their body conditions. Depending on species density, particularly impacted by harsh environmental conditions, niche overlap fluctuated across years, leading to niche enlargement of densely populated species, except for catfish.
5. These mechanisms enabled species coexistence, allowing the co-occurrence of alien and native predators within the same ecosystem.
6. This work advocates for time-integrated studies of trophic webs to not limit our view to a static picture and partial conclusions and to capture the variability of their dynamics. This is particularly true for critical stages like juveniles whose survival strongly depends on their capacity to cope with competition. Information from trophic mid-term studies

III.B Variability of the trophic niche of a freshwater predator community

of juveniles stand as a key point to obtain valuable guidance for an optimized management of species.

Keywords : *Esox lucius*, *Perca fluviatilis*, *Sander lucioperca*, *Silurus glanis*, stable isotopes

Introduction

In aquatic ecosystems, both trophic complexity and consistency have manifold implications for the functioning and stability of trophic webs (Rooney & McCann, 2012). Trophic webs are characterized by the flow of energy reflecting trophic interactions among organisms and ultimately leading to a community structuring (Rooney et al., 2008; Thompson et al., 2012). Within insular systems (such as lakes), resources tend to be limited (Essington & Carpenter, 2000). External and internal stressors can induce fluctuations that lead to shifts in the flow of energy and thus, relocation of biomass and changes in species interactions and trophic positions (Sentis et al., 2017; Su et al., 2021). Organism groups like fish are prone to express variability in their trophic placement and thus the occupied niche space, which in turn may reflect the use of resources or occupied habitats (Haubrock et al., 2021a).

Predatory fish species play a crucial role within trophic webs by exerting predatory pressure on lower trophic level, limiting the competition among species within the same guild (top-down control) (e.g. Rosenfeld, 2000; Baum & Worm, 2009). They also compete with each other for prey, resulting in a fragile context-dependent equilibrium, with changes in their abundance having cascading consequences for lower trophic levels (Carpenter et al., 1985; Rooney et al., 2006). In Europe, northern pike *Esox lucius* Linnaeus, 1958, hereafter pike, European perch *Perca fluviatilis* Linnaeus, 1958, hereafter perch, pikeperch *Sander lucioperca* (Linnaeus, 1958) and European catfish *Silurus glanis* Linnaeus, 1958, hereafter catfish, are four widespread predators in lakes, the last two being known alien invasive species in many regions (Kottelat & Freyhof, 2007; Copp et al., 2009; Cucherousset et al., 2018). Although these species can frequent multiple habitat types with seasonal variations (e.g. De Santis & Volta, 2021; Vagnon et al., 2022), they have some habitat preferences. Pike are mainly littoral and prefer vegetated areas (Chapman & Mackay, 1984a; Craig, 1996; Jepsen et al., 2001) while pikeperch are nocturnal and mainly frequent the pelagic area (Vehanen & Lahti, 2003; Huuskonen et al., 2019). Perch are in-between pike and pikeperch (Schulze et al., 2006; Hölker et al., 2007; Westrelin et al., 2021) whereas catfish prefer benthic habitats and mainly the lower third of the water column (Pohlmann et al., 2001; Copp et al., 2009; Cucherousset et al., 2018). These differences also seem to exist in juvenile stages (Treasurer, 1988; Luchiari et al., 2006; Slavík et al., 2007; Craig, 2008; Slavík et al., 2012), which could favor a trophic segregation.

These four species are primarily piscivorous as adults, even if variability in their diet has been reported (Campbell, 1992; Dörner et al., 2003; Craig, 2008; Vejřík et al., 2017). In general,

III.B Variability of the trophic niche of a freshwater predator community

pikeperch is a piscivorous specialist (Kangur & Kangur, 1998; Huuskonen et al., 2019) that occupies the highest position in the trophic web (Pérez-Bote & Roso, 2012), often higher than pike, which is also mainly piscivorous but more plastic (Craig, 2008; Kopp et al., 2009; Pedreschi et al., 2015). On the other hand, perch is a generalist species and catfish opportunistic (Dörner et al., 2003; Schulze et al., 2012; Vejřík et al., 2017; Vagnon et al., 2022). These species also undergo some ontogenetic variations in diet. Pike, pikeperch, and perch feed on zooplankton and other invertebrates when juveniles but then become piscivorous (Matěna, 1998; Mittelbach & Persson, 1998; Vašek et al., 2018; Yazıcıoğlu et al., 2018; Jacobson et al., 2019), while catfish shift from a diverse diet composed of crustaceans, molluscs and fish when juveniles to a mainly piscivorous diet when adults (Rossi et al., 1991; Syväranta et al., 2010). Yet, while their function in freshwater ecosystems has often been examined within trophic webs, most studies on trophic interactions between these species concern adults only and, in contrast, the feeding ecology of young-of-the-year (YOY) remains poorly understood (Nunn et al., 2012).

Resource partitioning is one of the important mechanisms allowing species coexistence (Schoener, 1986a; Chesson, 2000; Chase & Leibold, 2003). The competitive exclusion principle (niche theory) states that sympatric species can not have completely overlapping niches (Gause, 1934; Hardin, 1960), and the theory of limiting similarity that there is some maximum level of similarity bearable (Abrams, 1983). Niche differences are stabilizing mechanisms of species coexistence in the niche theory as well as in the more recent coexistence theory, and the intraspecific variability which affects intraspecific competition is also a crucial process (Chesson, 2000; Chu et al., 2017). As an outcome of high intra- and/or interspecific competition and limited resource availability, lower body condition is expected (Verdiell-Cubedo et al., 2006; Gaygusuz et al., 2013; Kamimura et al., 2021; De Santis et al., 2022).

The introduction of invasive fish species has a direct impact on recipient ecosystems by restructuring trophic webs (Haubrock et al., 2019; Bissattini et al., 2021) and increasing the interspecific variability, which can lead to negative interactions with native species (Martin et al., 2010; Haubrock et al., 2018; Champneys et al., 2021), for example in some cases when invasive and native species have overlapping niches (Haubrock et al., 2021b). The analysis of carbon and nitrogen stable isotopes is a powerful tool to obtain long-term and time-mediated information on the trophic structure of communities (Post, 2002; Layman et al., 2012) and can give useful insights into how species coexist and how alien species integrate into the native food web (Gutmann Roberts & Britton, 2018; Stellati et al., 2019). Although stable isotope

analysis (SIA) is now widely applied, comparatively few studies investigate temporal variations within the same ecosystem (Haubrock et al., 2021a). Indeed, most of such studies focused on seasonal variations in trophic niches within one year (Fitzgerald et al., 2017; Neves et al., 2021), and little is known about interannual and same-season variations occurring within one ecosystem.

In the present work, we sampled the YOY community of four predatory fish species over three years in a shallow natural lake in south-eastern France. We aimed to evaluate the interspecific trophic interactions and the degree of trophic niche partitioning (as opposed to niche overlap) occurring between these coexisting cohorts. By investigating variations of trophic interactions across years, we hypothesized that (i) predatory YOY coexisted by partitioning their trophic niches; (ii) trophic interactions (niche segregation vs niche overlap) among species were stable across time; (iii) the rising abundance of the YOY of alien invasive fish species would enhance competitive pressures on YOY of native species.

Materials and methods

Study site

“Etang des Aulnes” is a shallow lake (mean depth 3.8 m, maximum depth 6 m, 104 ha area), located in southeastern France in a protected natural area. Previous samplings revealed that the fish assemblage consists of pikeperch, catfish, pike, and 13 other species, the most abundant ones being bream (*Abramis brama*, relative abundance 65%), perch (13%), pumpkinseed (*Lepomis gibbosus*, 8%) (Westrelin et al., 2022). The “Etang des Aulnes” is eutrophic (see Suppl. Mat. III.B.1 for chemical element concentrations). Seasonal temperatures are given in Suppl. Mat. III.B.2.

Sample collection and measurements

The fish community of “Etang des Aulnes” was sampled in autumn over three years (October 2018, 2019 and 2020). October was chosen as the sampling period because SIA of fin tissues (detailed below) is integrative of the three previous months (Willis et al., 2013; Busst & Britton, 2018), corresponding to the summer period. The feeding intensity is usually very high in summer (Dominguez & Pena, 2000; Balik et al., 2006; Copp et al., 2009; Yazıcıoğlu et al., 2016) which encompasses the important growth period of YOY in northern temperate lakes

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before winter (Kubečka, 1994; Nunn et al., 2002). Fish were caught using fyke nets set equally in the pelagic and littoral zones, and using fish traps and electrofishing in the littoral zone. In each sampling, the YOY of pike, perch, pikeperch, and catfish were collected. Based on informations on the growth of these species in our site or neighboring ecosystems and in the literature (Goubier, 1975; Schlumberger & Proteau, 2001; Beeck et al., 2002; Poulet, 2004; Dubois et al., 2008), we used the following upper limits for YOY as total length: 400, 140, 280 and 350 mm, respectively for pike, perch, pikeperch and catfish.

Due to the very high number of fish, we could not handle all individuals and therefore guesstimated size class for most of them. The catch per unit effort (CPUE, number of caught fish per net per day) was calculated accordingly (Figure III.B.1).

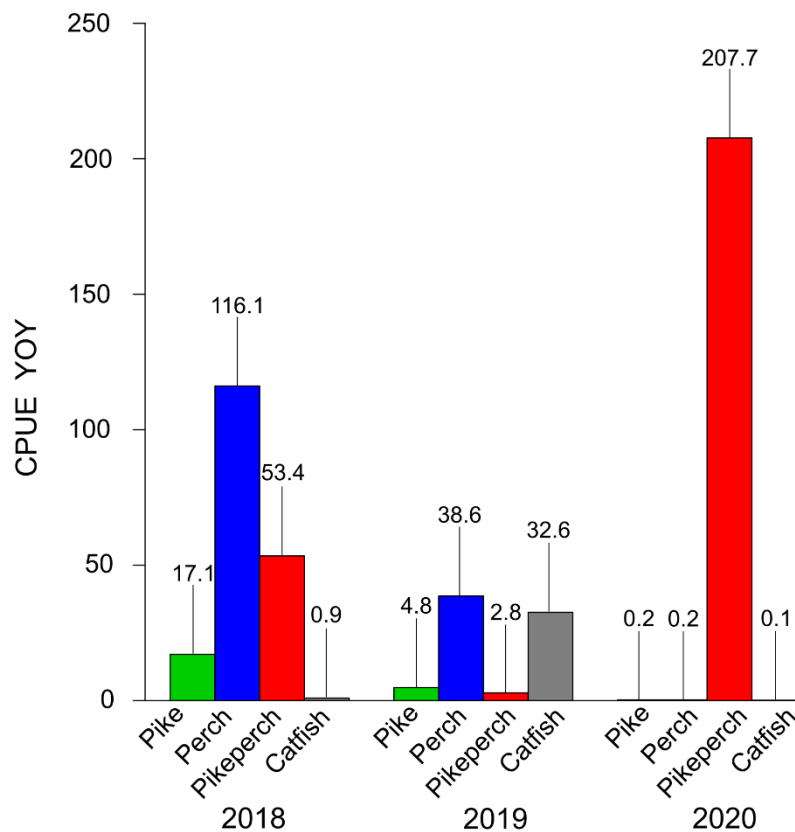


Fig III.B.1 Catch per unit effort of YOY per species per year. The unit is the number of fish per net in a day. CPUE values are given at the top of the graph. Barplots for pike, perch, pikeperch and catfish are respectively colored in green, blue, red and grey.

For SIA, specimens of each species were randomly selected (Table III.B.1). For catfish, however, all specimens were analyzed in the frame of another project focusing on this species,

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except in 2019 when the YOY cohort was very important and thousands of individuals were caught. They were stocked for a few hours in aerated basins, then anaesthetised in a tank containing a solution of benzocaine (80 mg/L) before being weighed (accuracy 1 g) and measured (total length, accuracy 1 mm). For SIA, a non-lethal and non-invasive tissue sampling technique was used (Jardine & Cunjak, 2005; Kelly et al., 2006; Hayden et al., 2015) by extracting 0.25cm² of the pelvic fin tips. Fish then spent 3 to 6 hours in recovery basins before being released. To evaluate the body condition of each individual, the relative weights were also calculated as the ratio of the observed weight over the expected weight calculated from the linear regression $\log(\text{Weight}) = a * \log(\text{Total_length}) + b$ where a and b are the regression coefficients (Blackwell et al., 2000; Kraus et al., 2020).

Table III.B.1. Characteristics of YOY sampled each year for SIA. Their number and mean ([range]) total length (in mm) are given.

		Pike	Perch	Pikeperch	Catfish
n	2018	16	16	13	36
	2019	13	38	14	111
	2020	14	4	34	9
Total length	2018	311	97	161	291
		[230; 382]	[76; 130]	[138; 248]	[179; 342]
	2019	299	122	254	271
		[239; 380]	[102; 140]	[181; 280]	[159; 350]
	2020	310	139	210	309
		[239; 393]	[136; 140]	[174; 273]	[279; 350]

To capture and account for the spatial and temporal variations at the base of the food web, snails and zooplankton were collected during the same field campaigns as fish to be used as baselines (i.e. representing primary consumers) (Post, 2002). Aquatic gastropods (*Radix sp.* and *Physa sp.*, n=7, 8 and 12 in 2018, 2019 and 2020 respectively) were collected along the lake littoral; only their feet was used for SIA. Bulk zooplankton (n=9, 10 and 15 in 2018, 2019 and 2020

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respectively) was collected from the pelagic zone by taking diagonal hauls from 1-meter above the lake bottom to the surface along a 10-m boat track. It was immediately sieved with a 250- μ m mesh. Samples were screened under a microscope to limit the debris contamination. These organisms represent the littoral and pelagic baselines, respectively, to account for these two distinct carbon pathways commonly found in lake webs (France, 1995; Post, 2002).

All fish and invertebrates samples were rinsed thoroughly with distilled water, stored individually without any chemical and preserved at -20 °C for a few days before being dried in an oven at 60 °C for 60 hours.

Stable isotope analysis

Carbon ratios relate to the major energy sources, while nitrogen to the trophic position of a consumer within a food web (Fry, 2006; Layman et al., 2012). SIA is based on predictable changes occurring in the isotopic ratios from prey to consumer, being enriched by 1‰ for carbon and by 2.5-5‰ for nitrogen for each trophic level (Post, 2002; Vanderklift & Ponsard, 2003). Dried samples were sent to the Cornell University Isotope Laboratory, New York for SIA. They were ground into a fine and homogenized powder with a Spex CertiPrep 6750 Mill and packed into tin capsules for isotopic analyses (approximately 1 mg of material per sample). Samples were analyzed with a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer. Isotope compositions were expressed as ‰ with the δ notation, based on $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \right]$ where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios. Results were referred to Vienna Pee Dee Belemnite for carbon and to atmospheric N_2 for nitrogen, with laboratory standards routinely calibrated against reference materials provided by the International Atomic Energy Association.

After analysis, $\delta^{13}\text{C}$ was corrected for lipid content according to Post et al. (2007) when the C:N ratio was greater than 3.5. Out of 318 values, 200 were corrected and corrections ranged in [0.15 ; 0.94].

We used the trophic position and the littoral reliance of fish to correct for differences in basal resources for nitrogen and carbon. For a two-source food web, the trophic position of a fish is calculated as follows (Post, 2002):

$$TP_{fish} = 2 + \frac{(\delta^{15}N_{fish} - [\delta^{15}N_{gastropod} \times LR_{fish} + \delta^{15}N_{zooplankton} \times (1 - LR_{fish})])}{3.4}$$

where 2 is the trophic position of the baseline (i.e. primary consumer), 3.4 is the enrichment in $\delta^{15}N$ per trophic level and LR_{fish} is the proportion of nitrogen in the fish ultimately derived from the base of littoral food web (Post, 2002), also called littoral reliance as it quantifies the percentage contribution of littoral pathway, and calculated as follows (Vander Zanden & Vadeboncoeur, 2002):

$$LR_{fish} = \frac{\delta^{13}C_{fish} - \delta^{13}C_{zooplankton}}{\delta^{13}C_{gastropod} - \delta^{13}C_{zooplankton}}$$

LR_{fish} greater than 1 means that the ^{13}C enrichment of the fish is higher than the littoral baseline one (Gastropods). TP_{fish} and LR_{fish} are unitless numbers.

Because life history traits (optimum spawning temperature -Souchon & Tissot, 2012-, growth rates, size) of the four species differ, we used multiple linear regressions to test if species, year of sampling and size of species could explain TP and LR. To smooth these differences already comprised within the ‘species’ factor, for each species, the size was divided by the maximum size of YOY over the three years. The model could be written as follows:

$$\overline{\text{Trophic metric}} = \alpha + \text{SPECIES} \times \text{YEAR} \times \text{NormalizedSIZE} + \varepsilon$$

where $\overline{\text{Trophic metric}}$ is the expected mean TP or LR, NormalizedSIZE is the size normalized by the maximum size of YOY of the considered species over the study period, α is the overall intercept and ε is the error term following a normal distribution with zero mean.

When significant, interactions were further analyzed by Tukey comparisons of pairwise estimated marginal means of the different factor levels of predictors at the 5% significance level (emmeans R package; Lenth, 2016).

Isotope niche analysis and overlap

For each species of YOY and year, the isotopic niche size was estimated in the LR-TP space with standard ellipse areas (SEA): considering 40% of data points, SEA40% were plotted to visualize the isotopic niche, and their Bayesian distribution (SEAb 40%) used for statistical comparisons (95% credible intervals based on 200 iterative draws) (SIBER R package; Jackson et al., 2011). Additionally, Layman metrics (Layman et al., 2007) were calculated for each YOY

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species and year as well as for the whole YOY community. TP and LR ranges (TP_range and LR_range) as well as TA are measurements of the extent of the LR-TP bi-plot, reflecting the species/community niche width. TA is the total area of the convex hull encompassing all the individuals (at the species level) or the centroids of each species' trophic niche (at the community level). The mean distance to the centroid (CD) provides a measure of the trophic diversity among individuals when calculated on species and between species when calculated on the whole community. The mean nearest neighbor distance (MNND) and its standard deviation (SDNND) relate to the distance of individuals/species and indicate the degree of trophic redundancy.

Within a year, the degree of isotopic niche overlap between pairwise species was estimated by using the equation of Stasko et al. (2015) which gives the proportion of total ellipse space occupied in overlap:

$$\%Overlap = \frac{(area\ of\ overlap\ between\ SEA1\ and\ SEA2) \times 2}{SEA1 + SEA2} \times 100$$

where SEA1 and SEA2 are the ellipse areas calculated from species 1 and species 2 samples, respectively. This metric stands as a quantitative measure for diet similarity among different species (Jackson et al., 2012). %Overlap was calculated for each posterior draw of the Bayesian estimates of overlap and SEAb (*SIBER* R package) to get its distribution (95% credible intervals based on 200 iterative draws).

Additionally, to test the degree of partitioning among species' niches in each year, we also used a PERMANOVA (Euclidian distance, permutations=999) on LR and TP followed by multiple comparisons with Pillai–Bartlett statistic (Hand & Taylor, 1987) using false discovery rate adjusted p-values (Jafari & Ansari-Pour, 2019). PERMANOVA was performed with the *vegan* R package (Oksanen et al., 2020) and multiple comparisons with *RVAideMemoire* R package (Hervé, 2021).

All statistical analyses were made with R version 3.6.3 (R Core Team, 2020).

Results

Morphometrics and CPUE

Sample sizes and total lengths of fish are given in Table III.B.1. We found significant differences in morphometric measures within each species across the sampled years as well as

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among species within the same year (Suppl. Mat. III.B.3). The greatest CPUEs were observed in perch and pikeperch, while pike and catfish had the lowest, albeit large variations between years (Figure III.B.1). Pikeperch in 2019 and catfish in 2020 both had very low CPUE values, which were not associated with higher body conditions (Suppl. Mat. III.B.3). Conversely, high CPUEs, in 2020 for pikeperch and in 2019 for catfish, were associated with lower body conditions (Suppl. Mat. III.B.3). On the contrary, for pike and perch in 2018, when their CPUE were the highest, their body conditions were higher than in both other years.

Table III.B.2. Numeric results from the multiple linear regressions that tested the fixed effects of species, year and normalized size and their interactions on YOY trophic position (panel a) and littoral reliance (panel b). At the bottom of each table is shown the F-Test of overall significance that tests whether or not the linear regression model provides a better fit to the dataset than a model with no predictor variables. p is the associated p-value.

	Trophic position		a
	d.f.	F	p-value
Species	3	20.067	< 0.001
Year	2	317.515	< 0.001
Normalized size	1	47.864	< 0.001
Species: Year	6	12.575	< 0.001
Species: Normalized size	3	3.403	0.018
Year: Normalized size	2	0.172	0.842
Species: Year: Normalized size	6	9.239	< 0.001
Residuals	294		
Multiple R-squared		Adjusted R-squared	
0.751		0.731	
F = 38.46, (23, 294 d.f.), p < 0.001			

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	Littoral reliance		b
	d.f.	F	p-value
Species	3	133.384	< 0.001
Year	2	1526.759	< 0.001
Normalized size	1	6.978	0.009
Species: Year	6	21.250	< 0.001
Species: Normalized size	3	19.596	< 0.001
Year: Normalized size	2	11.671	< 0.001
Species: Year: Normalized size	6	4.384	< 0.001
Residuals	294		
	Multiple R-squared	Adjusted R-squared	
	0.926	0.921	
F = 160.7, (23, 294 d.f.), p < 0.001			

Trophic dynamics

Both TP and LR varied among species differently across different years and sizes (Tables III.B.2a, III.B.2b). TP and LR showed significant interannual variations within species (Figures III.B.2a, III.B.2b). In 2018, TP and LR of each species were higher than in 2019 and 2020 (Tables III.B.2a, III.B.2b, Figures III.B.2a, III.B.2b). TP and LR also showed significant interannual variations among species. Each year, the TP hierarchy between species changed, except for perch which always had the lowest TP (Figure III.B.2a). Perch LR was however as high as those of pike and/or pikeperch (Figure III.B.2b). Perch in 2018 and pikeperch in 2020 showed a particularly wide range for LR (Table III.B.3), when their CPUE was the highest (Figure III.B.1). Pike and pikeperch often had among the highest TP, but lower than catfish in 2020 (Figure III.B.2a). Catfish considerably shifted its TP, having the highest in 2020, the lowest - with perch - in 2019, and an intermediate one in 2018. Catfish LR followed the same variations as TP across years (Figures III.B.2a, III.B.2b); catfish had the highest correlation

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between TP and LR (Pearson coefficient = 0.84, df=154, $p<0.001$; 0.39 for perch, df=56, $p=0.002$; 0.68 for pikeperch, df=59, $p<0.001$ and 0.61 for pike, df=41, $p<0.001$). The largest variability in TP, of about one trophic position, was found for pike in 2018 and catfish in 2019 (Table III.B.3). LR was significantly correlated to TP (Pearson coefficient = 0.66, d.f.= 316, $p<0.001$), yet to different degrees depending on species as shown above. All YOY had a LR >1 in 2018, all < 1 in 2019 and only a few individuals (six pike, two pikeperch and one catfish) > 1 in 2020. In 2018, catfish had a lower LR than pike and perch; in 2019, it had a lower one than all three other species, while in 2020 pike and catfish both had a higher LR than perch and pikeperch.

Table III.B.3. Layman metrics of YOY species each year. TP_range range of TP, LR_range range of LR, TA total area of the data convex hull, CD mean distance to centroid, MNND mean nearest neighbour distance, SDNND standard deviation of the nearest neighbour distance

		Pike	Perch	Pikeperch	Catfish
TP_range	2018	0.937	0.553	0.508	0.681
	2019	0.350	0.698	0.555	0.998
	2020	0.429	0.055	0.681	0.301
LR_range	2018	0.554	1.331	0.484	0.502
	2019	0.287	0.539	0.241	0.360
	2020	0.461	0.238	1.047	0.449
TA	2018	0.250	0.402	0.126	0.180
	2019	0.054	0.276	0.067	0.266
	2020	0.117	0.007	0.382	0.043

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CD	2018	0.232	0.357	0.139	0.134
	2019	0.123	0.182	0.155	0.113
	2020	0.168	0.092	0.260	0.119
MNND	2018	0.114	0.137	0.098	0.041
	2019	0.053	0.051	0.058	0.023
	2020	0.065	0.069	0.063	0.077
SDNND	2018	0.110	0.082	0.087	0.072
	2019	0.032	0.043	0.042	0.042
	2020	0.032	0.010	0.041	0.097

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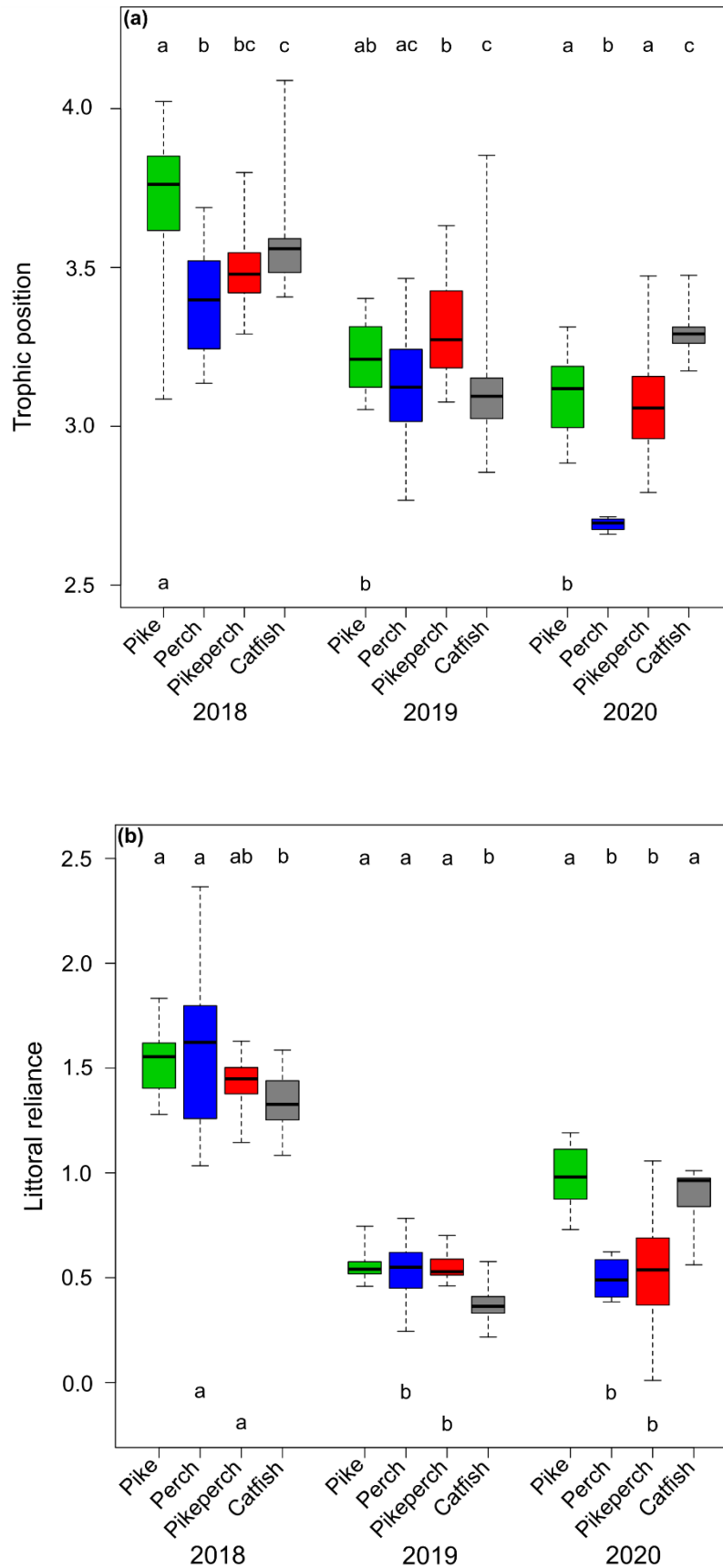


Fig III.B.2 Distribution of trophic position (panel a) and littoral reliance (panel b) of YOY by species and year. Boxplots for pike, perch, pikeperch and catfish are respectively colored in green, blue, red and grey. Above the boxplots, within a year, distributions for species that share a same letter are not different (5% significance level). Below the boxplots, within a species, distributions for years that share a same letter are not different (5% significance level); for better readability, no letter is present for species for which the distributions of the three years are different.

Trophic niche space

The graphical representation of the trophic niches in the LR-TP space illustrates the variations of species niche size and trophic interactions among species across years (Figure III.B.3). As for TP and LR, no consistent pattern of niche size was visible across years (Figure III.B.4). In 2018, perch occupied a larger niche than pikeperch and catfish, which had occupied comparable niche sizes (0.986, 0.301 and 0.269, respectively), while pike showed an intermediate niche size (0.663).

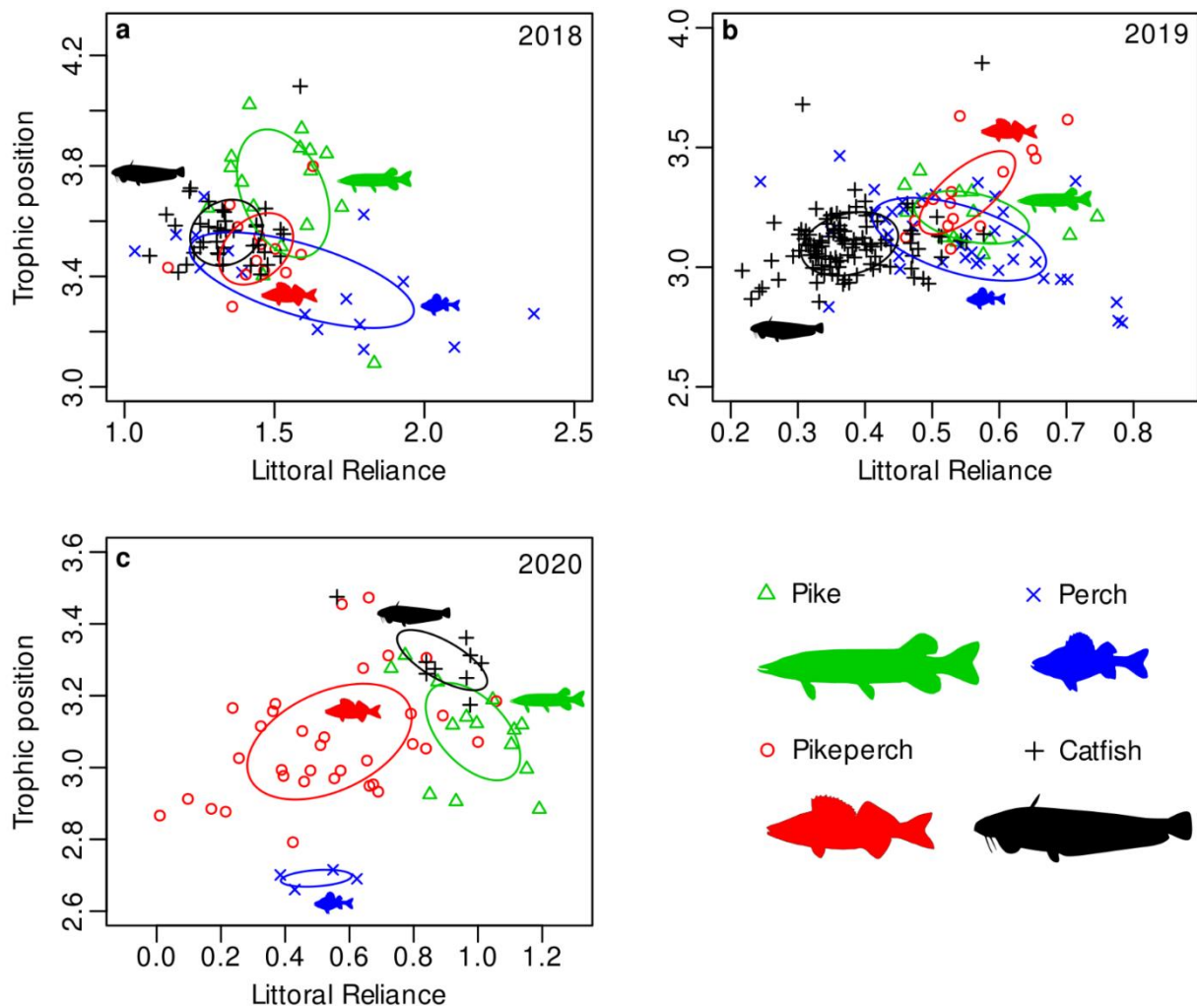


Fig III.B.3 Trophic niche of YOY per predator species and isotopic niche of corresponding community over the years 2018 to 2020. Each symbol (triangle, cross, circle and plus for pike, perch, pikeperch and catfish, respectively) represents the position of an individual in the bidimensional isotopic space (Littoral reliance - Trophic position). For each species is represented the SEA 40% (solid line). Pike, perch, pikeperch and catfish are respectively represented in green, blue, red and black. Panels a, b and c respectively represent years 2018, 2019 and 2020.

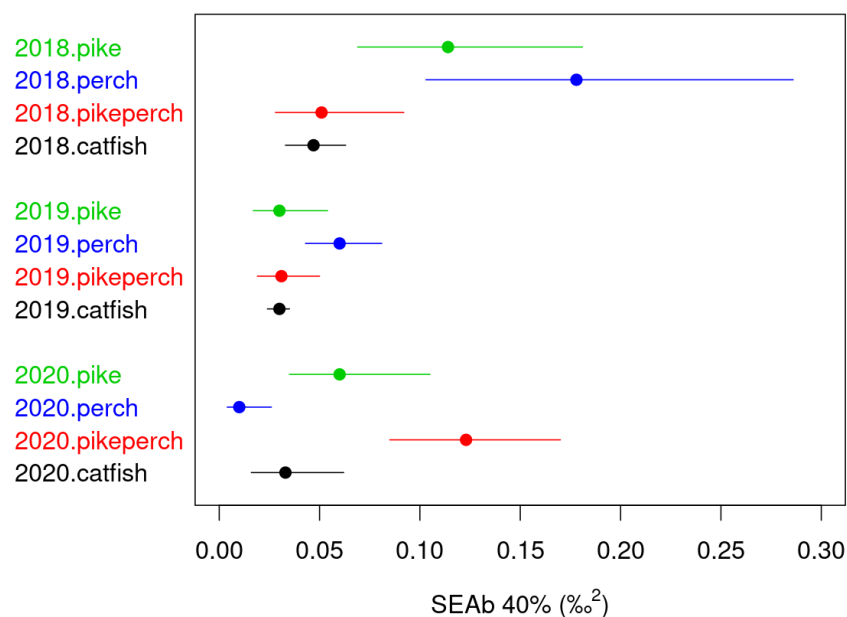


Fig III.B.4 Isotopic niche size for each species of YOY and year. The SEAb 40% is calculated in the LR-TP space; its mean is represented by a dot and its 95% credible interval is represented by a solid line.

In 2019, niche sizes appeared very similar among species and overall narrow compared to other years; this was typically the case for the numerous sampled catfishes ($n=111$; Table III.B.1), although their niche was comparably small. In 2020, pikeperch had the largest niche, when their resource range was very large (Table III.B.3) and their CPUE the highest (Figure III.B.1), while perch had the smallest one (Figure III.B.4). Within species, catfish showed the most stable niche size across years while perch niche significantly differed from one year to another. Pike niche showed varying size across years, albeit to a lesser degree, with the largest niche observed in 2018 when their range of TP was very large (Table III.B.3) and their CPUE the highest (Figure III.B.1). Pikeperch had a comparable niche size in 2018 and 2019 but occupied a much larger niche in 2020 (Figure III.B.4).

The trophic diversity of catfish, quantified by CD, was noticeably stable across years and often the lowest compared to other species. The CD of the three other species varied by a factor of two between years (Table III.B.3), but in 2018 and 2019 perch had the largest CD among species (in 2020 the sample size was low). Catfish had the lowest MNND in 2018 and 2019, meaning that, on average, individuals had a higher trophic redundancy than other species. The three other species showed comparable trophic redundancy. In 2020, catfish trophic redundancy

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was comparable to other species (Table III.B.3). Variations around this pattern were high as the SDNND was of the same order of magnitude as MNND (Table III.B.3).

At the community level, in 2018 and 2019, Layman metrics were quite similar (Table III.B.4). In 2020, these metrics all increased, indicating a higher trophic diversity within the food web and a greater trophic diversity between species (as indicated by the higher CD and MNND, Table III.B.4). As a result of the distance between species niches, the community TA considerably varied across years, being especially high in 2020 when the niches of the four species were more segregated compared to other years (Table III.B.4, Figure III.B.3).

Table III.B.4. Layman metrics of the YOY community each year. TP_range range of TP, LR_range range of LR, TA total area of the data convex hull, CD mean distance to centroid, MNND mean nearest neighbour distance, SDNND standard deviation of the nearest neighbour distance

	TP_range	LR_range	TA	CD	MNND	SDNND
2018	0.314	0.252	0.034	0.134	0.160	0.053
2019	0.214	0.182	0.017	0.106	0.114	0.034
2020	0.608	0.488	0.130	0.295	0.302	0.093

Overlapping niches showed very large confidence intervals (Figure III.B.5). Nevertheless, if we exclude perch in 2020 (n=4), the mean SEAb 40% overlap laid in 0-9% (Figure III.B.5). PERMANOVA results showed significant differences among the species niches in all three years (2018: $F_{3,79}=8.853$, $p = 0.001$; 2019: $F_{3,173}=22.389$, $p = 0.001$; 2020: $F_{3,57}=18.156$, $p = 0.001$). In particular, the species niches were all segregated ($p < 0.01$ for all pairwise comparisons in all the three years), except for perch and pikeperch in 2018 ($p = 0.151$), pike and perch in 2019 ($p = 0.086$) and pike and pikeperch in 2019 ($p= 0.168$).

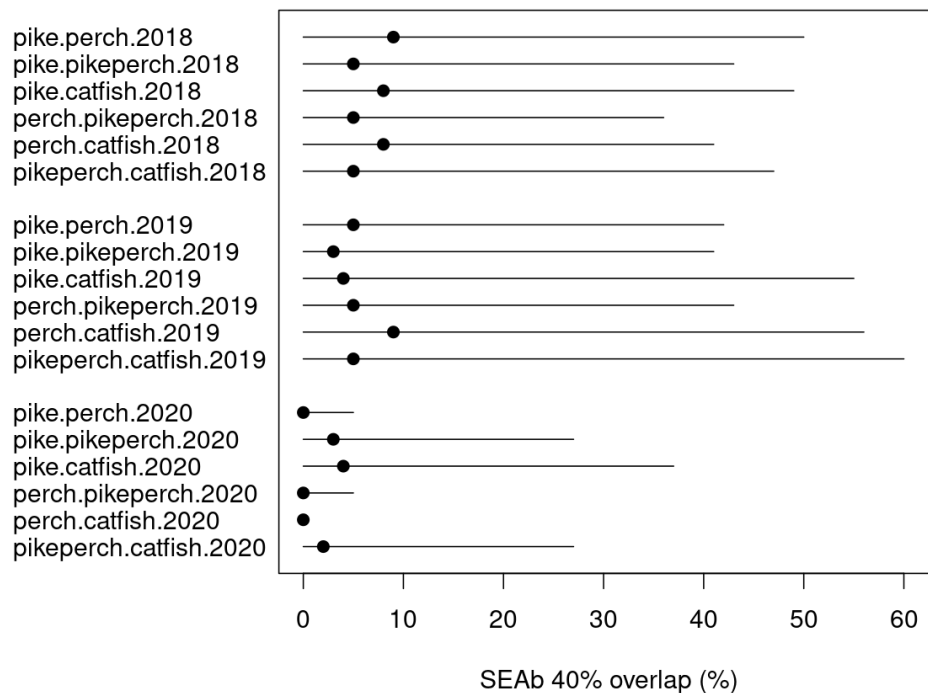


Fig III.B.5 Isotopic niche core overlap between YOY species each year. The mean SEAb 40% overlap is represented by a black dot and its 95% credible interval by a solid line.

Discussion

Trophic webs are complex and fragile, especially when encompassing YOY of predatory fish species. These stages are indeed less resilient as they need for instance to maximize growth (Miller et al., 1988) during the months after hatching to surpass predator gape limitations, make ontogenetic shifts, and increase survival by reaching a sufficient size to escape harsh environmental conditions and predation (Cowan et al., 2000; Logez et al., 2021). We found that YOY had segregated trophic niches and identified some general patterns, especially in the trophic positionings, with perch always in a lower position than pike and pikeperch. On the other hand, we found a variable trophic positioning of pikeperch and especially catfish. Instead, no clear pattern appeared for the littoral reliance. All species presented a high temporal variability in their trophic position and littoral reliance, reflected in their respective niche size and interspecific relationships.

Trophic dynamic

Trophic interactions within predator communities are among the most faceted mechanisms (Schmitz, 2007). In general for adult stages, pike and pikeperch tend to occupy the highest TP throughout the ecosystems they occupy, whereas perch commonly occupies lower TP and catfish - an ubiquitous generalist species - expresses highly adaptive niche occupation. Here, we found similar patterns for the YOY, which is in agreement with our hypothesis that trophic interactions among YOY species would be consistent across time, but with large variations around a general pattern. The observed increase in TP with size (see also Syväranta et al., 2010; Linzmaier et al., 2018; Vašek et al., 2018) could correspond to a shift of the diet towards enhanced piscivory and by this way could reduce intraspecific competition between different ontogenetic stages (Beeck et al., 2002; Ginter et al., 2011; Vašek et al., 2018; Jacobson et al., 2019), but is not necessarily associated with better body conditions. Seemingly, interspecific variations within a year did not affect the body conditions of fish, as all species had comparable body conditions each year (Suppl. Mat. III.B.3). In 2018, the high TP and relatively greater use of littoral resources (e.g. Beaudoin et al., 1999 on pike) were accompanied by better or equal body conditions for all species compared to other years, but neither larger nor heavier individuals (Suppl. Mat. III.B.3) (see also Persic et al., 2004). Having identified LR to be greater than one, i.e. an enrichment in ^{13}C greater for fish than for gastropods, might indicate that YOY tend to consume relatively more matter of terrestrial origin (as suggested by Syväranta et al., 2010). Although this raises questions as it appeared only in one year but concerned almost all individuals. In 2018, the variability of the isotopic ratios of zooplankton was high, but the mean values remained in agreement with the two other years. Indeed, the observed pattern originated from an unusual enrichment in ^{13}C of fish compared to other years, which was identified in other sampled species like *Abramis brama*, *Tinca tinca*, *Scardinius erythrophthalmus* and *Lepomis gibbosus* (and also in *Oligochaeta* sp.), but not in *Pseudorasbora parva* and *Gambusia holbrooki* (Suppl. Mat. III.B.4). This observation remains challenging to explain. One hypothesis could be the role of environmental conditions: in anoxic conditions, the methane pathway is activated and biogenic methane has been shown to be ^{13}C -depleted compared to allochthonous terrestrial plant detritus and autochthonous phytoplankton (Grey, 2016). Yet, anoxic conditions regularly occur at the lake bottom in summer and the most severe events can even concern the whole water column, especially in shallow lakes (see Westrelin et al., 2022). Depending on environmental conditions, the relative contribution of the different carbon sources to the trophic web could thus change from one year to another, and be reflected in the

autumnal SIA of individuals that were present in summer. However, in summer 2019, a severe anoxia occurred without any apparent impact on stable isotope ratios. Not only the severity but also the occurrence of anoxic events might probably play a role. In 2018 for example, less severe anoxia events limited to the bottom layer could have occurred frequently, reflected in isotope ratios.

Inter- and intraspecific tradeoffs

Our results suggest that YOY adapt their trophic niche to minimize both intra- and interspecific competition, with variations across years, as it has been shown in several other ecosystems (Wellard Kelly et al., 2021). Fish species, especially predators, are capable of adapting their feeding strategy to their needs (Beaudoin et al., 1999; Svanbäck & Persson, 2004; Matich et al., 2011), resulting in the occurrence of intra- and interspecific tradeoffs. The degree of potential competition, as estimated by isotopic niches, fluctuates across years between and within species, depending on their density (Borcherding et al., 2019). Indeed, the observed variability in occupied niches' dimensions seemed to be linked to variations in CPUE. The most evident case in our study is that of pikeperch, which showed huge differences in its isotopic niche width, with a much wider population niche (SEAb40%) and increased trophic diversity between individuals (CD) when the CPUE was high. This was also the case for pike and perch. With increased intraspecific competition, pike, perch and pikeperch would enlarge their niche to decrease competition with conspecifics (Araújo et al., 2011), suggesting that individuals adopt individual strategies rather than a generalist pattern controlling the diet spectrum, although this may also be indicative of resource limitations (Latli et al., 2019). Perch niche size appeared as the most variable across years; as a trophic generalist, perch would adapt its diet according to the concurrent and predatory community (Schulze et al., 2012). Beaudoin et al. (1999) revealed that the trophic position of pike increases by shifting towards a greater importance of littoral prey, and that individuals could differ by as much as two trophic levels in the same population, lowering intraspecific competition. On the other hand, in 2019, the observed niche of catfish did not increase with the larger sample size and much greater CPUE, suggesting that catfish either focus on their niche to decrease interspecific competition, following the classic niche theory (Pianka, 1981), or that resources are not limiting, since the total YOY CPUE (and thus the potential intra- and interspecific competition) in 2019 was much lower than in the two other years. Catfish niche size was, however, the most stable and it was rather narrower than those of

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piscivorous specialists like pikeperch and pike, as also found in other studies (Haubrock et al., 2019; Haubrock et al., 2020), which differs from its adult opportunistic generalist trophic behavior (Vejřík et al., 2017).

Except for some occasional (i.e. not constant across years) overlaps, species niches were segregated as hypothesized, indicating that the potential interspecific competition is low. This partitioning probably contributed to preserving body conditions for all species as these were similar within years (Bašić et al., 2019). The observed divergence of niches and their varying interannual degrees of overlap (niche expansion) according to ecological gradients (e.g. environmental variations, community composition, etc.) advocate for the ‘resource diversity hypothesis’ prevailing in our lake (Costa-Pereira et al., 2019), which is indeed productive (eutrophic status), with resources appearing as abundant.

Importance of environmental factors

Predator assemblages are determined by a combination of local and regional factors - an important one being the environment - acting in synergy (Fernández et al., 2018) whereas their diversity ensures the ecosystem functioning under fluctuating conditions (Yachi & Loreau, 1999). In the end of August 2019, a severe hypoxia in the lake led to the death of numerous fish (see Westrelin et al., 2022 for details on this event). Pikeperch, whose CPUE collapsed, was probably impacted as it has the highest oxygen requirements among the four species (Dolinin, 1974). Perch and catfish were probably the least impacted (see their CPUE) as they are the least demanding in oxygen (Jones, 1964; Daněk et al., 2014; Westrelin et al., 2022). In 2019, the YOY community appeared released from competition, as the total YOY CPUE was the lowest, mainly due to the collapse of the pikeperch stock. Species niches were also narrowed but simultaneously less segregated (niches of pike and perch, and pike and pikeperch were not different). The niche variation hypothesis however states that the release from competition leads to population niche expansion due to increased interindividual variation and/or increased individual niche widths (Van Valen, 1965; Bolnick et al., 2010). While CPUE provides information on the species abundance in the community at one time, SIA on fin tissue provides time-integrated information on the diet of the three previous months and thus indicative of July-September diet. The juvenile pikeperch cohort is usually abundant in this lake (unpublished data) and could also have been abundant in 2019 before the anoxic event in the end of August, approximately one month before our SIA sampling. Thus, it could have happened that

interspecific competition was effectively strong before the anoxia, contributing to narrowed and segregated species niches, and that after the pikeperch collapse, the release from interspecific competition led to less segregation. Our SIA could then be representative of a period over which strong interspecific competition was ongoing for two-thirds of the time and competition was released for merely one-third. This could explain the mixed pattern we observed on niches. Natural environmental changes have already been shown to affect trophic niches (Persic et al., 2004). This indicates that pikeperch likely shapes the predator community and further strengthens the hypothesis that a species recruitment not only depends on the available resources and its natural enemies but also on its own response to the environment and abilities to adapt to fluctuations (Shea & Chesson, 2002). At the ecosystem level, this underlines the importance of biodiversity, and in this case of predators, which supports ecosystem functioning and resilience against environmental uncertainty (Thébault & Loreau, 2005; Mori et al., 2013).

Invasions

The integration of alien species into food webs has shown complex outcomes of competitive interactions within and between species, both alien and resident (Britton et al., 2019). We found no overlap between the catfish isotopic niche and those of native fishes. On the other hand, the niche of pikeperch occasionally overlapped with those of pike and perch, which nevertheless maintained abundant populations. Although this does not provide evidence of the detrimental effects of invasive YOY as hypothesized, yet, the introduction of a fish species leads to shared resources which can become limiting factors affecting food acquisition, assimilation, growth and survival rates of YOY (Gozlan et al., 2010; Dick et al., 2014; Dick et al., 2017; Gutmann Roberts & Britton, 2018). The successful introduction of alien species is often favored by their trophic plasticity and generalist diet (Comte et al., 2017; Cathcart et al., 2019; Balzani et al., 2021); this can lead to niche constrictions or shifts of native competing species via trophic specialization, as a way to preserve growth rates and conditions (Bašić et al., 2019). In our system though, the niche of these two alien species did not appear larger than those of native species. As discussed above, pikeperch isotopic niche size seemed to be larger when pikeperch density was higher, which could sign potential intraspecific competition, pikeperch adapting its trophic niche according to the density of conspecifics. Contrary to expectations, catfish, often labeled as generalist, did not have the largest niche. The abilities of species to partition their niche, along with abundant resources, facilitates the integration of alien species (such as catfish

and pikeperch), but with complex interactions between cohorts' strength and intra- and interspecific competition (Britton et al., 2018).

Conclusion

Apart from certain caveats (see Suppl. Mat. III.B.5), this study highlighted that YOY predators can partition their trophic niche, probably to decrease the potential interspecific competition. The temporal span of the study added interesting unexpected features: a general trophic pattern could effectively be found across years for the YOY community, but with a high variability which was not expected for such a closed system. This variability, however, seemed to be linked to the relative strength of the cohorts, which changed considerably between years and in turn could make the degree of the potential intraspecific competition vary. Environmentally harsh conditions contributed to the interannual variability and underlined the importance of the diversity of predators to maintain their functions in case of the decline of a particular species (Yachi & Loreau, 1999). Indeed, size- and stage-structured predator communities contribute to an efficient transfer of biomass and energy across the web (Gaedke, 2021), thereby increasing the stability of the trophic web (Caskenette & McCann, 2017). Surprisingly, YOY catfish expressed a consistently narrow niche compared to other species. The eutrophic status of this lake, offering rather abundant resources, probably facilitated the coexistence of these four predators. As such, this work demonstrates the importance of viewing trophic webs as dynamic systems and should encourage time-integrated studies to get the most exhaustive and informative picture. Concomitantly, we advocate for multiplying studies on juveniles, as they shape future communities.

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4. *Supplementary materials*

Suppl. Mat. III.B.1. Trophic status of the “Etang des Aulnes”.

Over the 4 seasons in 2018, 2019 and 2020 (one measurement per season over the whole water column), the mean and range (in mg/L) of mineral nitrogen (NO_3^- and NH_4^+), orthophosphate (PO_4^{3-}) and total phosphorus in the whole water column were respectively 1.42 ([0.55 ; 10.75]) , 0.12 ([0.02 ; 0.52]) and 0.14 ([0.01 ; 0.71]). These values classify the “Etang des Aulnes” as eutrophic (WFD2000/60/EC, 2000).

Suppl. Mat. III.B.2. Hourly mean (range) temperature (in °C) of the water column. Hourly temperatures have been averaged at 0.5, 3 and 5 m above the bottom at the deepest point of the lake, 5.5 m deep, to get a mean temperature for the water column. They are given in winter (21 December - 20 March), spring (21 March - 20 June), summer (21 June - 20 September) and autumn (21 September - 20 December) every year from 2018 to 2020.

	Winter	Spring	Summer	Autumn
2018	7.4 [3.0; 12.4]	17.9 [8.1; 24.2]	24.5 [21.2; 27.1]	14.5 [7.5; 23.4]
2019	7.1 [3.2; 12.9]	16.5 [11.4; 23.2]	24.8 [18.9; 29.1]	14.7 [8.0; 21.6]
2020	9.4 [6.8; 13.3]	18.7 [12.6; 24.1]	24.6 [21.8; 28.6]	13.8 [6.4; 24.1]

Suppl. Mat. III.B.3. Characteristics of YOY sampled each year for SIA. Their number, mean (range) total length (in mm), weight (in g) and relative weight (dimensionless) are given. For each species, total lengths, weights and relative weights were compared between years by an analysis of variance (ANOVA) and Tukey multiple comparisons of means (5% significance level). Each year, total lengths, weights and relative weights were also compared among

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species. A superscript number indicates when years significantly differ (5% significance level); the number corresponds to the ascending rank among years.

		Pike	Perch	Pikeperch	Catfish
n	2018	16	16	13	36
	2019	13	38	14	111
	2020	14	4	34	9
Total length	2018	311	97 ⁽²⁾	161 ⁽³⁾	291 ⁽¹⁾
		[230; 382]	[76; 130]	[138; 248]	[179; 342]
	2019	299	122 ⁽¹⁾	254 ⁽¹⁾	271 ⁽²⁾
		[239; 380]	[102; 140]	[181; 280]	[159; 350]
	2020	310	139 ⁽¹⁾	210 ⁽²⁾	309 ⁽¹⁾
		[239; 393]	[136; 140]	[174; 273]	[279; 350]
Weight	2018	189	12 ⁽³⁾	33 ⁽³⁾	150 ⁽¹⁾
		[80; 346]	[5; 26]	[16; 119]	[36; 291]
	2019	161	21 ⁽²⁾	122 ⁽¹⁾	110 ⁽²⁾
		[81; 332]	[11; 32]	[40; 161]	[23; 236]
	2020	187	32 ⁽¹⁾	64 ⁽²⁾	170 ⁽¹⁾
		[98; 386]	[28; 36]	[35; 140]	[120; 239]
Relative weight	2018	1.07 ⁽¹⁾	1.08 ⁽¹⁾	1.06 ⁽¹⁾	1.02 ⁽¹⁾
		[0.91; 1.32]	[0.95; 1.28]	[0.90; 1.47]	[0.76; 1.40]
	2019	0.97 ⁽²⁾	0.97 ⁽²⁾	1.00 ⁽¹⁻²⁾	0.96 ⁽²⁾
		[0.90; 1.06]	[0.74; 1.40]	[0.92; 1.10]	[0.81; 1.21]
	2020	1.03 ⁽¹⁻²⁾	1.01 ⁽¹⁻²⁾	0.95 ⁽²⁾	1.03 ⁽¹⁻²⁾
		[0.88; 1.27]	[0.85; 1.09]	[0.74; 1.33]	[0.94; 1.15]

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To evaluate the body condition of each individual, the relative weight was also calculated as the ratio of the observed weight over the expected weight calculated from the linear regression $\log(\text{Weight}) = a \times \log(\text{Total_length}) + b$ where a and b are the regression coefficients (Blackwell et al., 2000; Kraus et al., 2020). Within a year, relative weights did not differ between species, except in 2020 when pikeperch had lower relative weights than pike ($p=0.039$). Within a year, total lengths differed between all pairwise species except pike and catfish ($p=0.386$, 0.052 and 0.999 , respectively in 2018, 2019 and 2020), with pike and catfish larger than pikeperch, itself larger than perch. Only in 2019, pikeperch and catfish total lengths did not differ ($p=0.328$). The pattern was a bit different for weights with pike and catfish heavier than pikeperch and perch: in 2018 and 2020, weights did not significantly differ between pike and catfish ($p=0.161$ and 0.816 , respectively) and between perch and pikeperch ($p=0.781$ and 0.508 , respectively). In 2019, weights of pike and pikeperch and of catfish and pikeperch did not differ ($p=0.155$ and 0.791 , respectively); pike was heavier than catfish ($p < 0.001$).

Between years and within species, relative weights were the highest in 2018 for all species, the lowest in 2019 and not different from these two years in 2020 for all species except pikeperch. For pikeperch, the relative weights were the lowest in 2020 and not different from 2018 and 2020 in 2019. The total length did not change for pike between years, whereas perch was larger in 2019 and 2020 than in 2018, pikeperch was larger in 2019 > 2020 > 2018 and catfish was larger in 2018 and 2020 than in 2019. The weight did not change from year to year for pike. Perch was heavier in 2020 > 2019 > 2018; pikeperch was heavier in 2019 > 2020 > 2018 and catfish was lighter in 2019 than in 2018 and 2020.

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Suppl. Mat. III.B.4. Mean bulk stable isotope ratios for fish species and baselines of the “Etang des Aulnes” food web over the three years. Mean (*sd*) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are given for different species. All sizes of fish are mixed, but only YOY for pike, perch, pikeperch and catfish.

Species	Year	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Bulk zooplankton	2018	9	-25.2 (5.32)	2.66 (3.35)
	2019	10	-23.89 (0.47)	3.42 (1.34)
	2020	15	-23.98 (0.57)	6.53 (0.48)
<i>Gastropods sp.</i>	2018	7	-21.23 (1.33)	3.22 (0.65)
	2019	8	-18 (1.74)	3.61 (0.71)
	2020	12	-21.42 (2.5)	7.82 (0.54)
<i>Oligochaeta sp.</i>	2018	4	-24.52 (1.23)	6.1 (1.32)
	2019	5	-25.93 (0.34)	7.02 (0.24)
	2020	5	-25.9 (0.88)	6.11 (0.81)
<i>Gambusia holbrooki</i>	2018	7	-21.38 (0.95)	7.16 (0.67)
	2019	11	-21.02 (0.79)	6.44 (0.73)
	2020	8	-22.29 (0.64)	10.66 (0.39)
<i>Pseudorasbora parva</i>	2018	7	-20.72 (0.92)	5.14 (0.4)
	2019	8	-20.5 (0.75)	5.17 (0.5)
	2020	7	-21.24 (1.03)	9.88 (0.35)

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	2018	18	-19.55 (0.96)	7.21 (0.72)
<i>Abramis brama</i>	2019	35	-21.48 (1.21)	6.66 (1.81)
	2020	10	-23.2 (0.56)	8.91 (0.31)
	2018	15	-18.82 (0.86)	6.05 (0.57)
<i>Scardinius erythrophthalmus</i>	2019	21	-20.93 (0.68)	6.21 (0.47)
	2020	5	-22.62 (0.52)	9.11 (0.26)
	2018	25	-20.09 (1.54)	7.85 (1.17)
<i>Tinca tinca</i>	2019	38	-21.62 (1.05)	6.89 (0.97)
	2020	26	-22.57 (1.03)	9.77 (0.51)
	2018	29	-19.26 (1.07)	7.28 (1.04)
<i>Lepomis gibbosus</i>	2019	29	-21.18 (0.97)	6.4 (1.11)
	2020	25	-22.61 (0.76)	9.55 (1.38)
	2018	16	-19.13 (0.61)	9.3 (0.75)
<i>Esox lucius</i>	2019	13	-20.6 (0.5)	7.63 (0.36)
	2020	14	-21.46 (0.37)	11.54 (0.39)
	2018	16	-18.89 (1.47)	8.27 (0.48)
<i>Perca fluviatilis</i>	2019	38	-20.71 (0.75)	7.32 (0.57)
	2020	4	-22.7 (0.28)	9.52 (0.18)

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	2018	13	-19.49 (0.48)	8.57 (0.46)
<i>Sander lucioperca</i>	2019	15	-20.64 (0.42)	7.98 (0.59)
	2020	34	-22.6 (0.65)	10.87 (0.74)
	2018	38	-19.89 (0.47)	8.71 (0.42)
<i>Silurus glanis</i>	2019	111	-21.67 (0.42)	7.22 (0.45)
	2020	9	-21.7 (0.36)	12.09 (0.2)

Suppl. Mat. III.B.5. Caveats identified in the study.

The sampling of muscle is very commonly used for SIA but needs to sacrifice the fish. Surrogates such as fins or scales can be used instead. But fin isotopic ratios can be different from that of muscle and fractionation factor of N and C can be different among species. A lot of studies strengthen the importance of getting species-specific relationships between stable isotope values of muscle and fin when aiming at using fin tissue as a surrogate for muscle and even relationships that can depend on season and fish size (Willis et al., 2013; Busst et al., 2015; Winter et al., 2019a; Roberts et al., 2021). Although we did not sample muscle by favoring a non-lethal sampling, we followed Hayden et al. (2015) recommendations by standardizing sampling in selecting tissue only from the extreme tip of a fin and homogenizing fins prior to analysis. Concerning the trophic discrimination factors (TDF), they can indeed also vary between species, but even between closely related ones (Ceia et al., 2021) and also between ontogenic stages (Scharnweber et al., 2021). In the absence of available muscle conversion factor and TDF calibrated on our species and ontogenetic stages, the conversion of the data should be considered with great caution and could even be detrimental. In our specific case, we thus think it was more reasonable to use neither conversion factor to muscle nor different TDF. Moreover we conducted a sensitivity study that showed that by using conversion factor between fin and muscle, our results remained extremely similar.

We also tested the variations around the trophic discrimination factor by running the *tRophicPosition* package that uses Bayesian estimates (Quezada-Romegialli et al., 2018). Below is the equivalent of the original Fig III.B.2a (Fig III.B.2a-bis) of our paper with the *tRophicPosition* package (the raw posterior distribution of TP is plotted, based on 10,000

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simulated values). Results are very similar despite some small differences. Globally, differences which visually appear are less often significant. This does not change the TP pattern compared to what we found with a fixed TDF. If we recall Post (2002)'s comments "To integrate the variance around the mean trophic fractionation of 3.4‰ in estimates of trophic position is thus particularly recommended in studies which attempt to quantify trophic differences among just a few feeding links. But, when applied to entire food webs, with multiple trophic pathways and many species, a mean trophic fractionation of 3.4‰ is a robust and widely applicable assumption.", we are indeed in the second case. Moreover, in our study we need the TP values, not only its distribution based on 10,000 draws, to plot the isotopic niche and to fit linear regression using individuals' size among covariates. Based on these considerations, on the arguments from the literature and the results of tRophicPosition package here presented that are in agreement with our results presented in the paper core, we decided to keep a fixed TDF.

Only four YOY perch were caught in 2020, which inevitably impacted Layman metrics on this species as there is a tendency for underestimation at small sample sizes ($n < 10$) (Jackson et al., 2011). This was visible on estimation of niche overlaps, which need to be interpreted with caution, even if "The Bayesian estimate, SEAb, captures all the same properties as SEAc, being unbiased with respect to sample size and exhibiting more uncertainty with smaller sample size." (Jackson et al., 2011). Catfish in 2020, with a sample size just below the threshold of ten (nine), seemed to be less affected by this underestimation as their Layman metrics were not systematically lower than in other years. Nevertheless, these sample sizes were very linked to the CPUE and it was important to take into account all the four species in the community niche metrics.

Unfortunately, we could not conduct a similar study on adults as we captured very few adults pikeperch and perch. But this would have brought interesting results to review in light of the YOY's findings and this could be worth investigating in the future. Nor did we consider the predation risk from piscivorous adults, which can influence juvenile habitat use and consequently their trophic niche (Araújo et al., 2011). We actually hypothesized that competition within the same YOY predatory guild would be the dominant pressure as piscivorous adults can prey upon a much more abundant cyprinid community.

Our sampling was not intended to perform SIA on the preys of YOY (macroinvertebrate community and small fish for example), which could have highlighted some interesting

III.B Variability of the trophic niche of a freshwater predator community

features. Moreover, even if they only constitute a snapshot view of the diet, stomach contents would have brought informations on the prey spectrum of YOY species and their degree of overlap (e.g. Zhang et al., 2018; Haubrock et al., 2020; Bissattini et al., 2021). It could possibly have helped explain the high LR in 2018 as well, in case we missed something in the sampling. This should be considered in future investigations, even if focused on the trophic niche.

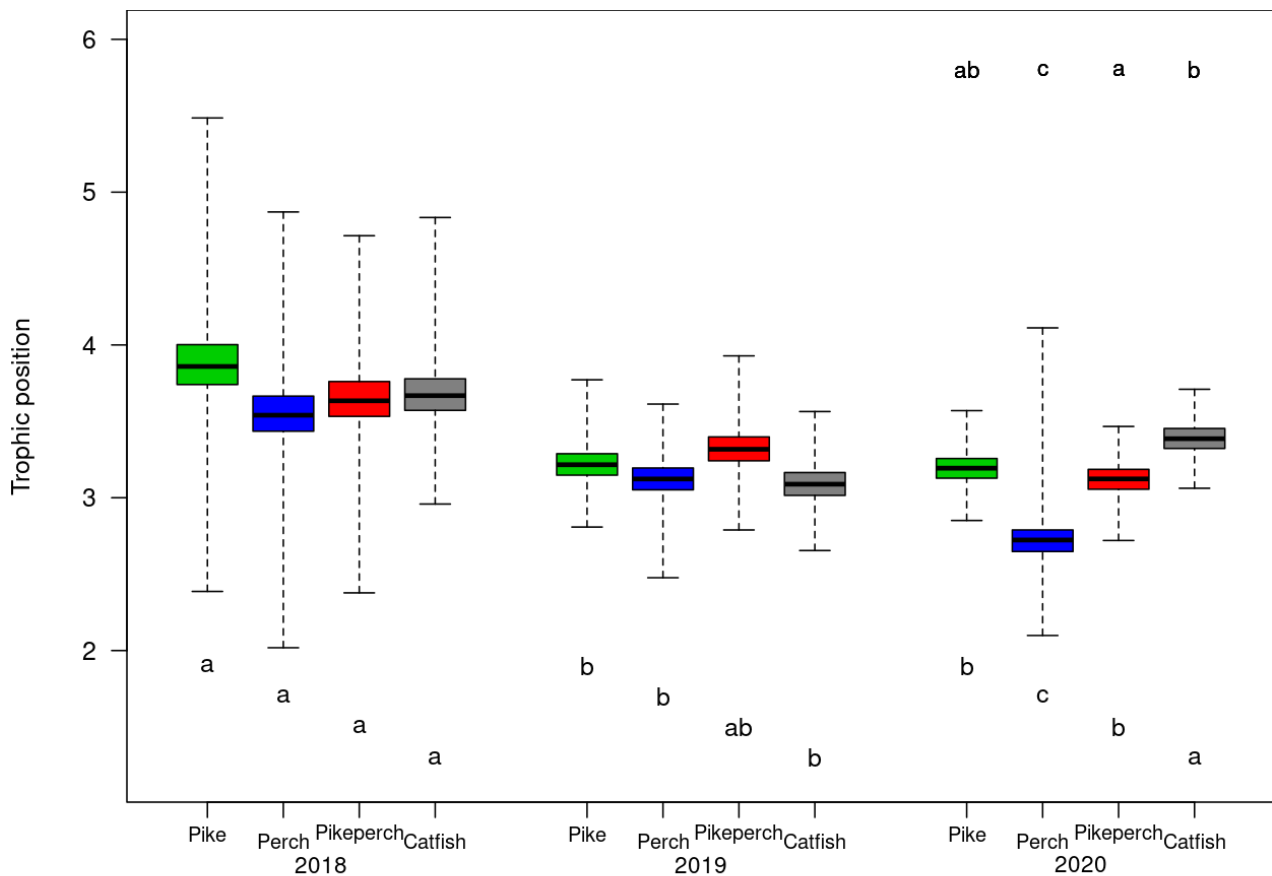


Fig III.B.2a-bis: Boxplots of the posterior distributions of trophic position calculated on fin SIA and using variance around the trophic discrimination factor (values from Post, 2002). The Bayesian distributions have been compared with the function `pairwiseComparisons` of `tRophicPosition` package. This figure compares to Fig III.B.2a of the core paper.

IV.A

Impact of environmental conditions
(seasons, water levels) on the habitat
niche of a population of freshwater
predators

IV. Impact of variable or harsh environmental conditions on the habitat niche of a population of freshwater predators

In the previous chapter, habitat and trophic niche partitioning among species along with intraspecific niche variation were highlighted as mechanisms of species coexistence. Environmental conditions are important factors that can impact intraspecific competition and, in turn, modify species' niches. The environmental changes that come with seasons themselves constitute a common periodic forcing. Time-limited but harsh conditions can impact species abundance as this anoxia in “Etang des Aulnes” in summer 2019 that led to the collapse of the least resilient YOY pikeperch population. Particular environmental conditions can also lead to the scarcity of preferred resources or habitat that could create a competitive bottleneck. In this chapter, we analyzed variation of the population habitat niche in response to environmental conditions.

A. Habitat use and preference of adult perch (*Perca fluviatilis* L.) in a deep reservoir: variations with seasons, water levels and individuals

1. *Synthesis (English)*

In reservoirs, water level fluctuations (WLF) considerably differ from natural lakes in amplitude, seasonality and frequency. In particular, they are often much larger and much more frequent, leading to rapid shifts in habitat availability and even detrimental effects on littoral habitats, thereby decreasing the biodiversity they host. In the Bariousses reservoir (WLF amplitude of 6 m), we tracked 21 adult perch over 2 years to evaluate how environmental variations due to WLF, combined with seasonal changes, could affect fish habitat niche. Perch is a widespread predator in European reservoirs that are frequent in open waters but are also known to commonly use the littoral zone. By relating positions to the available habitats (water depth and, in the littoral zone, substrate type, presence of emerging trees, and presence of tree stumps), we quantified perch habitat preferences across seasons and water levels (low, mean, high). Perch habitat niche was strongly dependent on season, except for the substrate component for which the more complex (stones, boulders and rocks) were favored regardless of season. Surprisingly, we did not find any significant impact of water level on perch habitat niche whereas low water levels reduced the structural complexity of the littoral zone (i.e. fewer emerging trees, less gravel, pebbles and stones and more silty ground). Irrespective of the water

IV.A Impact of environmental conditions (seasons, water levels) on the habitat niche of a population of freshwater predators

level, in spring and summer, a strong preference for the littoral zone and notably complex habitats was observed. Spring and summer are seasons of greater activity for perch and prey become abundant in littoral habitats. Moreover, perch spawns in spring and seeks suitable laying substrates, more abundant in the vicinity of the littoral zone. In summer, the hypoxic hypolimnion limits in part the use of the pelagic zone. In autumn and winter, perch migrated into deeper waters. Despite these general patterns, the individual variability of habitat niche was high. Several assumptions could explain why WLF did not impact perch habitat niche. Perch have been shown to have a plastic behavior and could possibly adapt to such variations. It is also possible that the availability of preferred habitats did not reach critical threshold for a long enough period to become detrimental. The seasonal shift of the perch habitat niche, related to temperature changes, strengthens the close links between habitat niche and environmental conditions.

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2. *Synthesis (French)*

Utilisation et préférence d'habitat de la perche adulte (*Perca fluviatilis*) dans un réservoir profond : variations avec les saisons, les niveaux d'eau et les individus.

Dans les réservoirs, les variations du niveau d'eau (VNE) diffèrent considérablement de celles des lacs naturels, que ce soit en amplitude, saisonnalité ou fréquence. En particulier, elles sont souvent plus amples et beaucoup plus fréquentes, ce qui engendre de rapides changements dans la disponibilité des habitats, et même des dégradations des habitats littoraux, affectant par là même la biodiversité qu'ils hébergent. Dans le réservoir des Bariousses (dont l'amplitude des VNE est de 6 m), nous avons suivi les déplacements de 21 perches adultes deux années durant pour évaluer comment les fluctuations environnementales, associées aux VNE ainsi qu'aux changements saisonniers, impactaient leur niche d'habitat. La perche est un prédateur répandu dans les réservoirs d'Europe, fréquentant largement la zone pélagique mais utilisant également beaucoup la zone littorale. En reliant les positions aux habitats correspondants (hauteur de la colonne d'eau et, dans la zone littorale, type de substrat, présence d'arbres émergents et présence de souches d'arbres), nous avons quantifié ses préférences d'habitat selon les saisons et les niveaux d'eau (bas, moyen, élevé). La niche d'habitat de la perche dépendait fortement de la saison, excepté pour le type de substrat dont les plus complexes (pierres, blocs et rochers) étaient toujours privilégiés. De façon surprenante, le niveau d'eau n'impactait pas significativement la niche d'habitat de la perche alors que les niveaux bas réduisaient pourtant la complexité structurale de la zone littorale (moins d'arbres émergents, moins de gravier, de cailloux et de pierres et plus de vase). Indépendamment du niveau d'eau, au printemps et en été, une forte préférence de la zone littorale, notamment de ses habitats complexes, était observée. Le printemps et l'été sont des périodes de forte activité de la perche et les proies deviennent abondantes en zone littorale. Qui plus est, la perche se reproduit au printemps et se met à la recherche de substrats de ponte, plus abondants au voisinage de la zone littorale. En été, l'oxygénation dégradée de l'hypolimnion limite en partie l'utilisation de la zone pélagique. En automne et en hiver, la perche migrait vers des zones plus profondes. Autour de ce patron général, la variabilité individuelle de la niche d'habitat était cependant élevée. Plusieurs hypothèses peuvent expliquer pourquoi les VNE n'impactaient pas la niche d'habitat de la perche. La perche est connue pour sa relative plasticité comportementale et pourrait alors

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s'adapter à de telles variations. Par ailleurs, il se peut aussi que la disponibilité de ses habitats préférés n'ait pas atteint de seuil critique suffisamment longtemps pour devenir délétère. Les variations saisonnières de la niche d'habitat de la perche, liées aux variations de température notamment, soulignent les liens étroits entre niche d'habitat et conditions environnementales.

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3. Core paper

Samuel Westrelin, Romain Roy, Laurence Tissot-Rey, Laurent Bergès, Christine Argillier, 2018. Habitat use and preference of adult perch (*Perca fluviatilis* L.) in a deep reservoir: variations with seasons, water levels and individuals. *Hydrobiologia*, 809(1), 121-139 <http://dx.doi.org/10.1007/s10750-017-3454-2>.

Abstract

Perch *Perca fluviatilis* is a widespread predator in European reservoirs, frequent in open waters but also known to spend a lot of time in the littoral zones. To get insight into how adult perch used and selected their habitat in an environment subject to water level fluctuations, 21 perch were continuously tracked using acoustic telemetry over 2 years in the Bariousses reservoir (France). The different available habitats were characterized by depth classes and substrate types, presence of emerging trees, and presence of tree stumps in the littoral zone. We showed that perch habitat preferences were strongly dependent on the season, except for substrate type, and in line with their habitat use. Surprisingly we did not find any influence of the water level which however reduced the structural complexity of the littoral zone when lowering. In spring and summer, whatever the water level, we observed a strong preference for the littoral zone and complex habitats. In autumn and winter, perch migrated into deeper waters. However, the individual variability of the habitat preferences was quite high. This type of research helps to understand the spatial ecology of fish and provides useful guidance to hydromorphological restoration for fish populations.

Keywords: acoustic telemetry; littoral zone; depth; seasonal migrations

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Introduction

Whatever their origin, lake littoral zones are transitional areas between terrestrial and aquatic habitats that generally host a high biodiversity (Schmieder, 2004). They provide resources available nowhere else in the lacustrine ecosystem (Zohary & Gasith, 2014) and most lake fishes use them during their life cycle (Winfield, 2004). Littoral habitats can also be composed of complex structures (e.g. rocks, woody debris, vegetation) that provide both spawning grounds and refuges to a diverse assemblage of microorganisms, algae, invertebrates (Gasith & Gafny, 1998) as well as fish larvae and juveniles (Diehl, 1993; Stoll et al., 2008).

Littoral habitats are highly influenced by water level fluctuations (WLF) which can be particularly pervasive in lentic systems exploited by humans for water use and hydropower. Habitat complexity changes with water level (WL), particularly in the littoral zone (Zohary & Ostrovsky, 2011). For instance, high WLF (frequent and wide) may engender coarser littoral substrate with less macrophyte coverage in the shallow zones of lakes (Evtimova & Donohue, 2016), which in turn reduce the productivity and biodiversity of these areas (Wetzel, 1990; Evtimova & Donohue, 2014). More specifically, studies have shown that WLF can affect various ecological aspects of fish species such as their growth, distribution and behaviour (e.g. Gaboury & Patalas, 1984; Rogers & Bergersen, 1995; Fischer & Ohl, 2005; Sutela & Vehanen, 2008; Logez et al., 2016). Indeed, WLF can lead to loss of potential prey (Winfield, 2004), loss of refuge areas (Kaczka & Miranda, 2014) and loss of spawning habitats (Hudon et al., 2005) for fish fauna. Finally, WLF may also decrease fish recruitment if WL drops after spawning (Kahl et al., 2008) and fish eggs desiccate (Michaletz, 1997; Winfield, 2004). Therefore, Coops et al. (2003) and more recently Tao et al. (2016) highlighted the urgency of collecting ecological data on fish–habitat relationship. Fish habitat use is a key driver of population dynamics (Hayes et al., 2009) and an essential knowledge for predicting how populations will respond to management interventions (Koster et al., 2015; Cooke et al., 2016). In particular, the identification of crucial habitats is important for efficient aquatic conservation in areas with strong human influence (Halpern et al., 2005; Sale et al., 2005).

A thorough *in situ* study of WLF effects on the behaviour of a species has rarely been conducted and can contribute to valuable knowledge on management decisions, as Gardner et al. (2015) recently showed on the common bream (*Abramis brama* L.) which altered their home range size according to the WL while keeping the same activity level. In the present work we propose

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to study habitat-use patterns of the Eurasian perch (*Perca fluviatilis* L.), a species present in most lowland reservoirs (Irz et al., 2006) and widespread in Europe (Kottelat & Freyhof, 2007) but on which the effects of WLF have never been investigated. Although frequent in open waters, their dependence on the littoral zone is high (Zamora & Moreno-Amich, 2002; Jacobsen et al., 2015). At night, they rest in the littoral zone on the bottom (Imbrock et al., 1996). They are highly selective in their choice of spawning habitat, generally preferring shallow and sheltered areas with rigid and structurally complex substrates (Probst et al., 2009; Snickars et al., 2010; Čech et al., 2012a) but can spawn in deeper waters depending on the environmental conditions (Čech et al., 2012a; Čech et al., 2012b). Perch spawning usually takes place when water temperatures reach about 5°C (Souchon & Tissot, 2012).

Given that the littoral zone is a critical habitat for the perch, we designed the present study to evaluate whether and how WLF affect its habitat preferences, here defined as the higher likelihood that an individual chooses a habitat type if offered on an equal basis to others (Johnson, 1980). As WLF can modify the availability of the different littoral habitat types (Zohary & Ostrovsky, 2011; Evtimova & Donohue, 2016), we expected a shift of perch habitat preferences with WL. For example, when an habitat becomes very scarce, if perch keeps on frequently using it, then its preference will automatically raise; on the contrary, if perch switches to another habitat, its preference will decline for this scarce habitat and raise for the other. In particular, we could expect this to happen during the spawning season, in spring in our case, when the habitat choice appears crucial. To answer this question, we set up a high spatial and temporal resolution study over a French reservoir, subject to human induced WLF ranging from days to seasons. More specifically, we tracked 21 large perch by acoustic telemetry over a 2 year period. We first evaluated how WLF affected the relative availability of the littoral and pelagic areas in the reservoir. Then, we assessed the effects of WLF and seasons on individual habitat preference. Lastly, perch habitat use and preferences were analyzed in detail.

Materials and methods

Study site

The study was conducted in the Bariousses hydropower reservoir (45.33°N, 1.49°E) in the west central part of France (Figure IV.A.1). The reservoir is located in a rural and natural

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environment, in a forest land cover dominated catchment with low anthropogenic activities (Logez et al., 2016). This reservoir, with a 229 km² watershed, is an impoundment of the Vezere River. It is the second dam on this river and it is located 42 km downstream the source; the average flow is 4.37 m³/s at Bugeat, 20 km upstream from the dam. The main inflow to Bariousses lake comes from deep waters of the first dam located 12 km upstream. As these waters are colder than those of the lake, especially in spring and summer, they probably flow at the bottom of the lake along the original river track. At the mean WL, altitude of 511.5 m, its area covers 86.6 ha, mean depth is 7.1 m and maximum depth reaches 19.4 m. The bathymetry of the reservoir was measured with a multibeam sounder (EDF, personal source), giving a 2×2-m resolution GIS map. The reservoir mean renewal time is 12 days.

The thermal regime of the reservoir is monomictic with four distinct temperature regimes. In spring (April to June), the water temperatures raise rapidly and the stratification is taking place; in summer (July to September), waters are warmer and stratified and the thermocline about 4.5m deep; the autumn (October to December) corresponds to a rapid decrease of water temperatures when the mixing is taking place and destratification is in progress and, in winter (January to March), the waters are homogeneously cold over the whole water column (Table IV.A.1). The summer thermocline is associated with an oxycline that separates saturated surface waters from deep waters; the deep layer has an oxygen saturation rate of 40%. These regimes can be linked with perch ecology. The broad range of optimum temperatures for perch spawning lies between 5°C and 19°C, depending on the region, and the limited one between 8°C and 15°C (Souchon & Tissot, 2012). Rising temperatures appeared to be the major factor inducing spawning (Hokanson, 1977; Thorpe, 1977; Craig, 2000) which suites well with spring. In addition, in the Bariousses reservoir, we observed some perch eggs laying on the shore in April and perch egg ribbons were also usually seen by regular anglers in early May in very shallow zones dewatered by the WLF. Perch activity was shown to raise with temperature (Craig, 1977) and to peak concomitantly with high summer temperatures (Jacobsen et al., 2002).

Depending both on human energy needs and hydrology, WLF are very variable in the Bariousses reservoir (Figure IV.A.2). Over the study period (June 2012 to March 2014), the hourly WL, measured by Electricité de France (EDF), ranged from 507.1 m to 513.5 m. The tertiles of the hourly WL distribution over the study period were used to split WL into low, mean and high WL. The mean lake area is 78.1, 86.6 and 90.5 ha respectively at low, mean and

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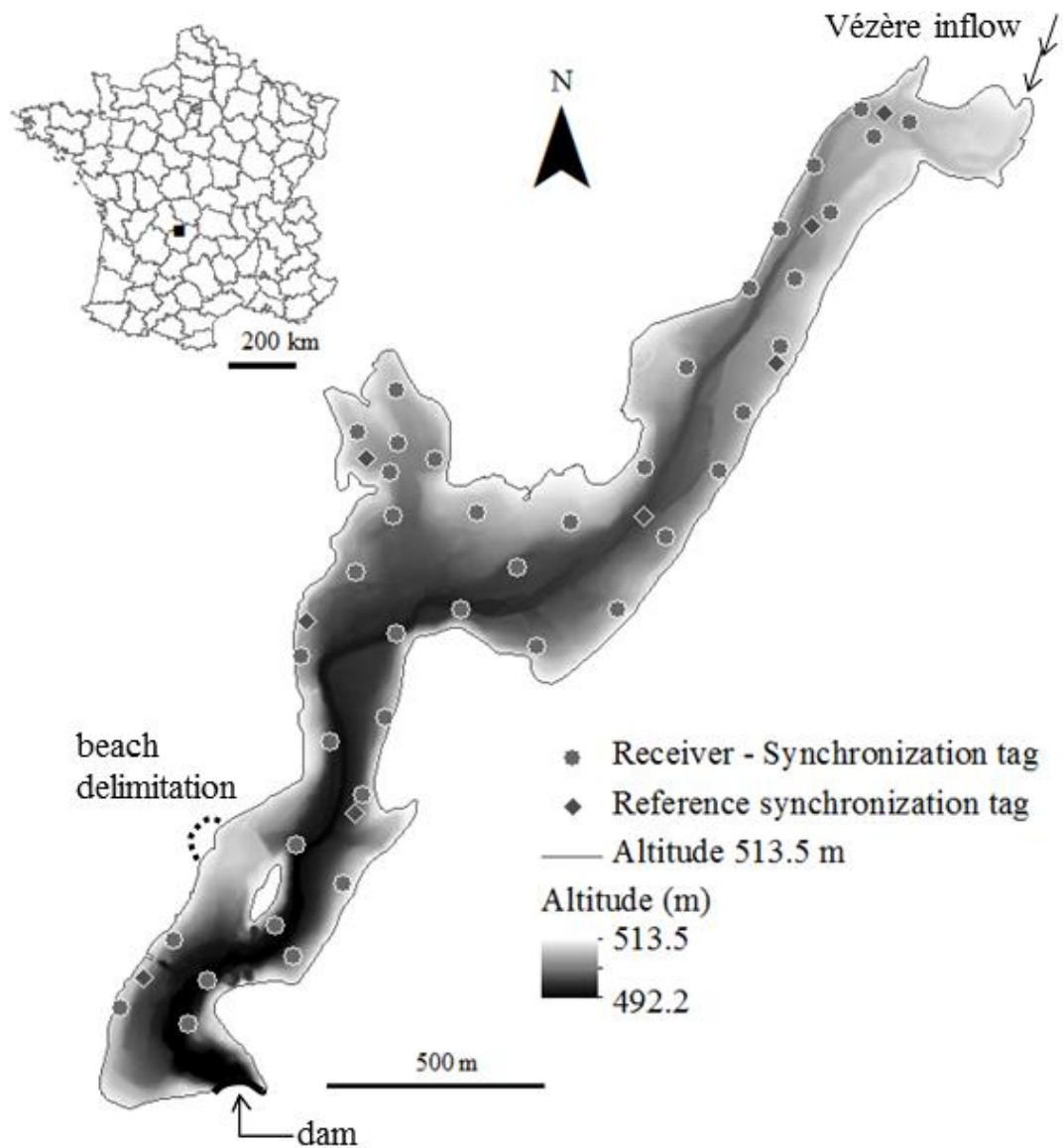


Fig. IV.A.1 Location of the study site on the inset map of France and bathymetric map of the reservoir with the location of the receivers and synchronizing tags

high WL. Typically, WL can shift from one class to a neighbouring class in a few days. Though, main annual features emerge. In spring, the high WL is from far the most frequent whereas the low one is in autumn because, at the beginning of this season, the WL is usually lowered in anticipation of rains (Logez et al., 2016). In winter the occurrence of the three WL classes is more evenly distributed. In summer the WL is kept stable around its mean value 95% of the

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time to sustain recreational activities which are concentrated close to a sandy beach located on the west shore in front of the island (Figure IV.A.1), motorboats being forbidden.

Table IV.A.1 Extent of the study period characterized by the mean, minimum and maximum temperatures (T, °C) over three depths (0.5, 4.5, and 18.5 m), the number of tagged perch (Nind) and their mean (range) total length (TL, mm) and weight (W, g). Npos is the total number of positions. The 4.5 m depth corresponds to the summer thermocline top

Season	Period	T 0.5m	T 4.5m	T 18.5m	Nind	Npos	TL	W
Spring	20/03/2013	- 11.0	9.9	8.4	12	169 999	409	990
	21/06/2013	5.0-18.6	5.0-14.6	4.8-11.7			320-486	383-1800
Summer	29/06/2012	- 20.7	17.3	15.0	18	211 266		
	07/08/2012	17.4-23.6	16.5-18.8	13.6-15.5			405	975
	21/06/2013	- 20.5	17.3	14.5			320-486	383-1800
	22/09/2013	15.3-24.6	13.9-20.3	11.7-15.9				
Autumn	05/10/2012	- 10.4	10.2	10.0	16	160 747		
	21/12/2012	4.6-16.4	4.5-15.7	4.6-14.7			415	1071
	22/09/2013	- 11.3	10.9	10.4			320-486	383-1800
	21/12/2013	3.4-18.4	3.4-16.7	3.8-15.0				
Winter	21/12/2012	- 4.7	4.7	4.7	12	263 292		
	20/03/2013	2.8-6.3	2.9-6.2	3.1-6.2			409	990
	21/12/2013	- 5.6	5.5	5.3			320-486	383-1800
	10/03/2014	4.2-6.4	4.2-6.3	4.3-6.0				

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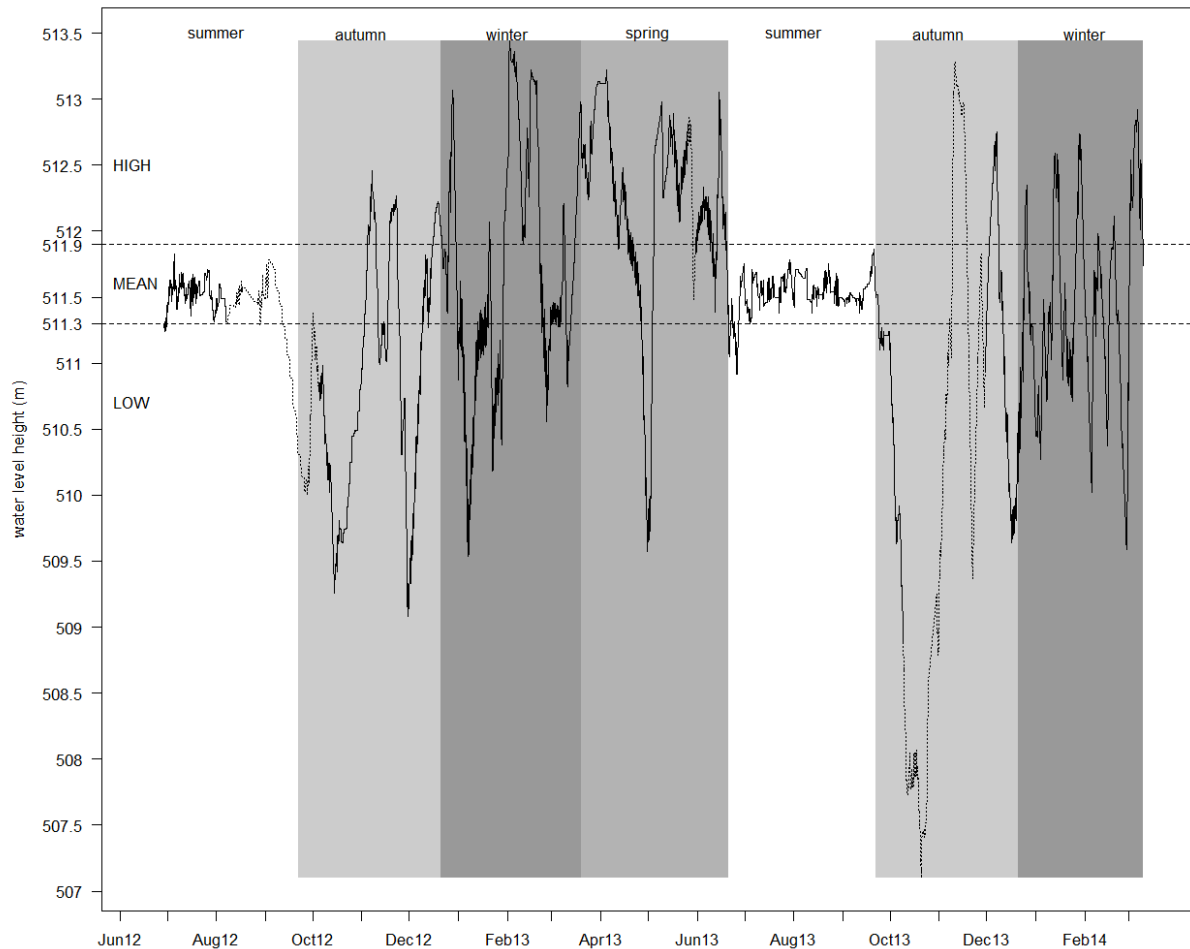


Fig. IV.A.2 Hourly water level in the Bariousses reservoir from 29 June 2012 to 10 March 2014. The solid (respectively dotted) black line corresponds to periods with (respectively without) fish positions. The dashed horizontal lines represent the first and second tertiles of this water level distribution which were used to split water levels into low, mean and high

The water conductivity is low over the whole water column all over the year. The Secchi transparency depth lies between 1.3 and 2.5 m. The characterisation of the phytoplankton community qualifies the reservoir as oligotrophic. Based on diversity, abundance and sensitivity to pollutants of invertebrates sampled in shallow waters, the reservoir appears in good condition (unpublished data). The fish fauna of the reservoir was determined with a standardized procedure (CEN, 2005) in 2010 and comprises 15 species. It is dominated by Cyprinids and Percids, characteristic of a lowland reservoir (Irz et al., 2002). The most dominant species, in terms of catch per unit effort, are roach (*Rutilus rutilus*), ruffe

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(*Gymnocephalus cernua*), Eurasian perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*) and common bream (*Abramis brama*). Beside Eurasian perch and pikeperch, another dominant predator, pike (*Esox Lucius*), is present. This community has been very little manipulated since a lake drainage in 1997. Fishing is allowed all along the year and only outside of spawning periods for pike and pikeperch.

Fish tagging

Following the suggestions of Thiem et al. (2011), below is detailed the followed surgical procedure. A total of 29 adult perch were caught with gillnets set at dawn, day and dusk for maximally 2 hours over four sampling campaigns: 16 in spring 2012, 1 in summer 2012, 7 in autumn 2012 and 5 in spring 2013. Once captured, to check their condition, they spent 3-6 hours in an aerated tank of lake water prior tagging, after a half an hour trip on the boat in another aerated tank to join the tagging site located in a building on the lake shore. Fishes were individually anesthetized, which took 8-10 min, by immersion in a 20 l tank filled with an aerated solution composed of 90% diluted clove oil (0.03–0.05% in lake water) and 10% ethanol. Once the fish had lost its balance (ventral side up), did not respond to stimuli anymore and had a very slow and steady operculum rate with large amplitude, it was weighted, measured and placed ventral side up on a V-shaped surgical table. The same anesthetic solution but less concentrated in clove oil (0.003%) was used to irrigate the gills during surgery. A 10 to 15 mm long incision was made posterior to the pelvic girdle to insert an acoustic transmitter, previously sterilized in surgical spirit, in the peritoneal cavity. We used Vemco V9P-2L (47 mm long, 6.3 g in the air, 90 s mean burst interval, mean battery life 385 days) or V8-4L (20.5 mm long, 2 g in the air, 90 s mean burst interval, mean battery life 163 days) acoustic transmitters. The transmitter weight in the air did not exceed 2% of the fish body weight (Winter, 1983). The incision was closed using 2 to 3 simple surgical sutures (3-0 Polydioxanone Ethicon monofilament Ltd.) placed 5 mm apart. An antiseptic and antibiotic cream (Fucidine 2%) was applied on the incision wound to help healing and limit the risk of infection. The surgical procedure took 5 to 6 min. The same person always carried out the surgery. Fishes were then put in an aerated recovery tank, where they were continually observed until the opercular activity, swimming ability, balance and behavioural reponse to stimuli became normal again, usually after 10 min. Then, in a couple of minutes, they were transferred to a net set in the lake

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where they spent 6 to 12 hours. Lastly, they were transported by boat within half an hour in an aerated tank back to their capture site to be released.

Fish tracking

An array of 40 underwater VR2W 69kHz omnidirectional acoustic receivers (Vemco) with their associated synchronization tag (V13-1L) was anchored at the bottom throughout the reservoir from January 2012 until March 2014 (Figure IV.A.1). Eight additional synchronization tags were settled in the reservoir to detect anomalies in the tracking system. On average, neighboring receivers were positioned 150 m from each other (range, 72-223 m), 6 m deep (range, 2-15 m) (Roy et al., 2014). Roughly every 6 months, receivers were removed from the lake to download fish detections. Fish positions were calculated by Vemco with their Vemco Positioning System (VPS) algorithm (Smith, 2013). The horizontal position error, a dimensionless parameter calculated by the VPS for each position that gives information on the quality of the position estimate, was used to filter the data set (Espinoza et al., 2011a). In this study, we followed the recommendations of Roy et al. (2014) for the same system and only positions with horizontal position error not exceeding 15 were retained; this limit represented a good compromise between the mean position error (3.3 m throughout the reservoir) and the percentage of positions kept (79%) (see Roy et al., 2014 for detailed calculations of these error and percentage). Moreover, the probability of location map, estimated by Roy et al. (2014), showed that some parts of the lake were not well sampled, all located at the ends of the lake or on the shore. In parallel, in some of these areas very few locations were recorded. Not to introduce biases, we then removed from our study areas where the probability of location was below 2.5%; this threshold appeared as a good compromise between the representativeness of the sampling and the number of removed positions. So as not to include positions affected by behavioural modification following the surgery, only the positions recorded at least 2 days after release were included in the analyses (Bridger & Booth, 2003; Vehanen & Lahti, 2003). Some fish were already tagged in March 2012 but a problem of receiver memory saturation only fixed on late June 2012 caused the loss of data; the same problem caused the loss of data from August to October 2012. The downloading of receivers led to an interruption of the tracking for a few days in May 2013. In early October 2013, due to a sharp lowering of the WL for dam inspection, receivers were again downloaded and the experiment interrupted as the shallowest receivers

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could be dewatered; the interruption lasted till late November as the receivers could not have been put back into water sooner because of extended unavailability of divers and staff.

In the end, among the 29 perch initially tagged, 2 stationary fish were supposed to be dead rapidly after release, and 6 other, sparsely located from a few days to a few weeks, were then never located. These 8 individuals were omitted from the analyses. Hence, 21 adult perch, 320 to 486 mm long (Table IV.A.1), corresponding to 12-18 individuals depending on the season, were followed. The time series of their positions used in this study are represented on Suppl. Mat. IV.A.1.

Data analysis

We first define several terms used in the following. The use of an habitat is the quantity that is utilized by perch; the availability of an habitat is the quantity accessible to the perch; the selection of an habitat is the process in which perch choose an habitat and preference is a reflection of the likelihood that perch choose an habitat if offered on an equal basis to others (Johnson, 1980). Habitat availability, use, selection and preference were evaluated at the reservoir scale as most of the individuals used the whole reservoir (Suppl. Mat. IV.A.2).

Habitat description and availability

Based on the Secchi transparency depth, ranging from 1.3 to 2.5 m, we defined the littoral area of the reservoir as the lake area connected to the bank with a depth lower than 2.5 m. The substrate types observed in the Bariousses were silt, sand, gravel, pebble, stone, boulder and rock; at high WL, lawn was also present thanks to flooded grasslands. Other available habitats were tree stumps, coming from tree felling at the time of the impounding, emerging trees i.e. living shrubs or trees with roots and trunk in the water at least in some periods, helophytes and undercut banks. The last two categories were very scarcely present and thus not used further in the study. Thus the different available habitats were characterized by four variables: depth (7 classes: [0; 2.5[, [2.5; 5[, [5; 7.5[, [7.5; 10[, [10; 12.5[, [12.5; 15[and [15; 22[m) and, in the littoral zone, main substrate, emerging trees and tree stumps.

All the habitats listed above were mapped on October 2013 by visual observation all around the lake when the WL was 507.5m. Dewatered habitats between 513.5m and 507.5m were

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described as well as those down to 506.5m thanks to the water transparency. For each habitat variable, homogeneous polygonal areas were delimited with a differential GPS (Leica 1200®) and the habitat map was discretized in $10 \times 10 \text{ m}^2$ squares. In each grid square, for each habitat variable the habitat type which was selected was the one that covered more than 50% of the square. The mean square depth was used for depth. All habitats were mapped with ArcGis 10.0.

The relative availability of habitat type i , π_i , was defined as the ratio of the number of grid squares with habitat type i on the total number C of $10 \times 10 \text{ m}^2$ grid squares in the study area (the whole lake if the considered habitat is depth, the littoral area for other habitat variables) at the considered WL. The different available habitats of the lake were quantified at low, mean and high WL. For each hourly WL of the study period and each habitat variable, the relative availability of each habitat type was estimated. Mean and standard deviation of these relative availabilities were calculated in grouping the data by the three WL classes.

Environmental variables impacting habitat preference

For each fish position, the used habitat corresponded to the habitat of the grid square in which the fish was. The number of positions in a grid square was corrected with the probability of location in this grid square, estimated by Roy et al. (2014), to minimize the spatial variability of the sampling inherent to a telemetry system. The proportion of each type was calculated for each habitat variable.

The corrected number of positions of fish j in habitat type i is then given by:

$$u_{ij} = \sum_{c=1}^C \frac{n_{ij}^c}{p_c}$$

where n_{ij}^c is the number of positions of fish j in the grid square c containing the habitat type i and p_c the probability for a tagged fish present in the grid square c to be located (see Roy et al 2014 for more details).

The corrected number of positions of fish j in all classes of habitat type i ($1, \dots, I$) is :

$$u_{+j} = \sum_{i=1}^I u_{ij}$$

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where I is the number of types in the considered habitat variable (for example, the “main substrate” habitat variable contains 8 types).

The relative use of habitat type i by fish j is the ratio of u_{ij} on u_{+j} .

The selection ratios were then used to quantify the habitat preference (Manly et al., 2002). For individual j and habitat type i , the selection ratio is as follows:

$$\hat{w}_{ij} = \frac{u_{ij}/u_{+j}}{\pi_i}$$

For each habitat variable, the effects of habitat type, season, WL and two-way interactions on perch individual selection ratios were explored using generalized additive mixed-effects models (GAMM) (Zuur et al., 2009). The fish identity was considered as a random effect to explicitly account for individual heterogeneity. To take into account the skewed distribution of individual selection ratios towards zero, a Tweedie family function with a log-link was used (Gilman et al., 2012). As water temperature regimes were very similar over the 2-year study period (Table IV.A.1), data from the same seasons of different years were merged.

For one habitat variable, the full model could be written as follows:

$$\log(\overline{SR}_{ind}) = \alpha + HAB + SEASON + WL + HAB:SEASON + HAB:WL + WL:SEASON + s(ind) + \varepsilon$$

where \overline{SR}_{ind} is the expected mean individual selection ratio, strictly positive; α is the overall intercept; HAB is the habitat variable (depth, main substrate, emerging trees, tree stumps) split into different types corresponding to the variable classes; SEASON is the season (four classes, Table IV.A.1); WL is the water level (three classes, Figure IV.A.2); $s(ind)$ is a smoothing function modeling the individual effects (Wood, 2008) having the advantage to get a significance test of these effects and an evaluation of the explained deviance of the model; and ε is the error term following a normal distribution with zero mean.

For each habitat variable, the most parsimonious simple model was selected by running a forward stepwise-based procedure (Venables & Ripley, 2002) and applying the recommendations of Richards (2008): all models having an AIC value within a range of 6 from the lowest AIC value were initially selected and, among them, the more complex models that

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did not have an AIC value lower than all the simpler models within which they were nested were removed.

The model fitting was assessed with regards to the homogeneity and normality of the residuals (Zuur et al., 2009) and to the percentage of explained deviance (Hastie & Tibshirani, 1990).

Habitat use and preference

For each of the habitat variables, habitat use and preference were explored according to those of the environmental variables that had significant effects in the GAMM.

The compositional analysis as proposed by Aebischer et al. (1993) was applied on each habitat variable to test for habitat selection and to investigate habitat use. For each habitat variable, this analysis tests with a Wilk's lambda if the different habitat types are used more or less than expected from their availability and ranks the habitat types in order of use by comparing them two by two. For each habitat variable, the compositional analysis was also used to test for the significance of the use of each habitat type compared to all other combined.

Although the aforementioned analysis (Aebischer et al., 1993) allows testing the significance of the relative habitat use and the occurrence of habitat selection, no absolute preference per habitat type is calculated (Pauwels et al., 2016). Therefore, we calculated selection ratios for the pool of individuals, hereafter called mean selection ratios, and their associated Bonferroni-adjusted 95% confidence intervals as proposed by Manly et al. (2002).

The mean selection ratio is given by:

$$\hat{w}_i = \frac{u_{i+}/u_{++}}{\pi_i}$$

where

u_{i+} is the corrected number of positions of all fish in habitat type i ,

$$u_{i+} = \sum_{j=1}^n u_{ij}$$

with n the total number of fish, and

u_{++} is the corrected total number of positions

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$$u_{++} = \sum_{i=1}^I u_{i+}$$

The variance of \hat{w}_i is estimated as:

$$\text{var}(\hat{w}_i) = \frac{1}{u_{++}^2} \frac{n}{n-1} \sum_{j=1}^n \left(\frac{u_{ij}}{\pi_i} - \hat{w}_i u_{+j} \right)^2$$

Simultaneous Bonferroni confidence intervals for mean selection ratios can then be constructed with an overall confidence level of $100(1-\alpha)\%$, so that the probability of all the intervals containing the true value is $1 - \alpha$. These intervals are of the form

$$\hat{w}_i \pm z_{\alpha/2I} \sqrt{\text{var}(\hat{w}_i)}$$

where $z_{\alpha/2I}$ is the value exceeded with probability $\alpha/2I$ by a standard normal random variable.

The mean selection ratio pools observations from all fish in the sample, but the confidence interval takes the variation in resource selection from individual to individual into account (Manly et al., 2002). When a selection ratio and accompanying confidence interval is higher than 1.0, habitat preference is considered significant (Manly et al., 2002; Rogers & White, 2007).

Compositional analysis and selection ratios were generated in R 3.0.1 (R Core Team, 2013) using `adehabitatHS` package (Calenge, 2006). GAMM were implemented using the `mgcv` package (Wood, 2006).

Methodological considerations

We can mention that the pool of individuals was not strictly the same from one season to another but we took this into account both in the GAMM, by modelling individual effects, and in the confidence interval of mean selection ratios. By construction, the habitat use analysis also considers this.

We also paid great attention to the crucial step of telemetry experiment design (Kessel et al., 2014; Steel et al., 2014) and evaluated its performance (Roy et al., 2014) as recommended by Biesinger et al. (2013). The spatial variability of the performance was assessed in a prior study (Roy et al., 2014): the performance (positioning error and probability to get a position) was

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lower in the littoral zone than in the pelagic one. At least two reasons can explain this: firstly, the littoral zone is a structurally complex zone what has been shown to affect the system performance in terms of detection and error (Baktoft et al., 2015); secondly, by construction of the receiver network, the littoral zone is mainly outside this network whereas the pelagic one is inside and the VPS theory tells that the performance of the system is lower outside the network (Smith, 2013). Hence, we brought a correction to smooth this artificial spatial variability by using the probabilities of positioning calculated by Roy et al. (2014) in winter when the mixing of water was complete. In addition, the performance of a system can vary in time due to the modifications of the thermocline gradient and thermocline depth (Huveneers et al., 2016). We checked this over the 40 synchronizing tags and eight reference tags and no strong seasonal pattern of detection was found in this reservoir making our positioning adequate to study seasonal variability of habitat preferences.

Results

WL influence on habitat availability

When the WL rose, the relative availability of the littoral area ($[0, 2.5[m$) dropped from 19.5% at low level to 13.3% at high level (Figure IV.A.3a). These proportions, applied to the mean lake area at the different WL, also showed that the surface of the littoral area diminished when the WL rose. In the littoral zone, the relative availabilities of stone and boulder/rock were quite low (less than 10%) and little influenced by WL (Figure IV.A.3b). Similarly, the relative availability of tree stumps was not strongly impacted by WL and remained stable around 20% (Figure IV.A.3d). On the contrary, the WL influenced the relative availability of finer substrates and lawn (Figure IV.A.3b). The relative availability of silt prevailed at the lowest WL and dropped rapidly when the WL rose; conversely, the relative availability of gravel/pebble and lawn (class almost not present at low WL) increased with increasing WL to reach 19.5 and 27.6% respectively, whereas the relative availability of sand peaked at the mean WL (Figure IV.A.3b). The relative availability of emerging trees increased with increasing WL, roughly from 18.9% at low WL to 59.6% at high WL (Figure IV.A.3c).

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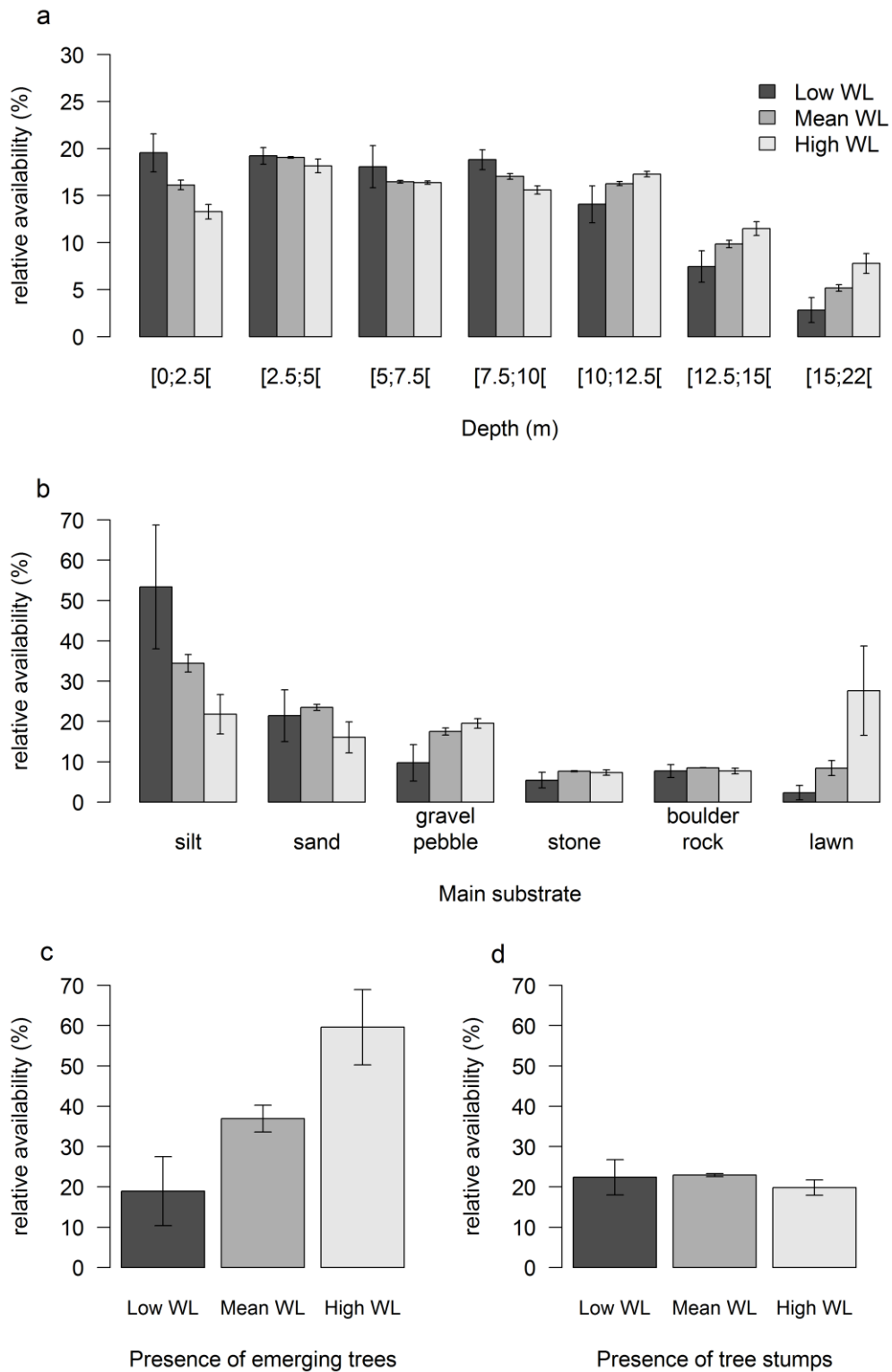


Fig. IV.A.3 Relative availability (%) of the different habitat types at low, mean and high water levels: (a) the depth classes, (b) the main substrate types, (c) the presence of emerging trees and (d) the presence of tree stumps. The error bar represents two standard deviations

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Which variables influence perch habitat preference ?

Depth selection ratios were the best modelled with 44.4% of the deviance explained (Table IV.A.2). This model showed that perch preferences were different between depth classes and influenced by the season with individual variability. The WL did not impact significantly the depth preferences. The models selected for tree stumps and emerging trees selection ratios explained respectively 33.4% and 24.3% of the deviance (Table IV.A.2) without significant individual differences. Perch preference for tree stumps and emerging trees had a significant seasonal component but was not influenced by WL. Main substrate selection ratios were the most poorly modelled with only 11.2% of deviance explained by the selected model in which neither the season nor the WL had a significant effect. The individual variability was not significant.

Table IV.A.2 Numeric results from the selected GAMM for each habitat variable. Pres/abs stands for presence/absence for both emerging trees and tree stumps

	Depth		
	d.f.	F	p-value
Depth class	6	42.17	< 2e-16
Season	3	11.24	3.07e-07
Depth:Season	18	7.72	< 2e-16
s(ind)	11.67	2.47	2.79e-8
Deviance explained (%)	44.4		

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Main substrate			
	d.f.	F	p-value
Substrate type	5	20.01	< 2e-16
Deviance explained (%)	11.2		
Emerging trees			
	d.f.	F	p-value
Pres/abs	1	50.000	2.52e-11
Season	3	3.293	0.0216
Pres/abs:Season	3	8.011	4.55e-05
Deviance explained (%)	24.3		
Tree stumps			
	d.f.	F	p-value
Pres/abs	1	44.864	2.09e-10
Season	3	6.258	0.000442
Pres/abs:Season	3	6.091	0.000550
Deviance explained (%)	33.4		

Depth use and preference

The selection of depth occurred in the four seasons. Whatever the season, perch used the [2.5, 5[m zone the most, significantly in spring, summer and autumn (Table IV.A.3). In spring and

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summer, the littoral zone use ranked second and was significantly more used than other depths only in summer whereas in autumn and winter the [5, 7.5[m depth ranked second. In autumn and winter, the littoral zone use only ranked four.

In spring and summer, perch preferred littoral and [2.5, 5[m zones (Figure IV.A.4a), in good agreement with the high use of these depths (Table IV.A.3). In autumn, perch preferred the [2.5, 5[m zone and tended to prefer the [5, 7.5[m depth, again in line with the high use of these depths, whereas they tended to avoid the littoral zone and avoided all other depths. In winter the littoral zone was avoided and areas between 2.5 and 10 m deep tended to be preferred, and also more used. Over the four seasons, the areas deeper than 10 m were avoided or rarely explored by perch, except by some individuals in the winter.

Table IV.A.3 Results of the compositional analysis (Aebischer et al., 1993) for each habitat variable (depth, main substrate, emerging trees, tree stumps). The habitat types are ranked from more used (top) to less used (bottom) and bold text indicates significance of the use of one habitat type compared to all other combined. The Wilk's lambda statistics is given with its associated 95% p-value which is in bold type when the habitat selection is significant

Depth (m)			
Spring	Summer	Autumn	Winter
[2.5, 5[[2.5, 5[[2.5, 5[[2.5, 5[
[0, 2.5[[0, 2.5[[5, 7.5[[5, 7.5[
[5, 7.5[[5, 7.5[[7.5, 10[[7.5, 10[
[7.5, 10[[7.5, 10[[0, 2.5[[0, 2.5[
[10, 12.5[[15, 22[[15, 22[[10, 12.5[
[15, 22[[10, 12.5[[10, 12.5[[12.5, 15[
[12.5, 15[[12.5, 15[[12.5, 15[[15, 22[
Lambda = 0.1040	Lambda = 0.0963	Lambda = 0.1102	Lambda = 0.1323
p-value = 0.0040	p-value = 0.0020	p-value = 0.0020	p-value = 0.0280

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Main Substrate			
Boulder/Rock			
Stone			
Sand			
Silt			
Lawn			
Gravel/Pebble			
Lambda = 0.3629			
p-value = 0.0040			
Emerging trees			
Spring	Summer	Autumn	Winter
Presence	Presence	Absence	Presence
Absence	Absence	Presence	Absence
Lambda = 0.1980	Lambda = 0.7851	Lambda = 0.9761	Lambda = 0.7527
p-value = 0.0040	p-value = 0.0460	p-value = 0.5480	p-value = 0.0940
Tree stumps			
Spring	Summer	Autumn	Winter
Presence	Presence	Absence	Presence
Absence	Absence	Presence	Absence
Lambda = 0.5471	Lambda = 0.7098	Lambda = 0.9984	Lambda = 0.8566
p-value = 0.0320	p-value = 0.0180	p-value = 0.9060	p-value = 0.1840

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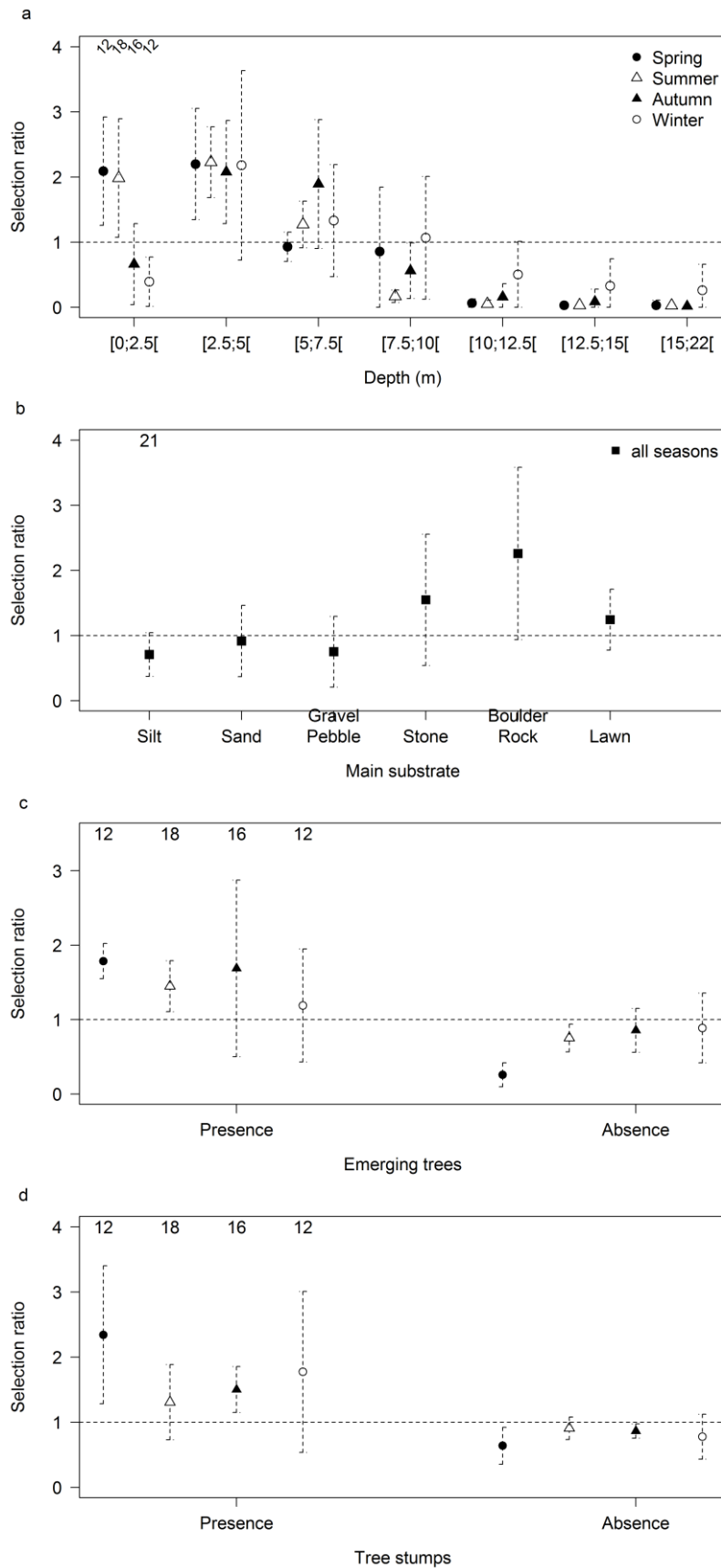


Fig. IV.A.4 Perch mean selection ratios of (a) depth and, in the littoral zone, of (b) the main substrate, (c) emerging trees and (d) tree stumps. The sample of perch used is given in the upper left corner. The 95% Bonferroni confidence intervals (vertical dashed bars) of the selection ratios are represented. The 1 threshold value, corresponding to “no preference,” is represented by a horizontal dashed line

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Use and preference of littoral habitats

Perch selected the littoral substrate (Table IV.A.3). In the littoral zone, boulder/rock was significantly the most used substrate type, followed by stone and sand which were not significantly more used than other substrates (Table IV.A.3). In line with their high use, boulder/rock and stone tended to be preferred (Figure IV.A.4b), as lawn although ranked second last regarding its relative use (Table IV.A.3). Perch tended to avoid finer substrates (silt, sand, and gravel/pebble) (Figure IV.A.4b). However, no preference/avoidance was significant due to a high individual variability, highlighted by large confidence intervals, especially for stone and boulder/rock.

Perch selected littoral zones with emerging trees in spring and summer; they were significantly more used than those without in these both seasons and also in winter (Table IV.A.3) but preferred only in spring and summer (Figure IV.A.4c). In autumn and winter, perch also tended to prefer them but the individual variability was high (Figure IV.A.4c).

The tree stumps were also selected in spring and summer and significantly more used (Table IV.A.3). Not completely in line with the habitat use analysis, they were preferred in spring and autumn and only tended to be in summer and winter, with a very high individual variability in spring and winter (Figure IV.A.4d).

Discussion

Variability of habitat availability with WL

Using a precise qualitative and quantitative description of the different habitats, we highlighted an influence of WL on the structure of the available littoral habitats of the Bariousses reservoir: they tended to become more homogeneous with a lowering structural complexity when the WL dropped. These results, based on the entire lake, are in agreement with other studies (Gasith & Gafny, 1990; Gasith & Gafny, 1998), and mean that lowering WL correspond to fewer refuge areas and probably fewer food resources for perch (Zohary & Ostrovsky, 2011; Zohary & Gasith, 2014). They also confirmed the trends observed by Logez et al. (2016) with a point sampling on the same lake, but brought additional information as the stable availability of littoral tree stumps with WL and the rise of the relative availability and surface of the littoral area when the WL dropped. The highest diversity of habitats was observed in spring, which

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corresponds to the perch spawning period, while the lowest diversity was noted in autumn. It was intermediate almost throughout the summer when WLF were very limited around the mean WL, and very contrasted in winter when WL were quite evenly distributed between low, mean and high classes.

Influence of WL on habitat preference

WLF directly impacted the relative availability of the different littoral habitats; however we did not observe any significant effect of WL on the habitat preference of adult perch. This suggests that the preference of littoral habitats remained the same whatever their availability, in the ranges and timing encountered in this reservoir. The scarcity of some preferred resources probably did not reach any critical threshold. Low WL were the most frequent in autumn and winter and corresponded to the highest relative availability of the littoral zone which was however much less used in these two seasons than in spring and summer.

In the same reservoir in summer and autumn, Logez et al. (2016) observed that the littoral fish assemblages, composed of juveniles and adults, were dependent on the WL and tended to homogenize when the habitat complexity lowered, suggesting variations in habitat use when its availability changed, even if adults seemed to be the less affected. Considering the advantages of the littoral zone for fish fauna (Schiemer et al., 1995; Schmieder, 2004; Lewin et al., 2014) and the importance of the habitats impacted by WLF for perch (Imbrock et al., 1996; Zamora & Moreno-Amich, 2002; Pekcan-Hekim et al., 2005; Čech et al., 2009; Muska et al., 2013), we expected some changes in the habitat preferences at different WL. As shown on some terrestrial species, variations in habitat availability can lead to changes in habitat preferences (Godvik et al., 2009; Hansen et al., 2009; Pellerin et al., 2010). With the loss of some emerging trees and boulder/rock habitat types when the WL dropped, we could have expected a higher attractiveness of tree stumps, whose availability remained stable, for feeding and spawning. In the Bariousses reservoir, the temporal scales of WLF (days) mainly changed the habitat availability without imposing great physical stress on organisms living in the littoral zone as short term WLF would (Hofmann et al., 2008). Moreover, the relative availability and surface of the littoral area rose when the WL dropped, which could mitigate the effects of the WLF. Above all, the relative availability of the complex preferred habitats by adult perch was the highest in spring and summer, respectively the period of spawning (Craig, 2000) and of highest

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activity (Jacobsen et al., 2002), when this type of habitat is the most required regarding perch ecology. In autumn and winter, when food requirements lessen because perch activity is reduced (Jacobsen et al., 2002), perch could cope with a limited availability of complex habitats. Aside this uneven distribution of WL between seasons, the lack of a net effect of WL on adult perch habitat preferences can also be related to their plastic nature regarding the environment (Craig, 2000). Besides, Čech et al. (2012b) have shown that, being able to spawn at various depths depending on the period and temperature, perch have evolved a mechanism to cope with a large spectrum of conditions.

Individual variability

Finally, even if the individual effect was globally significant only for depth selection, high individual variability, quantified by the confidence interval length of selection ratios, was observed on numerous habitat types. It is however important to emphasize that no link appeared between the individual variability and the number of individuals used in the sample. Regarding the substrates, the individual variability was very high especially for the most complex ones what could be linked to their relatively reduced availability in this reservoir.

Such variability is frequent among fish (Magurran, 1993) and contributes to the population adaptation to rapid changes in the environment. This variability could reflect different strategies adopted by perch, possibly related to sex-specific responses to environmental changes (Estlander et al., 2015) or to predation risk (Estlander & Nurminen, 2014) that also exists even if limited on these large individuals, as well as to the existence of different fish personalities in the population, for example bold or shy individuals, which have been shown to forage or manage the predation risk differently (Kekalainen et al., 2014; Harkonen et al., 2016). Unfortunately, despite the surgical operation, the gender of perch was seldom determined because the smallest possible incision was favored to provide the greatest chance of full healing.

Seasonal pattern of habitat use and preference

The high use of and preference for the shallow zones of the reservoir ([0, 5[m in depth) in spring and summer shown with high-resolution individual tracking are in agreement with previous conclusions obtained with fishing data (Craig, 1977; Muska et al., 2013). They also confirm

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results obtained with a comparable approach implemented in another temperate lake (Zamora & Moreno-Amich, 2002). However, even if these shallow zones were highly used and preferred, the individual variability was also significant. In stratified reservoirs, fish are usually distributed in the surface waters due to the attraction of warmer temperatures in spring and to avoid deoxygenated hypolimnion in summer (Kubečka & Wittingerova, 1998). What is more, the preference for shallow depths by adult perch could be related to the numerous juveniles of different fish species that live in this sheltered area and that provide food (Degiorgi & Grandmottet, 1993; Stoll et al., 2008) and, in spring, also to the search for spawning support (Čech et al., 2009). Emerging trees and tree stumps, which are rigid, structurally complex and strongly used and preferred in spring, correlate to the type of spawning substrate sought by perch (Gillet & Dubois, 1995; Čech et al., 2009; Snickars et al., 2010). This preference for complex habitats observed throughout the year for the substrate type and to a lesser extent in summer for emerging trees and tree stumps can probably be related to feeding given that they can shelter macro-invertebrates and fish (Czarnecka et al., 2014). With the beginning of autumnal mixing the perch migrated into slightly deeper waters as already described (Craig, 1977; Imbrock et al., 1996). We showed that, in the Bariousses reservoir, the most used and preferred depths shifted to [2.5, 7.5[m in autumn and winter. The low use of the littoral zone in these seasons was accompanied by a decrease of the attractiveness of emerging trees and tree stumps. Regarding the preferences, some exceptions could appear in winter, when littoral zones with emerging trees were still significantly more used than those without (Table IV.A.3) or in autumn, when the compositional analysis did not see any significant use or selection of tree stumps (Table IV.A.3) whereas the selection ratios showed a significant preference (Figure IV.A.4d). In this last case, the significance was however not very strong and a small variation in the sample could probably have led to a non significant result, especially as the availability of emerging trees was the lowest in autumn.

Such studies would be worth conducting on different species to improve knowledge of the impacts of human induced WLF in reservoirs. Even if we did not show any effect of WLF on adult perch habitat preference, they could act differently on other species such as pike, a more demanding species in terms of spawning substrate (Craig, 2008). Very recently, Cooke et al. (2016) submitted that: “quantifying and describing the spatial ecology of fish and their habitat is an important component of freshwater fishery assessment and management”. Fish habitat requirement is the basis for rehabilitation (Müller & Stadelmann, 2004; Cooke et al., 2016) and

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could help to adapt hydraulic management to efficiently preserve fish populations. Operational tools to quantify human influence (through hydraulic management, stocking, recreational use) and environmental drivers (temperature, water quality) on fish populations in reservoirs still remain scarce. In environments where the littoral zone is altered, hydromorphological rehabilitation programs are often implemented (Gonzalez et al., 2015). Any study that could provide insight into the impact of a hydromorphological restoration on the fish population is valuable (e.g. Boromisza et al., 2014; Rose et al., 2015), including species-habitat preference studies.

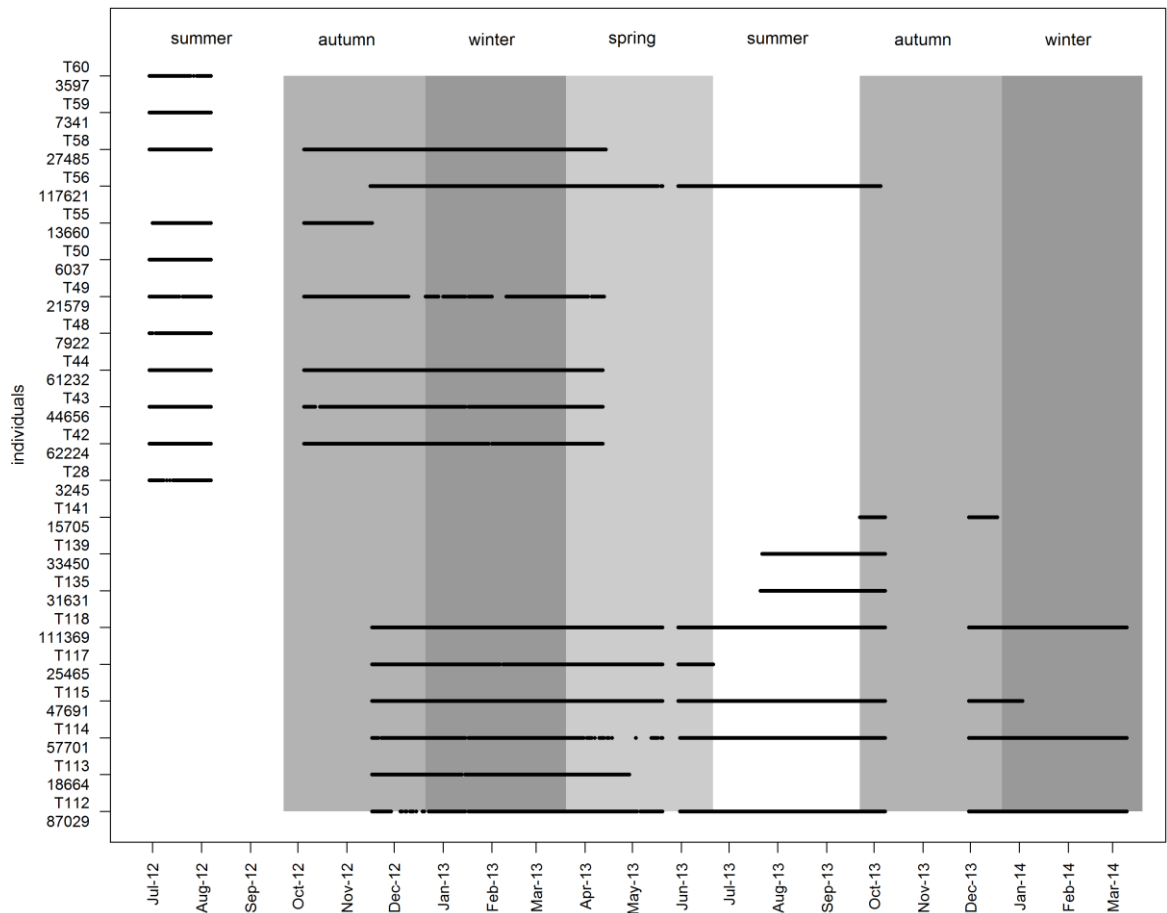
In conclusion, our study indicated that large perch selected zones at different depths in the reservoir mainly according to seasons without any effect of WL. In spring and summer, they highly used and preferred the littoral zone and the complex habitats it hosts, independently of the WL, even if the structural complexity of the littoral zone was reduced when the WL lowered. In autumn and winter they migrated to deeper zones. Our results also highlighted quite a high individual variability in the habitat preferences. This study contributes to the understanding of the spatial ecology of fish, which is essential to leading efficient management actions (Cooke et al., 2016). Based on these findings, even if WLF were shown not to impact perch habitat preferences, we can propose the following management actions to prevent eggs from being dewatered: in spring, to keep the WL stable at mean or high level or at least to avoid sharp lowering of WL from mid-April, the likely start of the spawning season, to mid-June when the majority of eggs have hatched; to add spawning substrates, woody structures for example, at mean and low WL to encourage perch to spawn deeper.

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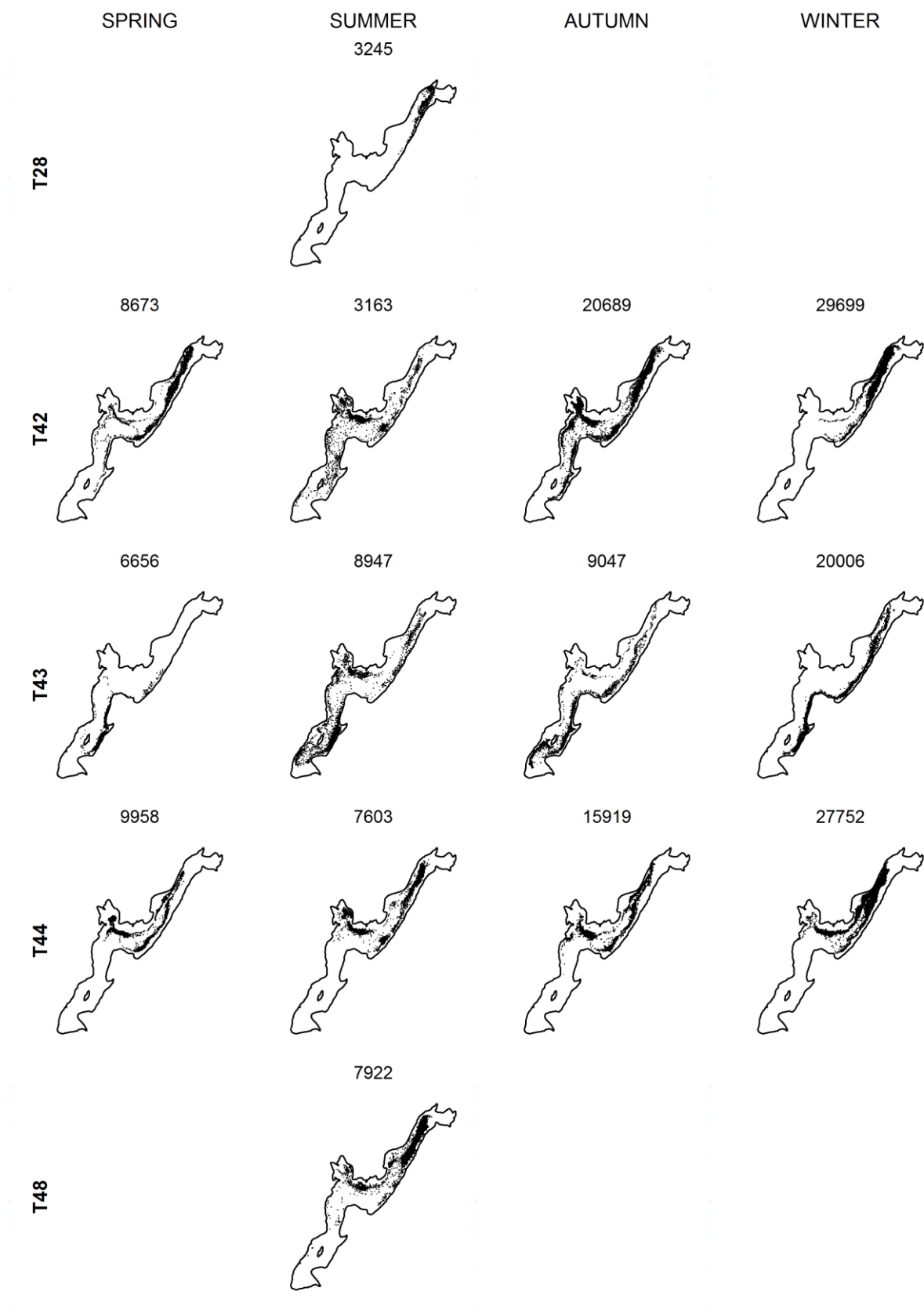
IV.A Impact of environmental conditions (seasons, water levels) on the habitat niche of a population of freshwater predators

4. *Supplementary materials*

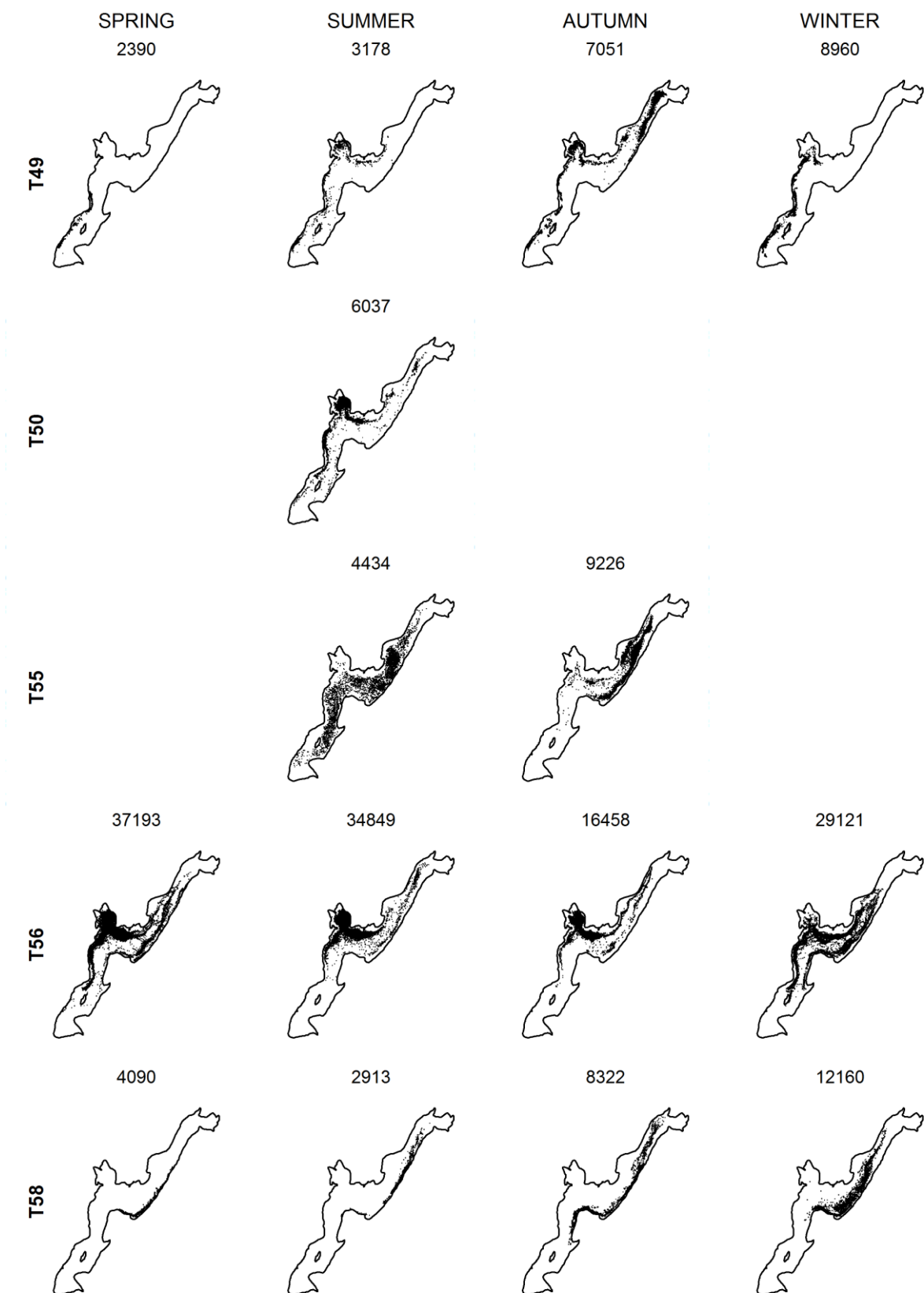


Suppl. Mat. IV.A.1 Time series of the positions of the 21 perch used in this study with their ID and corresponding number of positions labelled on the y-axis

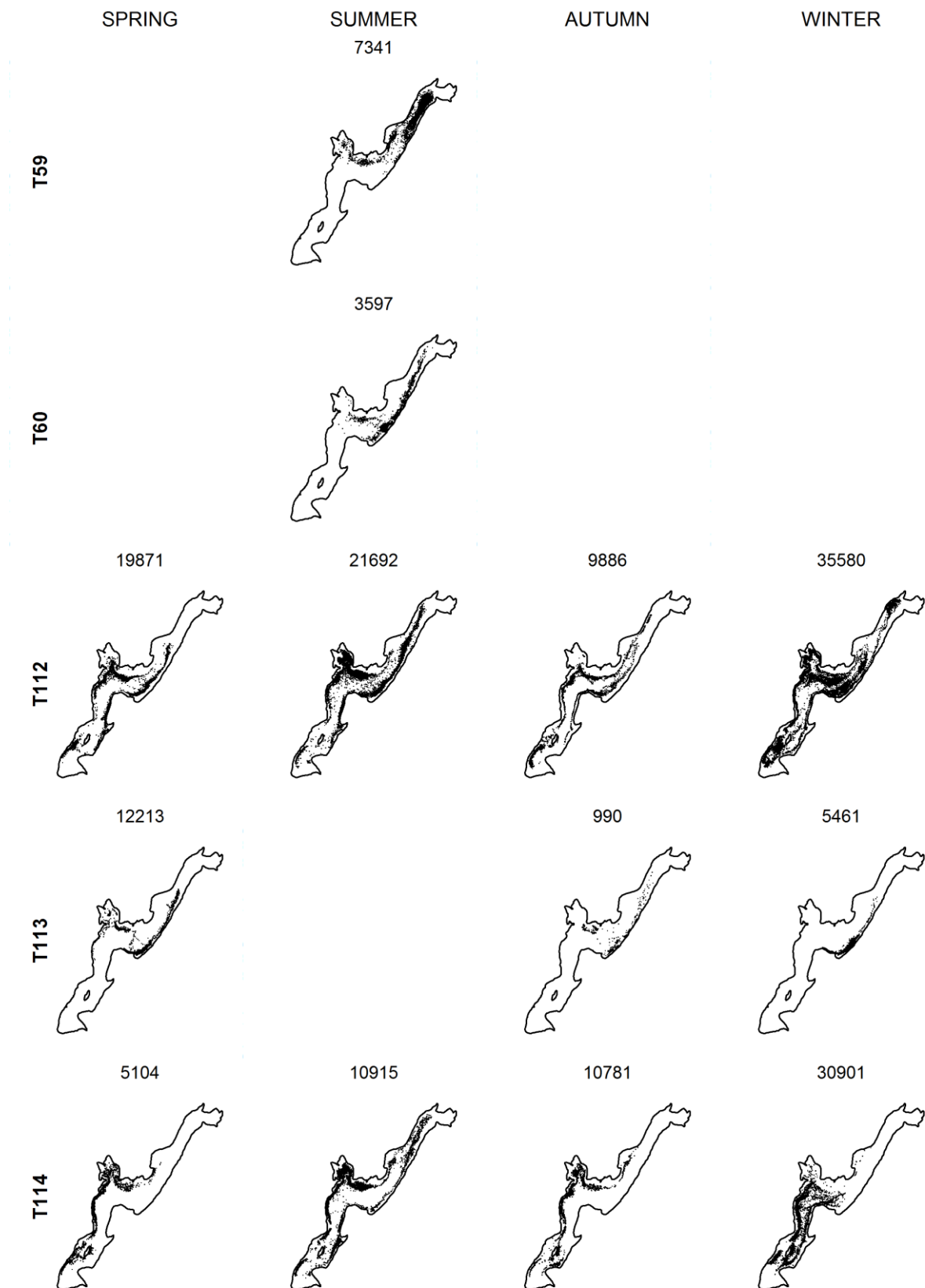
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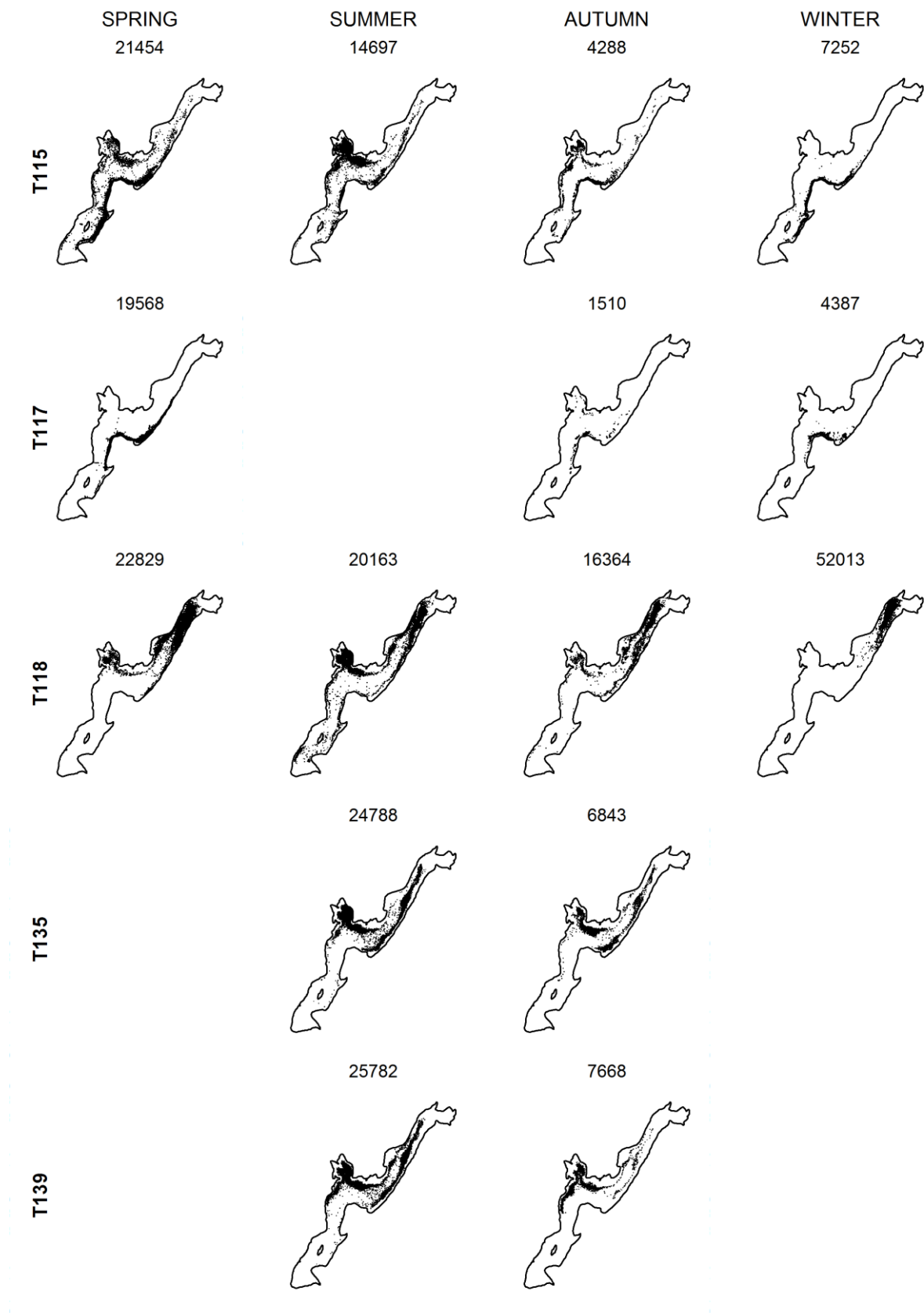
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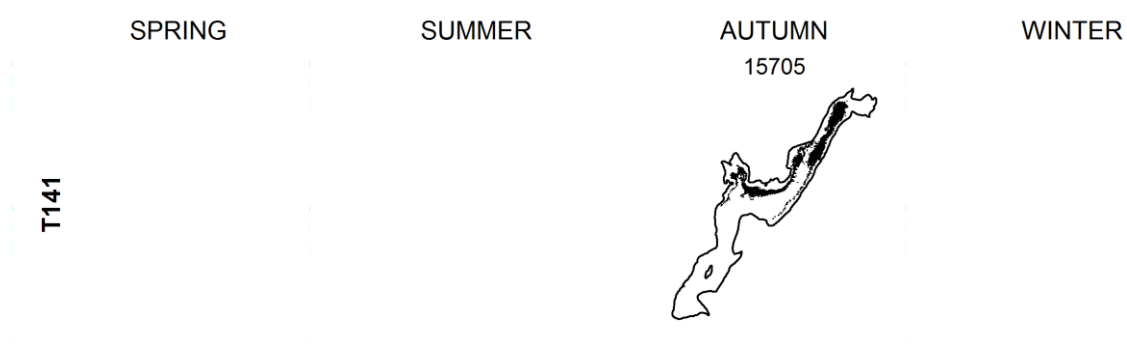
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Suppl. Mat. IV.A.2 Seasonal map and corresponding number of positions of the 21 perch used in this study

IV.B

Impact of winter conditions on the
habitat niche of a population of
freshwater predators

B. Overwintering aggregation patterns of a freshwater giant

1. *Synthesis (English)*

By their associated environmental changes, seasons drive habitat shifts in fish. The winter period imposes a thermal stress on fish as cold temperatures can drop far below their physiological optimum. This is the case for catfish that prefer relatively warm temperatures, typically above 20 °C. To evaluate the impact of this thermal stress on their habitat niche, we tracked 47 subadult and adult catfish (total size range [727; 2150] mm) over four years in “Etang des Aulnes” where water temperatures can drop down to 4 °C in winter. We then analyzed their movements over four winters (2017 to 2020). By synchronizing individual tracks and displaying them all together in a video, we highlighted an aggregative behavior every winter. We then investigated the dynamics of this aggregation (formation, stability, dislocation), and the factors that could govern it, either external (temperature, time of the day) or specific to the fish (size, key individuals), by implementing time series analysis and Cox proportional hazard models. The aggregation lasted 1.5 to 2 months and mainly took place in the same small 4 m-deep area, which did not constitute the deepest area (6 m-deep lake). In this area, the temperature, dissolved oxygen concentration and substrate did not differ from other parts of the lake. In some periods, all tagged fish were aggregated suggesting that a large proportion of the lake’s population gathered there. Low temperatures (below 9 °C) triggered the aggregation formation that became more stable with decreasing temperatures. When temperatures increased, individuals more often left the aggregation, preferentially at dusk and at night in agreement with their nocturnal activity. Interestingly, during the milder winter 2019, the aggregation was not as clustered as in other winters and was even split into two zones, including the common aggregation area. This strengthens the driving role of temperature on this behavior. The larger specimens more frequently moved to and from the aggregation, which could be linked to feeding to satisfy their higher metabolism associated with their larger body size. This huge grouping of individuals for such a long time possibly led to an enhanced competition for resources. This could be buffered by limited feeding activity in the cold season though. Irrespective of their size, some individuals consistently arrived at the aggregation early in the winter and left late which could mean that, in this long-lived species, some individuals seek for sociality while others are more independent. The fidelity to the same site enhances the non-random character of this aggregating behavior which is another argument for social interactions. In the end, this predictable seasonal grouping of individuals could provide an opportunity for

IV.B Impact of winter conditions on the habitat niche of a population of freshwater predators

lake managers to efficiently control catfish populations if needed, as concerns are often raised of the impact of this giant predator on other populations.

2. *Synthesis (French)*

Patrons d'agrégation hivernale d'un géant d'eau douce.

Par les changements environnementaux qui les caractérisent, les saisons s'accompagnent de changements d'habitat des poissons. L'hiver impose un stress thermique dans la mesure où les températures peuvent chuter bien en-deçà de leur optimum physiologique. C'est le cas du silure qui a un préférendum thermique relativement élevé, au-dessus de 20 °C. Pour évaluer l'impact de ce stress sur leur niche d'habitat, nous avons suivi les déplacements de 47 silures subadultes et adultes (longueur totale comprise entre 727 et 2150 mm) durant quatre années dans l'étang des Aulnes, où les températures peuvent chuter jusqu'à 4 °C en hiver. Nous avons ensuite analysé leurs mouvements au cours des quatre hivers (2017 à 2020). En synchronisant les trajectoires individuelles pour les visualiser simultanément sur une vidéo, nous avons mis en évidence un comportement d'agrégation qui avait lieu chaque hiver. Nous avons ensuite investigué la dynamique de cette agrégation (formation, stabilité, dislocation) et les facteurs qui la gouvernent, externes (température, phase de la journée) ou caractéristiques de l'individu (taille, individus clés), en mettant en œuvre des analyses de séries temporelles et des modèles de Cox. L'agrégation durait un mois et demi à deux mois, principalement en une même petite zone de 4 m de profondeur environ, l'étang atteignant 6 m de profondeur dans ses zones les plus profondes. Dans cette zone, la température, la concentration en oxygène dissous ainsi que le substrat ne différaient pas des autres zones de l'étang. A certains moments, tous les silures suivis étaient agrégés, suggérant ainsi qu'une large proportion de la population se rassemblait à cet endroit. Les températures basses (sous 9 °C) déclenchaient le processus de formation de l'agrégation, l'agrégation devenant de plus en plus stable avec la baisse des températures. Quand les températures augmentaient, les individus quittaient plus souvent l'agrégation, de préférence au crépuscule et la nuit, conformément à leur caractère nocturne. Durant l'hiver 2019 particulièrement doux, l'agrégation n'était pas aussi compacte que durant les autres hivers et était même répartie sur deux zones, incluant la zone régulière. Cela souligne le rôle moteur de la température sur ce comportement. Les plus grands specimens faisaient de plus fréquents allers-retours, ce qui peut être lié à une activité d'alimentation visant à satisfaire un métabolisme total plus élevé en lien avec leur grande taille. Ce rassemblement conséquent d'individus pendant une si longue période a potentiellement engendré une compétition accrue pour les

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ressources. Cela a cependant pu être tamponné par une activité d'alimentation plus limitée en saison froide. Indépendamment de leur taille, des individus arrivaient de façon consistante plus tôt sur le lieu d'agrégation et repartaient plus tard ; pour cette espèce qui a une longue durée de vie, cela pourrait être relié à une recherche de liens sociaux, alors que d'autres individus seraient plus indépendants. La fidélité à un site donné renforce l'hypothèse de liens sociaux. Pour finir, ce regroupement hivernal prévisible peut constituer une opportunité de régulation efficace de la population si besoin était, dans la mesure où ce grand prédateur suscite de nombreuses inquiétudes quant à son impact sur les populations sympatriques.

3. *Core paper*

Samuel Westrelin, Mathieu Moreau, Vincent Fourcassié & Frédéric Santoul. Overwintering aggregation patterns of a freshwater giant. In prep. for “Movement ecology” journal.

Abstract

Aggregations of animals, particularly large-bodied species, have always been both fascinating and questioning. Here we analysed the overwintering behaviour of European catfish, *Silurus glanis* Linnaeus, 1758, the largest freshwater fish in Europe. In tracking 47 subadults and adults (total length [727; 2150] mm) in the lake “Etang des Aulnes” (France, 104 ha, mean depth 3.8 m), we reported a consistent aggregative behaviour across four winters. By implementing time series analysis and Cox proportional hazard models, we investigated the dynamics of this aggregation (formation, stability, dislocation), and the factors that could govern it, either external (temperature, time of the day) or specific to the fish (size, key individuals). The aggregation lasted 1.5 - 2 months and mainly took place in one same small 4m-deep area whose environmental conditions (temperature, oxygen, substrate) did not differ from other parts of the lake. In some periods, all tagged fish were aggregated which suggests that a large proportion of the lake population gathered over there. Low temperatures (below 9 °C) triggered the aggregation formation that became more stable with decreasing temperatures, while individuals more often left the aggregation, preferentially during dusk and night, when temperatures increased. The larger specimens made more frequent back and forth to the aggregation. Irrespective to their size, some individuals consistently arrived early in the winter and left late the aggregation which could mean that some individuals seek for sociality while others are more independent. In the end, this predictable seasonal grouping of individuals could give the opportunity for lake managers to efficiently control catfish population if needed. The knowledge provided by such studies on how species use the space has important operational values and is as useful for species conservation as for species control.

Keywords: space use, fish behaviour, survival curves, *Silurus glanis*

Introduction

Aggregations of individuals are widespread in the animal kingdom and embrace a large range of sizes and time durations (Parrish & Edelstein-Keshet, 1999). Though they have been observed for a long time, they still remain striking and questioning for biologists (Krause & Ruxton, 2002). Aggregations are particularly common among fishes, both marine and freshwater, most of which form cohesive social groups at some stage of their life history (Pitcher, 1998). In fish, aggregations have been shown to bring numerous benefits, including protection from predators (Larsson, 2009; Herbert-Read et al., 2017), increased chance of mate encounter (Fox et al., 2015; Daly et al., 2019; Clevestine & Lowe, 2021), increased foraging efficiency (Day et al., 2001; Herbert-Read et al., 2016), reduction of energy expenditure (Hemelrijk et al., 2015; Marras et al., 2015), centralized information (Mourier et al., 2012), which should outweigh the costs among which within-group competition for resources (Webster & Hart, 2006) and exposure to parasites (Ward et al., 2005; Tobler & Schlupp, 2008). On the evolutionary time scale, aggregation behavior is thus expected to increase individual fitness (Heupel & Simpfendorfer, 2005).

Aggregations in fish range from relatively small shoals, usually in freshwater streams and lakes (e.g. Freeman & Grossman, 1992; Krause et al., 2000; Ward & Krause, 2001; Currie et al., 2021), to structured schools of up to hundred of thousands of individuals in marine systems (e.g. Weber et al., 2009). In most fish species, aggregations are stable over time (Sumpter, 2010) but for some others they can be transitory, for example when fish are attracted by aggregating devices (e.g. Moreno et al., 2016) or when they spawn (e.g. Penne & Pierce, 2008; Daly et al., 2019; Clevestine & Lowe, 2021).

In addition to spawning, for some species, temporary aggregations have been described for overwintering, a phase of fish's life during which individuals are exposed to a lot of stressors - starvation, thermal stress-, but which has been understudied (Thayer et al., 2017). In freshwaters, these wintering aggregations have long been described on the common carp *Cyprinus carpio* (Johnsen & Hasler, 1977; Pitcher, 1998; Penne & Pierce, 2008; Bajer et al., 2011; Vanovac et al., 2021) and more recently on another large and long-lived species, the lake sturgeon *Acipenser fulvescens*, the largest freshwater fish in North America (Thayer et al., 2017). Winter aggregations also occur on centrarchid fishes during the light phase of the day (Suski & Ridgway, 2009). However, it is still an understudied aspect of their ecology. One

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study reported aggregations in the European catfish *Silurus glanis* - 15 to 44 adults -, the largest European freshwater fish (Boulêtreau & Santoul, 2016). These aggregations occurred throughout the year at the same place in a large river (Boulêtreau et al., 2011). Brevé et al. (2014) observed such an aggregation of adults in a river section underneath boats, but just once. Yet, in a small shallow eutrophic lake, Vanovac et al. (2021) found that common carp were aggregating during winter while European catfish, the population of which came from stocked individuals, were not. European catfish has been reported to be a solitary forager (Carol et al., 2007), preferentially at night, and to expend more energy when in contact with conspecifics in preferred areas of habitat (Slavík & Horký, 2009), at least in its native range. Therefore, aggregations in European catfish warrant further work (Cucherousset et al., 2018).

While the ultimate causes of aggregations have been extensively studied and, in some cases, are well established, the proximate mechanisms underlying the formation and dislocation of aggregations have been less investigated (Tien et al., 2004). The transitory character of winter aggregations gives the opportunity to study their formation, stability and dislocation, as well as their triggering factors. Moreover, most studies on animal aggregations have dealt with collective coordinated behaviors emerging from interactions between individuals all considered equivalent (Sumpter, 2010). Yet, there is growing evidence that individual variability can play an important role in fish aggregation (Jolles et al., 2020) and the recent advances in high resolution tracking of individuals now provide tools to investigate its role in aggregation dynamics (Nathan et al., 2022).

In this paper, we present the results of an experiment in which 47 subadults and adults of the European catfish have been tracked by acoustic telemetry for four years in a 104-ha shallow eutrophic lake located in southeastern France. We focus on their overwintering behaviour by analysing their movements over four winters showing contrasted temperatures; every winter catfish showed an aggregative behaviour. We investigated its dynamics (formation, stability, dislocation), and the factors that could govern it, either external (temperature, time of the day) or specific to the fish (size, key individuals).

Materials and methods

Study site

“Etang des Aulnes” is a shallow natural lake, mean depth 3.8 m, maximum depth 6 m, 104 ha area, located in South-Eastern France in a protected natural area (Figure IV.B.1).

The fish assemblage, determined by fyke nets, fishing traps and electro fishing in October 2017, 2018 and 2019 was composed of 16 species. The most dominant species were common bream (*Abramis brama*, relative abundance 65%), European perch (*Perca fluviatilis*, 13%), pumpkinseed (*Lepomis gibbosus*, 8%), tench (*Tinca tinca*, 4%), pikeperch (*Sander lucioperca*, 4%), European catfish (*Silurus glanis*, 3%) and Northern pike (*Esox lucius*, 2%). In addition, two crayfishes were present: *Procambarus clarkii* and *Faxonius limosus*. Fishing is allowed but only during daytime from the eastern bank of the lake and no other activity is authorized.

Physical and chemical lake conditions

The “Etang des Aulnes” is eutrophic (see Westrelin et al., 2022 for chemical element concentrations). Hourly temperature profiles were recorded with HOBO data loggers U22 (0.2°C accuracy) at the deepest point in the lake (location 42 on Figure IV.B.1) and at different other locations among which points 5 and 38 which will be presented later on. During the winter period, temperatures are mainly homogenized in the water column; the characteristics of each winter are given in Table IV.B.1. At the deepest point in the lake, hourly profiles of dissolved oxygen concentration were also recorded with HOBO data loggers U26 (0.2 mg/L accuracy).

Fish tagging

The surgical procedure followed for fish tagging is detailed in Westrelin et al. (2022). Specifically, a total of 47 catfish, subadults and adults, were caught by fyke nets, angling or electrofishing over four sampling campaigns: 10, 32, 2 and 3, respectively in October 2017, 2018, 2019 and 2020. At the end of the 2018 and 2019 winters, respectively 2 and 3 tags were stationary and, consequently, the corresponding individuals were discarded from the analyses as they were supposed to be dead or to have expelled their tag. Vemco V13-1L acoustic transmitters (length: 30.5 mm, weight: 9.2 g in the air, mean battery life: 1825 days, mean burst

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interval: 180 s - range 120-240s - for the 12 used in 2017 and 320 s - range 260-380s - in 2018) were used. The transmitter weight in the air did not exceed 2% of the fish body weight (Winter, 1996; Snobl et al., 2015). The characteristics of the tracked fish are given in Table IV.B.1.

Fish tracking

52 underwater omnidirectional Vemco acoustic receivers (20 VR2W 69kHz and 32 VR2Tx 69kHz) with their associated synchronization tag (additional V16-1L transmitter for VR2W and built-in V16-like transmitter for VR2Tx, 500-700 s, used to correct for receiver internal clock drift) were anchored to the bottom of the lake in October 2017 (Figure IV.B.1). Seven reference tags (V13-1L, 840-960s) were added to detect anomalies in the tracking system. On average, neighboring receivers were positioned 155 m from each other (range, 100-209 m), in 3.9 m water depth (range, 1.5 - 6 m), 0.5 m above the bottom. Receivers were removed roughly every 6 months to download fish detections. From these detections, fish 2D positions were calculated with the Vemco Positioning System (VPS) (Smith, 2013). The horizontal position error, a dimensionless parameter calculated by the VPS for each position, gives information on the quality of the position estimate, and was used to filter the data set (Espinoza et al., 2011b). Here, we retained only positions with horizontal position error below 100; this limit represented a good compromise between the mean position error (7.4 m, calculated on reference tags) and the percentage of positions kept (87%).

Space use metrics

Fish were continuously tracked from October 2017. As our study focuses on the winter period, only the data recorded from the 15th of October to the 15th of March of the next year were analyzed. Individual raw positions were interpolated using the R package trajr (McLean & Skowron Volponi, 2018) for each quarter hour between the first and the last position recorded to get synchronized individual tracks. In order to visualize catfish space use in winter, all tracks were then plotted on the lake map to create videos of the catfish displacements (Suppl. Mat. IV.B.1). The videos clearly show an aggregation in the western part of the lake.

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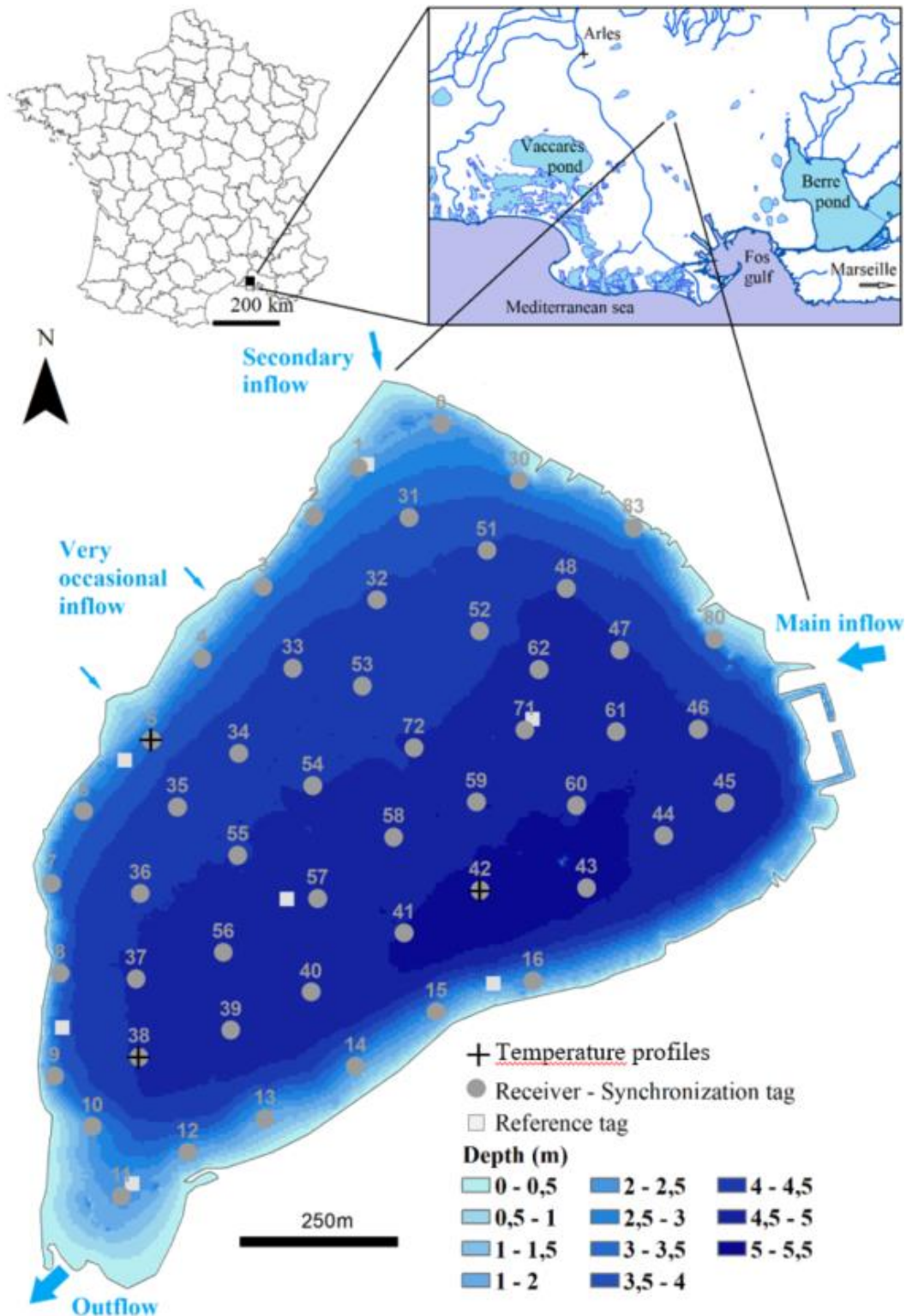


Fig IV.B.1 Bathymetric map of “Etang des Aulnes” at the water level of 11.14 m above sea level and experimental setup. Acoustic receivers and their associated synchronising tags are represented by grey dots. Reference tags are symbolised by pale grey squares. Hourly temperature profiles are located by crosses; location 42 is the deepest in the lake.

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Table IV.B.1. Temperature and catfish characteristics in each winter from 2017 to 2020. The daily temperature (mean, (*sd*) and [range], in °C) at 3 m above the bottom of the lake at the deepest point (point 42 on figure IV.B.1), the number of tracked catfish (*n*) and their total length (mean, (*sd*) and [range], in mm) are given for the extended aggregation period analyzed in each winter.

		Winter 2017	Winter 2018	Winter 2019	Winter 2020
Period		12/02/2017	12/03/2018	11/10/2019	11/22/2020
		17:15	06:15	06:00	14:00
		01/21/2018	03/06/2019	03/02/2020	02/06/2021
		11:15	20:30	05:30	19:00
Daily temperature (°C)		6.5 (1.5)	6.8 (2.3)	9.5 (1.3)	7.0 (2.0)
		[4.7; 8.9]	[3.3; 11.4]	[6.9; 13.9]	[3.2; 11.0]
All individuals	n	10	42	42	42
	Total length	893 (187)	1028 (309)	1056 (326)	1064 (313)
	(mm)	[727; 1465]	[727; 2150]	[727; 2150]	[727; 2150]
Small < 850 mm	n	5	9	9	8
	Total length	791 (33)	812 (34)	812 (34)	812 (36)
	(mm)	[727; 839]	[727; 847]	[727; 847]	[727; 847]
Medium [850; 1100[mm	n	4	26	24	23
	Total length	876 (15)	942 (59)	944 (59)	945 (59)
	(mm)	[855; 902]	[855; 1060]	[855; 1060]	[855; 1060]
Large ≥ 1100 mm	n	1	7	9	11
	Total length	1465	1623 (335)	1600 (311)	1495 (322)
	(mm)		[1100; 2150]	[1100; 2150]	[1100; 2150]

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To identify the aggregation zone over the 5-month periods, the home ranges were estimated with an Epanechnikov kernel as the utilization distribution with probability levels 95%, 50% (Worton, 1989) and the level corresponding to the highest percentage delineating only the aggregation zone that could be identified on the videos. The home ranges were estimated for each phase of the daily cycle, i.e. dawn, day, dusk and night, defined at an hourly resolution. Dawn was defined as the period including the hour preceding the sunrise hour, the sunrise hour itself and the following hour. Dusk was defined as the period including the hour preceding the sunset hour, the sunset hour itself and the following hour. These two periods of the day lasted three hours each. Daytime was the period following dawn and preceding dusk; night was the period following dusk and preceding dawn. These spatial analyses were conducted using the R package *adehabitatHR* (Calenge, 2006). To quantify the degree of aggregation over time, the mean distance between individuals was calculated each quarter hour using the R package *spatstat* (Baddeley et al., 2015) and the number of fish in the aggregation zone was counted.

Statistical analyses

To isolate the aggregation period, we applied an algorithm to detect possible breakpoints corresponding to structural changes in the 5-month time series of the mean distance between individuals (*strucchange* R package, Zeileis et al., 2002; Zeileis et al., 2003). In each of the four winters, the periods with the lowest mean distances between individuals corresponded to the time at which aggregation occurred; these periods were confirmed by watching the videos. To investigate the formation and dislocation of the aggregation, these periods were extended before, until no individual had joined the aggregation zone yet, and after, until all individuals had left it. In the following, these periods will be referred to as the extended aggregation periods.

To investigate whether some individuals consistently joined the aggregation earlier than others at the beginning of the aggregation period, we performed a comparison of the ranks at which individuals first joined the aggregation over successive winters using a Friedman test. To highlight whether fish size influenced the timing of aggregation, we then compared the mean rank of joining the aggregation of the different size classes with a Kruskal-Wallis test. Fish size was defined from the total body length measured during fish tagging and was categorized into three classes: “Small”, “Large” and “Medium”, corresponding to total length < 850 mm, ≥ 1100 mm and in-between, respectively (Table IV.B.1). The same analysis was performed at

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the end of the aggregation period, when the aggregation was dislocating, by considering the rank at which individuals permanently left the aggregation. To quantify a possible link between the mean rank of arrival in and the mean rank of departure from the aggregation, the Spearman correlation coefficient was calculated. These analyses were performed only over the three last winters, when a common significant pool of individuals was present (38 individuals throughout these 3 winters).

To investigate the effect of temperature, time of day and fish size on the stability of winter aggregations, we used two multivariate Cox proportional hazard models (coxme R package, Therneau, 2022a). The first model was used to assess the effect of the covariates on the rate of temporary leaving the aggregation for an excursion outside the aggregation while the second model was used to assess the effect of the covariates on the rate of coming back into the aggregation after an excursion. The two models can be formulated this way:

Survival(Start, Stop, Event) ~ TEMPERATURE + FISH SIZE + TIME OF DAY + (1|Fish identity)

where TEMPERATURE is the temperature at 3m above the bottom of the lake at its deepest point, FISH SIZE is the fish class size (Small, Medium, Large) and TIME OF DAY is the day period (Dawn, Day, Dusk, Night).

In the first model, Event corresponds to the behaviour “to leave the aggregation”; for each Event, the time-to-event goes from the time at which a given individual joined the aggregation (Start) to the next time at which it left it (Stop). In the second model, the Event corresponds to “to join the aggregation”; for each Event, the time-to-event goes from the time at which a given individual left the aggregation (Start) to the time at which it joined it (Stop).

The fish identity was considered as a random effect to explicitly account for individual variability and to take into account the repeated measurements made on the same individuals. The Cox models were run on the whole database which included the four pooled winters. Since two of the fixed effects (temperature and time of day) varied with time, the dataset was rearranged so that each quarter hour observation of a given individual fish appeared as a separate observation in the database containing a Start and Stop time and the corresponding Event type (Therneau, 2022a). The effects of significant categorical covariates were further analyzed by Tukey comparisons of pairwise estimated marginal means of their different levels (*emmeans* R package, Lenth, 2016).

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The survival functions, which represent the probabilities of time-to-event over time, were estimated by the Kaplan-Meier method (Schober & Vetter, 2018) and plotted for the different covariates (survival R package, Therneau, 2022b). For the temperature effect, the following classes were used to plot the survival curves: [3; 5[, [5; 7], [7; 9[and [9; 14] °C; the range of the warmest class is larger to avoid small sample size as temperatures above 11°C rarely occurred in winter.

All statistical analyses and graphics were made with R version 3.6.3 (R Core Team, 2020).

Results

Aggregation characteristics

The aggregation period lasted 41.9, 67.4, 55.2 and 59.7 days and the extended aggregation 49.8, 93.6, 113.0 and 76.2 days, respectively in 2017, 2018, 2019 and 2020 (Table IV.B.1) (Suppl. Mat. IV.B.2 details the breakpoints analysis). The difference between these two periods corresponds to the time for the formation and dislocation of the aggregation, i.e., 7.8, 26.2, 57.8 and 16.5 days, respectively in 2017, 2018, 2019 and 2020.

Catfish showed a strong fidelity to the same aggregation zone across the four winters, although they were more scattered in the milder 2019 winter (Figure IV.B.2, Table IV.B.1). The aggregation area ranged between 2.1 and 3.2 ha, if we exclude 2019 when the aggregation was not as dense as in other winters (see Suppl. Mat. IV.B.1) and was split into two main zones yielding a total area of 4.4 ha. However, one of the two zones was the same as in the other winters and spread over 2.0 ha (Figure IV.B.2). The aggregation zones corresponded to a probability of utilization of 35%, 50%, 30% and 40% over the 15 October – 15 March period, respectively in 2017, 2018, 2019 and 2020, which means that fish spent 30 - 50% of their time in this zone over this 5-month period. If this spatial analysis is restricted to the extended aggregation period, the probability of utilization raises to 60%, 70%, 40% and 70%, respectively in 2017, 2018, 2019 and 2020. In the 2017, 2018 and 2020 winters, during the identified aggregation period, most individuals were indeed located inside the aggregation zone (in average 68.0, 72.4 and 68.9 % over the extended aggregation period in 2017, 2018 and 2020 respectively; Figures IV.B.3a, IV.B.3b, IV.B.3d), which was not so much the case in 2019 (in average 38.7 %, Figure IV.B.3c). Over all winters, each quarter hour, the percentage of fish

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inside the aggregation zone ranged in $[2.4 ; 100]$ %. The identified aggregation periods corresponded to the time at which the coldest temperatures were recorded (Figure IV.B.3 and Table IV.B.1). The aggregation zones were very stable across the different times of day (Figure IV.B.4).

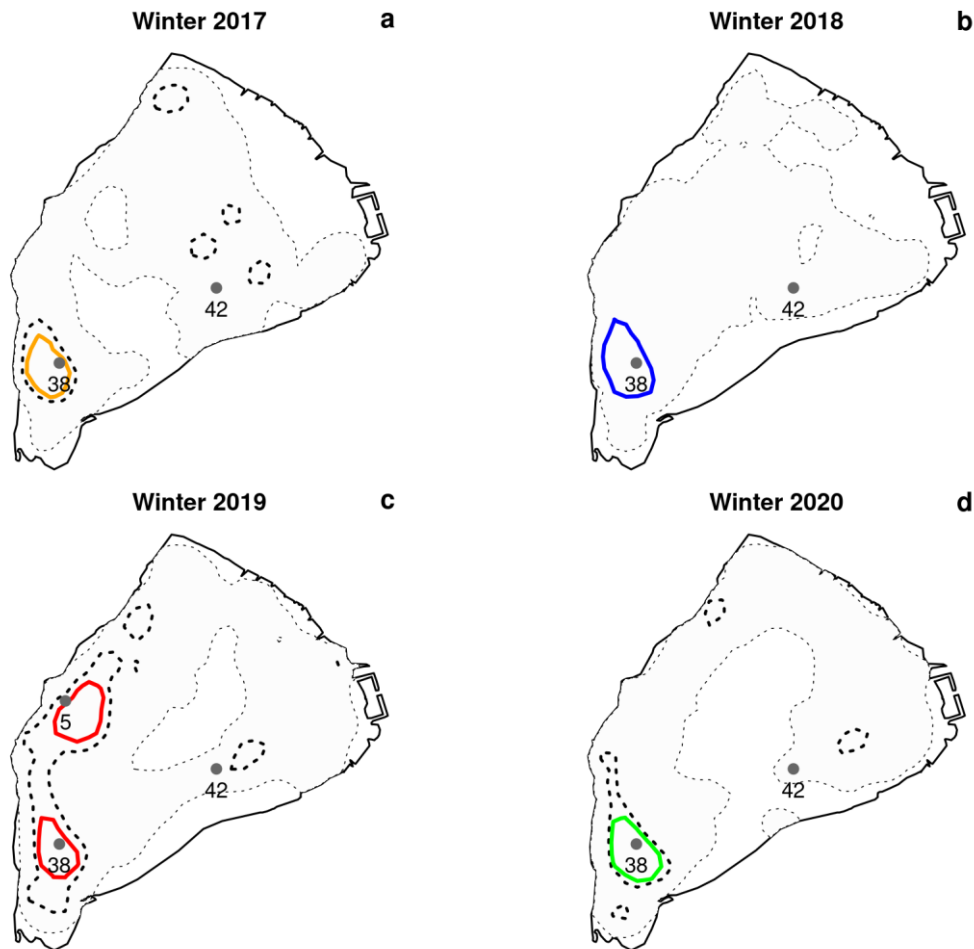


Fig IV.B.2 Catfish's home ranges over 15 October-15 March in winters 2017 to 2020. Home range 95% is filled in pale grey and delineated with a thin dotted line; home range 50% is delineated with a bold dotted line. The contour of the aggregation zone is colored in orange, blue, red and green, respectively in 2017 (panel a), 2018 (panel b), 2019 (panel c) and 2020 (panel d). The aggregation zone corresponds to the utilization distribution with probability level of 35% (21 352 m² area), 50% (32 141 m² area), 30% (44 050 m² area) and 40% (26 035 m² area), respectively in 2017, 2018, 2019 and 2020. The aggregation zone exactly matches with the home range 50% in 2018. The total area of the lake is 1 036 888 m². The grey dots symbolize the locations 5, 38 and 42 where hourly temperature was measured. The points 5 and 38 are

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close or inside the aggregation zone and the point 42 is the deepest point of the lake which stands as a reference point.

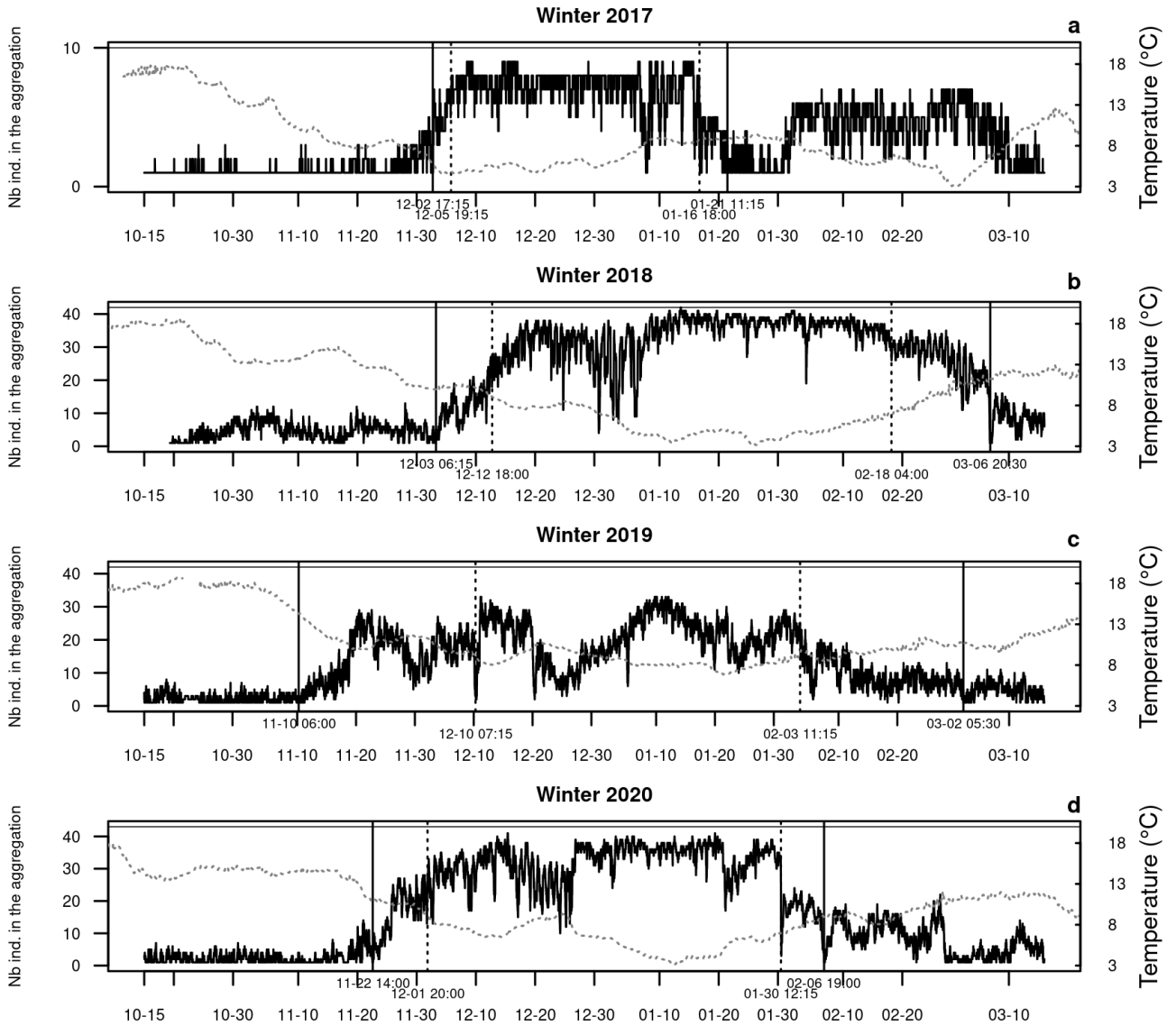


Fig IV.B.3 Time series of the number of individuals in the aggregation zone in winters 2017 to 2020 (15 October-15 March). The dates of aggregation given by the breakpoint detection algorithm are represented by vertical dotted lines. The period extended to the formation and dislocation of the aggregation is delimited by vertical solid lines. On the right y-axis, the temperature at the deepest point in the lake (3 m above the bottom) is plotted in dotted line. The horizontal gray solid line at the top of each panel corresponds to the number of catfish tracked in the corresponding winter.

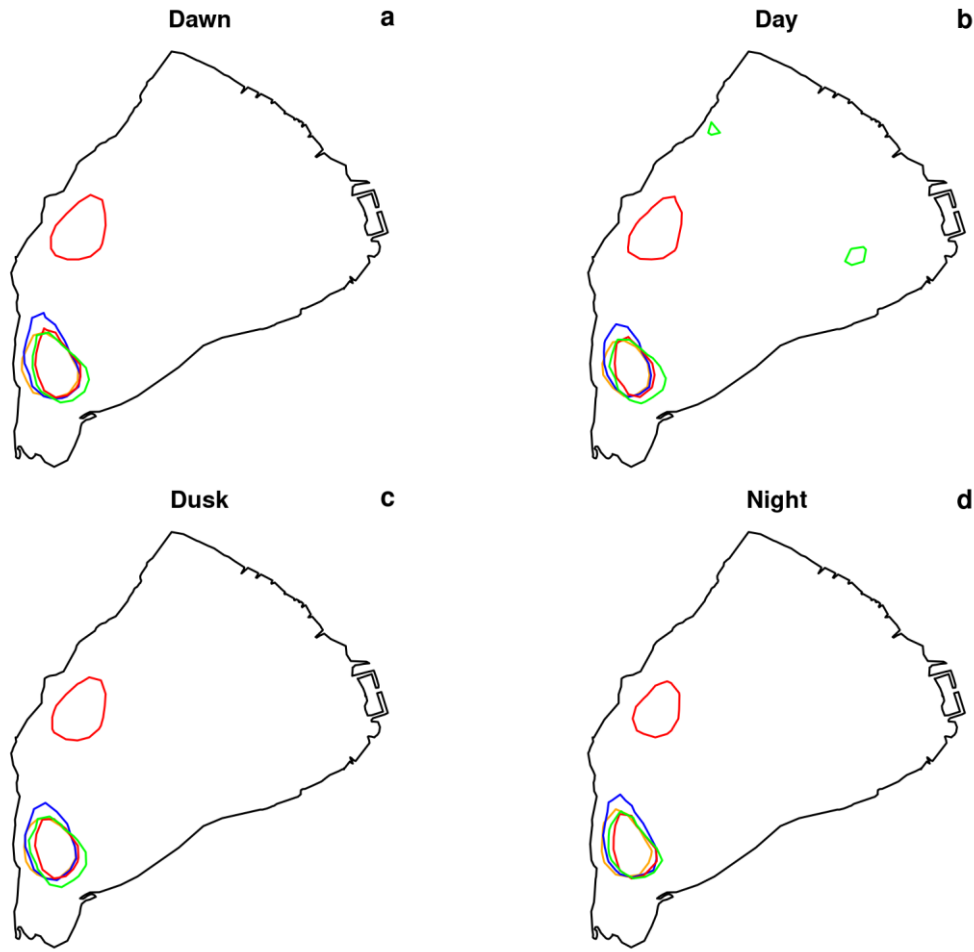


Fig IV.B.4 Catfish's aggregation zone in winters 2017 to 2020 according to the period of the day. The contour of the aggregation zone is colored in orange, blue, red and green, respectively in 2017, 2018, 2019 and 2020. The plotted home ranges correspond to the utilization distribution of figure 2, i.e., with probability level of 35%, 50%, 30% and 40%, respectively in 2017, 2018, 2019 and 2020. Dawn, day, dusk and night are respectively plotted on panels a, b, c and d.

Environmental conditions

The regular aggregation zone, which could be identified throughout the four winters, was in average 4.3 m deep (range [2.8; 4.8] m) and 107.2 m from the bank (range [42.8; 196.6] m). The secondary aggregation zone, which appeared only in winter 2019, was in average 4.2 m deep (range [3.7; 4.6] m) and 134.1 m from the bank (range [62.5; 215] m). The mean daily differences of temperature between the regular aggregation zone and the deepest point in the

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lake, which stands as a reference point, ranged in $[-0.2; 0.4]$ °C throughout the extended aggregation period and had a 0.0 °C mean over this period (Figure IV.B.2, Suppl. Mat. IV.B.3). The mean daily differences of temperature between a location close to the secondary aggregation zone and the deepest point in the lake ranged in $[-0.4; 0.5]$ °C throughout the aggregation and had a -0.1 °C mean over this period (Figure IV.B.2, Suppl. Mat. IV.B.4).

Over the extended aggregation period, at the deepest point, mean daily oxygen concentrations ranged in $[9.8; 14.2]$, $[6.1; 15.1]$, $[9.4; 12.9]$ and $[8.2; 13.7]$ mg/L, corresponding to saturation rates ranging in $[83.5; 113.9]$, $[48.3; 134.8]$, $[81.3; 112.8]$ and $[70.2; 105.4]$ %, respectively in 2017, 2018, 2019 and 2020.

Aggregation dynamics

There was no significant consistency in the rank of first arrival of individuals in the aggregation between the three last consecutive studied winters (Friedman test: $\text{Chi}^2 = 51.56$, $\text{df} = 37$, $p = 0.056$). However, there was little variability in the rank of first arrival of the individual with the lowest mean rank (mean rank 4; range $[1; 8]$ for individual 1030_18b) and of the two individuals with the highest mean ranks (mean rank 34.3 and 34.7; range $[31; 37]$ and $[34; 36]$, respectively for individuals 920_18 and 866_17) (Figure IV.B.5a). Moreover, the rank of first arrival did not depend on fish size (Kruskal-Wallis test: $\text{Chi}^2 = 2.13$, $\text{df} = 2$, $p = 0.345$), although the mean rank of arrival in the aggregation of 5 out of the 8 small fish was higher than that of 70% of all fish considered in the analysis ($n = 38$). Neither was there any consistency in the rank of last departure of the fish from the aggregation (Friedman test: $\text{Chi}^2 = 45.10$, $\text{df} = 37$, $p = 0.169$), nor any size effect (Kruskal-Wallis test: $\text{Chi}^2 = 0.97$, $\text{df} = 2$, $p = 0.614$). But, there was much less variability in the rank of last departure of the three individuals with the lowest mean ranks (mean rank 3.33, 3.67 and 4.47; range $[2; 5]$, $[1; 9]$ and $[3; 7]$, respectively for individuals 920_18, 866_17 and 839_17) and of the two individuals with the highest mean ranks (mean rank 30.7 and 33.7; range $[28; 34]$ and $[29; 36]$, respectively for individuals 873_18 and 1030_18b) (Figure IV.B.5b). The correlation between the mean rank of arrival and mean rank of departure was significantly negative (Spearman $\rho = -0.43$, $p = 0.007$) meaning that, in average, the first individuals arriving in the aggregation were the last to leave and *vice versa*.

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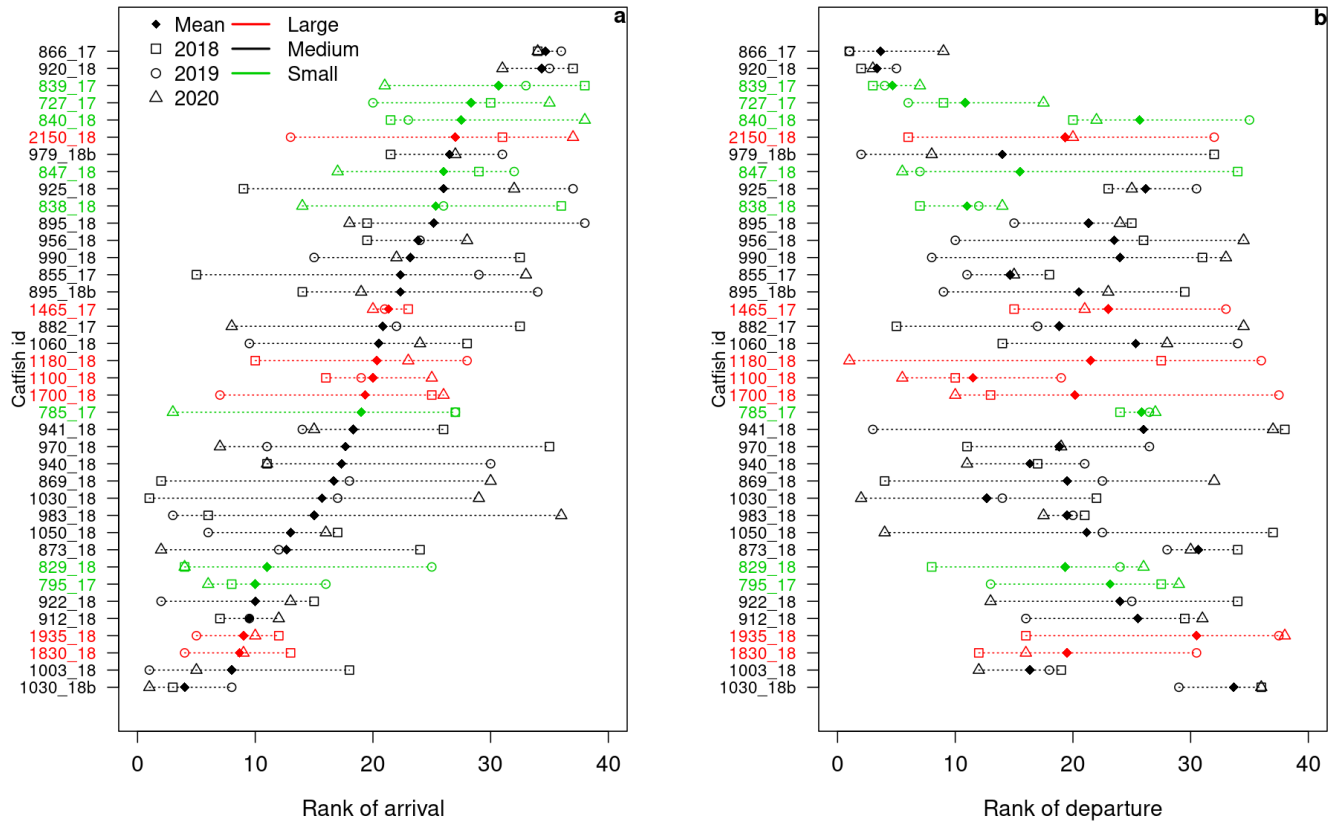


Fig IV.B.5 Rank of arrival in (panel a) and departure from (panel b) the aggregation of the 38 individuals present in the 2018, 2019 and 2020 winters. Individuals are labelled on the y-axis with the following convention: the first part of the label corresponds to the fish total length (in mm) and the two last digits to the year it was tagged; when two fish of the same length were tagged the same year, a “b” has been added at the end of the label of the heavier fish. In panel a, individuals are ordered by increasing mean rank of arrival; in panel b, the same order has been kept. Different colors are used for fish of different sizes (green, black and red for small, medium and large, respectively) and different symbols for the three winters (square, circle, triangle and filled losange for 2018, 2019, 2020 winters and the mean rank, respectively). A dotted line joins both extreme ranks among winters for each individual.

There was a significant effect of temperature, fish size and time of day on the probability of leaving the aggregation for an excursion (Table IV.B.2a, b) and on the probability of coming back into the aggregation after an excursion (Table IV.B.3a, b). The probability of leaving the

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aggregation significantly increased with increasing temperature (Fig. IV.B.6a, Table IV.B.2c), which meant that, in average, fish made longer stays in the aggregation when the water temperature remained low. This probability almost did not differ between small and medium fish but increased for large fish (Fig. IV.B.6b, Table IV.B.2c, d). Small and medium fish therefore made longer stays in the aggregation than large fish. Moreover, the probability of leaving the aggregation did not vary between dawn and day (Fig. IV.B.6c, Table IV.B.2d) but increased between day and dusk (Table IV.B.2c). It decreased between dusk and night and between night and dawn (Fig. IV.B.6c, Table IV.B.2c), which meant that fish left the aggregation mostly at dusk and at night, but even more often at dusk.

The probability of coming back into the aggregation after an excursion significantly decreased with increasing temperature (Table IV.B.3c), especially when temperature exceeded 9 °C (Fig. IV.B.6d). Therefore fish made longer excursions out of the aggregation when the temperature increased. The probability of coming back into the aggregation did not differ between fish of small and medium size (Table IV.B.3d) but significantly decreased for large fish (Table IV.B.3c, Fig. IV.B.6e). Large fish thus made longer excursions out of the aggregation than small or medium fish. Finally, the probability for fish to come back into the aggregation decreased between dawn and day and between dusk and night (Table IV.B.3c, Fig. IV.B.6f). It increased between day and dusk and between night and dawn (Table IV.B.3c, Fig. IV.B.6f). Ranked in order of importance, fish thus went back into the aggregation first at dawn, then at dusk and last at night.

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Table IV.B.2. Numerical results of the Cox model: Survival(Start, Stop, “Leaving the aggregation”) ~ TEMPERATURE + FISH SIZE + TIME OF DAY + (1|Fish identity). Part a gives the significance of each covariate. Part b compares this model with the model without random effect and gives goodness-of-fit of the corresponding model without random effects which is not accessible for the mixed model ; the Wald test tests the null hypothesis that the coefficients of covariates are null; the Concordance should be greater than 0.5 for the model to be informative. Part c shows the covariate coefficients of the mixed Cox model; the exponentiated coefficients are multiplicative effects on the hazard: for continuous covariates, as Temperature, $\exp(\text{coef}) = 1.23$ means that when temperature raises by 1°C, the probability to leave the aggregation increases by 23%. For categorical covariates, for example the coefficient of large fish in reference to small fish, $\exp(\text{coef}) = 1.44$ means that the probability for large fish to leave the aggregation was 44% higher than that of small fish. Coefficients are exposed only for significant contrasts shown in part d and, for time of day, only between consecutive classes in the diel cycle (Day/Dawn, Dusk/Day, Night/Dusk and Dawn/Night).

a	Log-likelihood	Chi2	df	p-value
NULL	-139012			
Temperature	-137329	3365.39	1	< 0.001
Fish size	-137322	14.64	2	< 0.001
Time of day	-136845	954.25	3	< 0.001

b

Model without random effects:

Log-likelihood=-137257; Concordance= 0.641; Wald statistic = 3421 (df=6, $p < 0.001$)

Comparison between model with and without random effects (deviance analysis):

Chi2=825.04 df=1 $p < 0.001$

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c				
	Coef	Exp(coef)	z	p
Temperature	0.21	1.23	46.70	< 0.001
		[1.22; 1.24]		
Large/Small	0.37	1.44	2.77	0.006
		[1.11; 1.87]		
Large/Medium	0.44	1.55	4.14	< 0.001
		[1.26; 1.90]		
Dusk/Day	0.68	1.98	25.07	< 0.001
		[1.88; 2.10]		
Night/Dusk	-0.21	0.81	-9.28	< 0.001
		[0.78; 0.85]		
Dawn/Night	-0.45	0.64	-16.24	< 0.001
		[0.61; 0.68]		

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d				
Contrast	ratio	df	z ratio	p
Small/Medium	1.07	Inf.	0.61	0.817
Small/Large	0.69	Inf.	-2.77	0.016
Medium/Large	0.65	Inf.	-4.14	< 0.001
Dawn/Day	1.03	Inf.	0.89	0.811
Dawn/Dusk	0.52	Inf.	-20.35	< 0.001
Dawn/Night	0.64	Inf.	-16.24	< 0.001
Day/Dusk	0.50	Inf.	-25.07	< 0.001
Day/Night	1.23	Inf.	-21.81	< 0.001
Dusk/Night	1.23	Inf.	9.28	< 0.001

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Table IV.B.3. Numerical results of the Cox model: Survival(Start, Stop, “Joining the aggregation”) ~ TEMPERATURE + FISH SIZE + TIME OF DAY + (1|Fish identity). The legend is the same as in Table IV.B.2.

a	Log-likelihood	Chi2	df	p-value
NULL	-137700			
Temperature	-137256	889.09	1	< 0.001
Fish size	-137248	15.56	2	< 0.001
Time of day	-137159	178.78	3	< 0.001

b

Model without random effects:

Log-likelihood=-137385; Concordance= 0.557 ; Wald statistic= 619.5 (df=6, p<0.001)

Comparison between model with and without random effects (deviance analysis):

Chi2=452.3 df=1 p<0.001

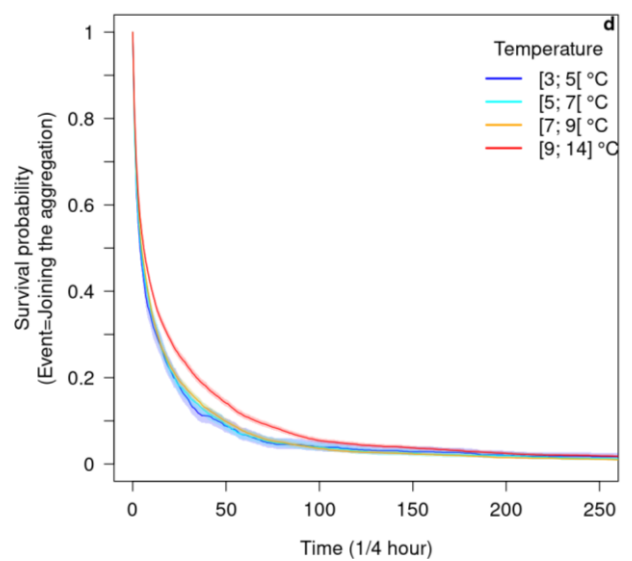
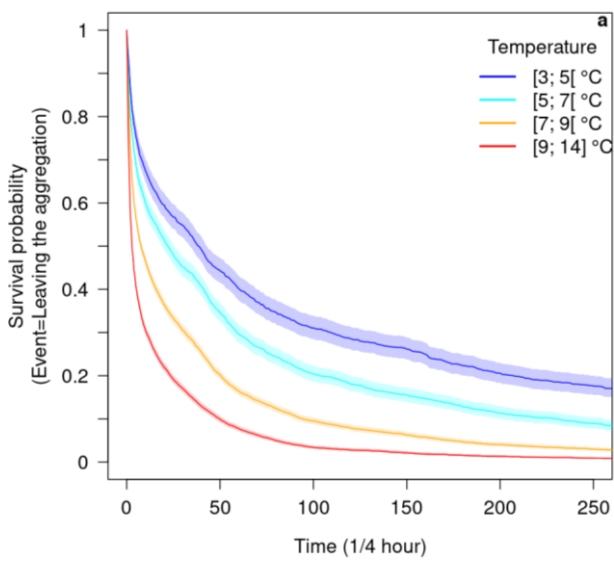
IV.B Impact of winter conditions on the habitat niche of a population of freshwater predators

c				
	Coef	Exp(coef)	z	p
Temperature	-0.06	0.95 [0.94 ; 0.95]	-12.94	< 0.001
Large/Small	-0.40	0.67 [0.54 ; 0.83]	-3.72	< 0.001
Large/Medium	-0.33	0.72 [0.60 ; 0.85]	-3.77	< 0.001
Day/Dawn	-0.37	0.69 [0.65 ; 0.73]	-13.27	< 0.001
Dusk/Day	0.21	1.23 [1.16 ; 1.31]	7.08	< 0.001
Night/Dusk	-0.05	0.95 [0.90 ; 1.00]	-2.15	< 0.001
Dawn/Night	0.22	1.24 [1.18 ; 1.30]	9.19	< 0.001

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d

Contrast	ratio	df	z ratio	p
Small/Medium	1.08	Inf.	0.81	0.700
Small/Large	1.50	Inf.	3.72	< 0.001
Medium/Large	1.39	Inf.	3.77	< 0.001
Dawn/Day	1.45	Inf.	13.27	< 0.001
Dawn/Dusk	1.18	Inf.	5.21	< 0.001
Dawn/Night	1.24	Inf.	9.19	< 0.001
Day/Dusk	0.81	Inf.	-7.08	< 0.001
Day/Night	0.86	Inf.	-7.04	< 0.001
Dusk/Night	1.06	Inf.	2.15	< 0.001



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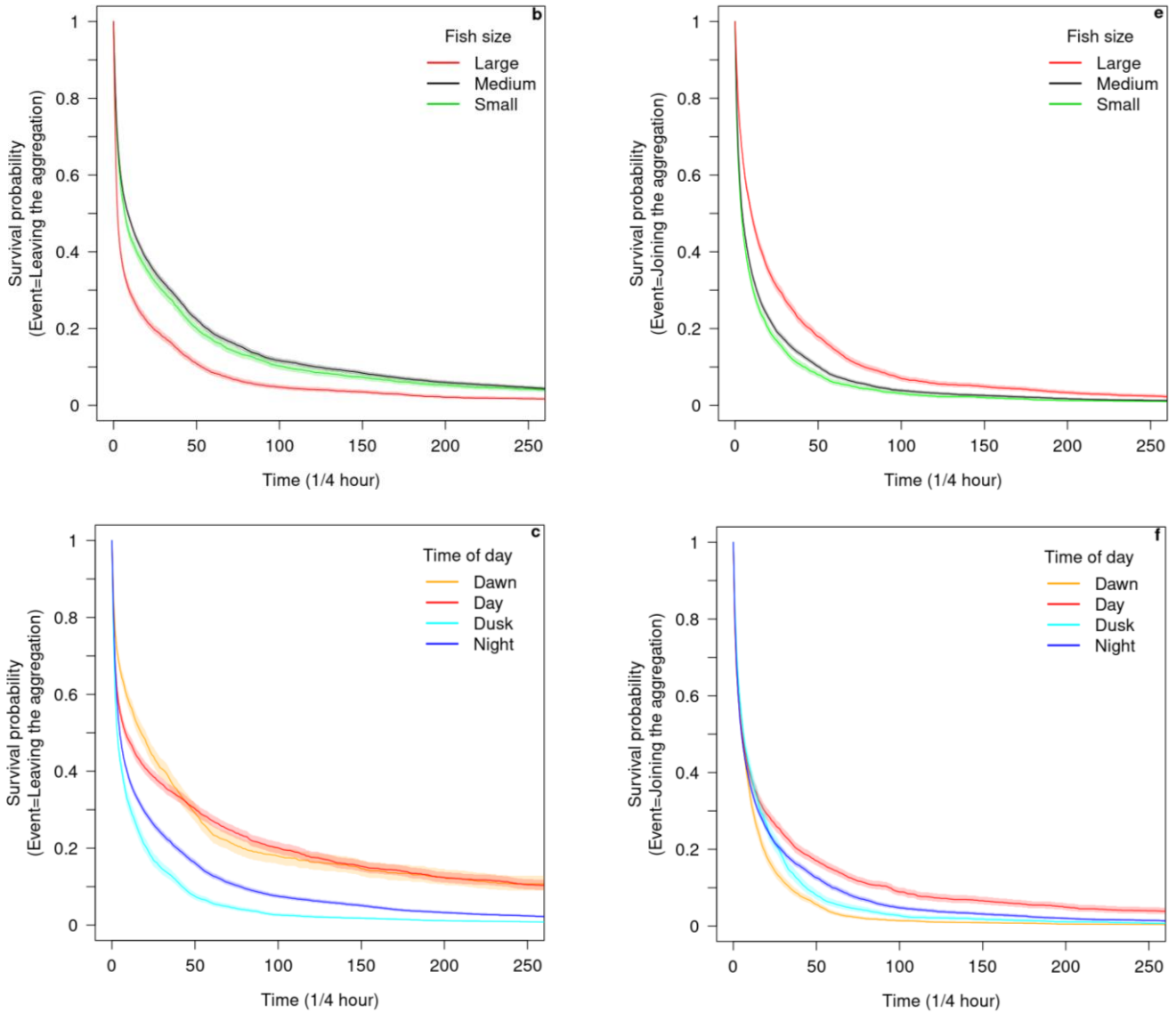


Fig IV.B.6 Kaplan-Meier survival curves corresponding to the events “leaving the aggregation” (panels a ,b, c) and “joining the aggregation” (d, e, f) during the period of winter aggregations for different water temperatures (a and d), different fish sizes (b and e) and the different times of day (c and f). These curves, which represent the survival function as a function of time, describe the probability that the event of interest has not yet occurred by this time point. As an example, in panel a, the probability for an individual of not leaving the aggregation after time=100 (25 hours), in other words, the probability of staying in the aggregation after 25 hours spent inside, is 0.03 at $[9; 14[$ °C, 0.10 at $[7; 9[$ °C, 0.20 at $[5; 7[$ °C and 0.31 at $[3; 5[$ °C. The curves have been computed on the four studied winters together. The shading around the curves represents the 95% confidence interval of the mean survival curve. It is sometimes barely discernible because very narrow.

Discussion

Aggregation zone

Catfish aggregated across the four winters for 1.5 to 2 months and showed a strong fidelity to a same zone representing 2-4% of the lake area. Even in other seasons, catfish has been shown to have a strong site fidelity (Carol et al., 2007; Slavík & Horký, 2009; Brevé et al., 2014; Capra et al., 2018), but such an aggregation behavior has been described in detail and shown repeatedly all over one year only once and in a large river (Boulêtreau et al., 2011). Quite often, fidelity to a site can be linked to environmental features that give individuals an advantage as warmer temperatures (Brevé et al., 2014; Capra et al., 2018) or a refuge area for catfish (Brevé et al., 2014), deep and slow pools for lake sturgeon *Acipenser fulvescens* (Thayer et al., 2017), proximity to beds of emergent vegetation or open water formed by turbulence from a lake aerator for common carp *Cyprinus carpio* (Penne & Pierce, 2008) or current updrafts that reduce energy expenditure for aggregating grey reef sharks *Carcharhinus amblyrhynchos* (Papastamatiou et al., 2021). In our case, the aggregation zone was not warmer than anywhere else in the lake and oxygen conditions were not limiting; moreover, a scan of the aggregation area with an acoustic camera in February 2020 revealed no particular structure at the bottom. In this region where the prevailing winds blow from the north, the secondary aggregation zone is relatively sheltered and could offer calmer waters, especially in this shallow lake, but this appears much less the case for the regular aggregation zone.

Aggregation dynamics

The aggregation formation and stability were closely linked to temperature; common carp aggregated when water dropped below 8°C (Johnsen & Hasler, 1977). Few movements associated with the aggregation behavior is a way to save energy (Domenici et al., 2013). It was stable across times of day, but most movements took place at dusk and night when some individuals left the aggregation or at dawn and dusk when they came back. This is in agreement with the preferential nocturnal activity of catfish (Carol et al., 2007; Brevé et al., 2014). The largest individuals spent more time outside the aggregation. The whole-organism metabolic rate of an individual depends on its body size (allometric equation, see Brown et al., 2004) which suggests large fish would more often leave the aggregation for feeding.

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Even if not significant, the rank of arrival of individuals was more or less consistent across winters ($p=0.056$), which could suggest that some individuals had a leading position (e.g. Jacoby et al., 2016). But this was not the case for the rank of departure. However, on one side, there was a tendency for some individuals to spend as much time as possible inside the aggregation (earlier arrived, later left) and, on another side, for some others to minimize it. Thus, leaders in the aggregation formation would not be leaders in its dislocation, quite the contrary. The possible leading position was not linked to fish size as leadership in roach shoals (Krause et al., 1998) or dominance in catfish itself (Slavík et al., 2016).

Aggregation causes and consequences

Up to 100% of tagged fish could be found in the winter aggregation, which is much greater than the 23% of lake sturgeon (Thayer et al., 2017) or 70% of common carp (Penne 2008). Based on capture-recapture data (unpublished data), the estimated catfish population (individuals greater than 600 mm) in “Etang des Aulnes” would be 770 individuals (95% confidence interval [184 ; 1356]). As all tagged individuals could be found in the aggregation, this means that possibly a great proportion of the population could gather over there. This would make a huge winter aggregation of roughly 770 individuals in comparison to the 44 individuals in Bouletreau et al (2011). European catfish have been reported to actively defend their access to resources (Cucherousset et al., 2018), to be a solitary forager (Carol et al., 2007), and to expend more energy when in contact with conspecifics in preferred areas of habitat (Slavík & Horký, 2009). In an aggregation of such a size that lasted 1.5 - 2 months, competition between individuals could considerably increase (Krause & Ruxton, 2002), even if catfish usually feed very little during cold season (Cucherousset et al., 2018). The cause or function of this aggregative behavior remains unknown. The temperature was far below suitable temperatures for spawning (between 20 and 25 °C, Souchon & Tissot, 2012), and this period appears far too early to identify potential mates for spawning several months later (usually in May-June in this lake). Unlike size-assortative schooling (e.g. Peuhkuri et al., 1997), individuals of various sizes could be found in the aggregation (range [727; 2150] mm from our tagged individuals), among which the smallest had probably not reached a refuge size against the largest individuals yet, since the prey-to-predator length ratio for catfish can reach 0.57 (Vejřík et al., 2017). But we do not know whether or not even smaller individuals also aggregated. We tried to get supplementary

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information on these aggregations by scuba diving but the usually low water transparency in this lake (mean Secchi depth = 2.5 m in winter) hinders any visual observation. Some studies on fish aggregation suggested that social interactions between conspecifics probably play a role, challenging the classical view of aggregation formation around floating devices (Robert et al., 2014). Moreover, the site fidelity for aggregating could favor social interactions (Wolf et al., 2007) as non-random aggregations in sharks (Mourier et al., 2012). As discussed above, whatever their size, some individuals tended to prolong the aggregation compared to others that seemed to shorten it. Irrespective to a possible hierarchy between individuals, to prolong the grouping could favor social interactions with conspecifics. These social interactions have been shown to regulate the stress in some species (Allen et al., 2009; Magnhagen, 2015). However, Slavík & Horký (2009) reported that catfish increased their energy consumption when in contact with conspecifics, assuming this was a stressful situation. This experiment was led on males only and in spring though, when catfish recover a significant activity and while they prefer solitary hunting (Carol et al., 2007). But catfish could decrease their activity in presence of conspecifics, if these conspecifics were familiar (Slavík et al., 2016). This raises the importance of animal personality, with shy individuals that would be more likely to cooperate and bold that would act more independently (Krause et al., 2008; Conrad et al., 2011), and the role of individual heterogeneity in collective behaviour (Jolles et al., 2020). Based on a proximity index, Vanovac et al. (2021) concluded that catfish did not display within-species interactions whereas common carp was, especially in winter. We may however question the sensitivity of this index to the sample size of fish. In their figure IV.B.4 which represents location of species across seasons with kernel densities, one can however see a tendency for catfish to clustering in winter, similar to what we showed.

Due to adults being at least twice larger than native predators, catfish is considered as a ‘giant’ top predator (Cucherousset et al., 2018) and is suspected to threaten the fish communities (Martino et al., 2011; Guillerault et al., 2015; De Santis & Volta, 2021; Vagnon et al., 2022). In numerous ecosystems, managers thus try to control their population. But, a fundamental constraint of control methods is a lack of selective removal methods that target the non-native fish species only (Britton et al., 2011). As a considerable fraction of the population gathers in a same zone during the coldest periods, tagging only a few individuals could help to locate and remove most individuals (population control by the Judas technique) (Bajer et al., 2011).

Conclusion

Long-lasting winter aggregations of catfish, that very probably concern a large fraction of the population, have been shown to consistently occur in a same small area of “Etang des Aulnes” every year, though less compact during mild winter. The aggregation formation and stability was closely linked to temperature: it seemed to be triggered by temperatures below 9 °C and became more stable with decreasing temperatures, while catfish made more frequent and longer excursions outside the aggregation when temperatures increased. Night and dusk were the preferred periods for these excursions. The area where they gathered was moderately deep, about 4 m, but not the deepest in the lake (6 m), and its abiotic environmental conditions (temperature, oxygen concentration, substrate) apparently did not differ from other parts in the lake. Individuals of various sizes took part in the aggregation, but larger specimens made more frequent excursions outside the aggregation. Irrespective to their size, some individuals consistently arrived early in the winter and left late the aggregation. This needs further research, but it could correspond to different coexisting behavioural types, some individuals seeking for sociality and others being more independent. In the end, this predictable seasonal grouping of individuals could give the opportunity for lake managers to efficiently control catfish population if needed. As for species conservation, if the overwintering habitat was a critical one, it could constitute a bottleneck habitat, crucial to secure and maintain. The knowledge provided by such studies on how species use the space has both academic and operational values.

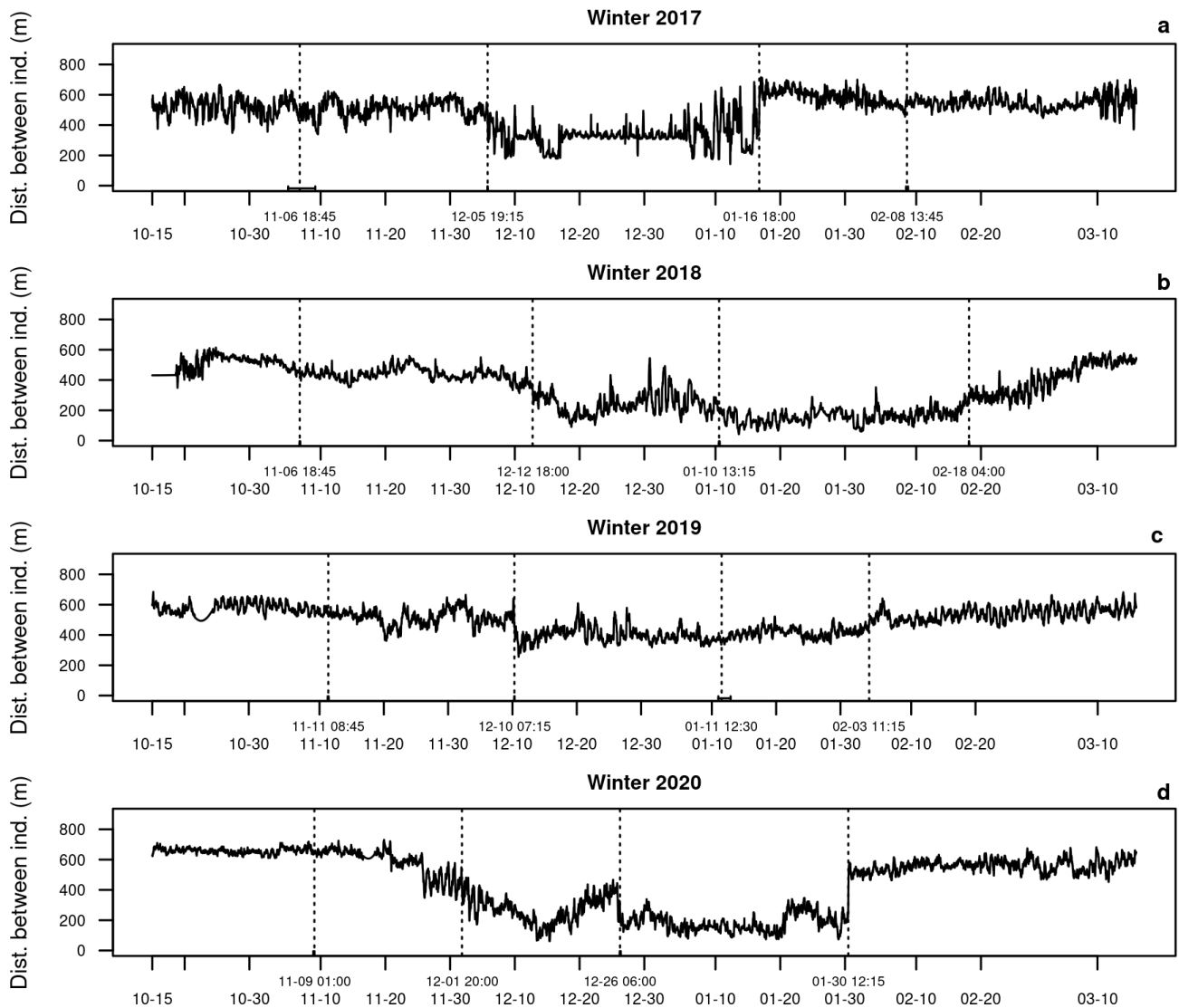
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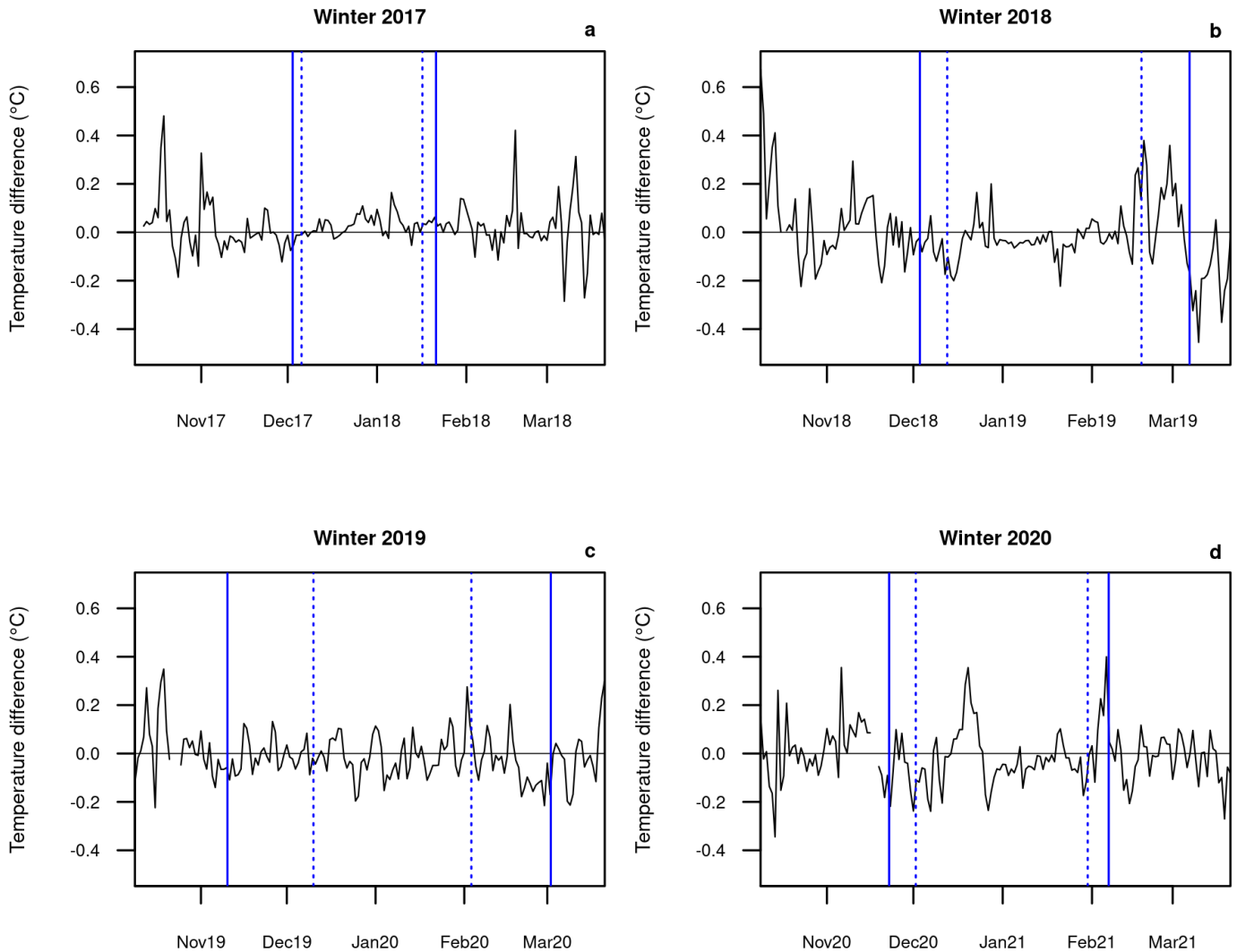
4. Supplementary materials

Suppl. Mat. IV.B.1 Synchronized tracks of European catfish over the four winters 2017-2020 in “Etang des Aulnes” <https://doi.org/10.57745/U7UG5D>



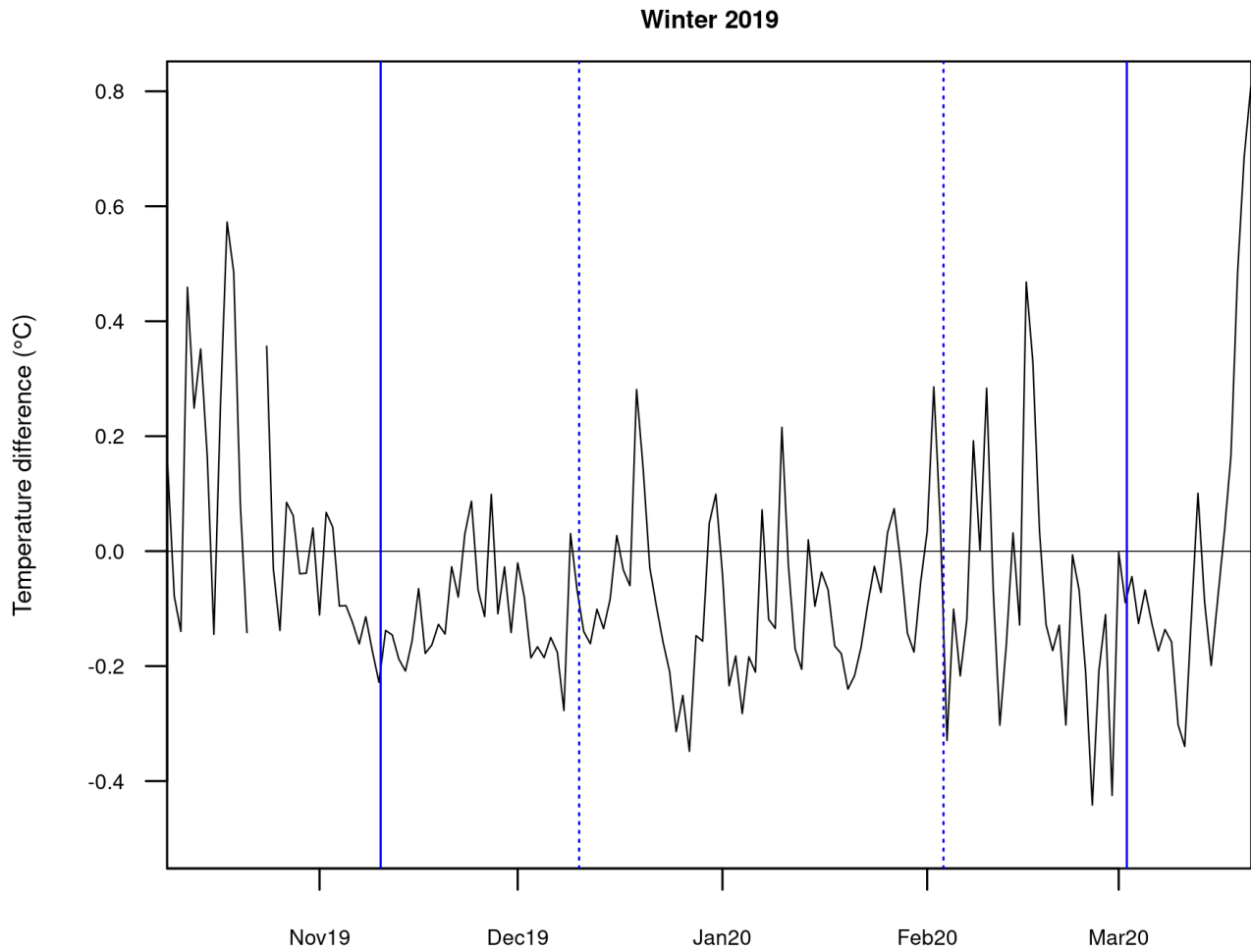
Suppl. Mat. IV.B.2 Time series of the mean distance between individuals in winters 2017 to 2020. The dates of structural changes over the 5-month time series (15 October-15 March) and their 95% confidence interval are labelled on the x-axis and represented by vertical dotted lines and interval at their basis (very tight intervals are not visible).

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Suppl. Mat. IV.B.3 Time series of temperature differences between the common aggregation point and the deepest point in the lake in winters 2017 to 2020 (panels a–d). The solid black line represents the mean daily temperature differences at 0.5 m above the bottom between locations 38 and 42 (see Figure 1) over the 5-month time series (15 October–15 March). Location 38 is inside the aggregation zone that showed off each winter. Location 42 corresponds to the deepest point in the lake and stands as a reference point. The dates of aggregation given by the breakpoint detection algorithm are represented by vertical blue dotted lines. The period extended to the formation and dislocation of the aggregation is delimited by vertical blue solid lines.

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Suppl. Mat. IV.B.4 Time series of temperature differences between a point close to the secondary aggregation point and the deepest point in the lake in winter 2019. The solid black line represents the mean daily temperature differences at 0.5 m above the bottom between locations 5 and 42 (see Figure 1) over the 5-month time series (15 October-15 March). Location 5 is very close to the secondary aggregation zone that showed off only in winter 2019. Location 42 corresponds to the deepest point in the lake and stands as a reference point. The dates of aggregation given by the breakpoint detection algorithm are represented by vertical blue dotted lines. The period extended to the formation and dislocation of the aggregation is delimited by vertical blue solid lines.

IV.C

Impact of hypoxic conditions on the
habitat niche of a population of
freshwater predators

C. European catfish *Silurus glanis* behaviour in response to a strong summer
hypoxic event in a shallow lake

1. *Synthesis (English)*

The seasonal cycle and related changes in temperature have a marked impact on the habitat niche of fishes. Another key driver of fish spatial distribution is the dissolved oxygen concentration (DOC) in the water, each species having its own optimal values. Depending on biological processes (photosynthesis, respiration, decomposition), DOC can rapidly vary and reach unsuitable thresholds for some species in some parts of the lake, thus compressing fish habitat. Here we analyzed the movements of 40 subadult and adult catfish ([727; 2150] mm) tracked in “Etang des Aulnes” during a severe summer hypoxic event. This event led to the mass mortality of fish, including species known to be resilient to low oxygen conditions such as carp and eel. We found that catfish could withstand very low DOC, down to 1.3 mg/L in the upper half of the water column (corresponding to a mean dissolved oxygen saturation rate of 16%), when their preferred benthic habitats were anoxic. When hypoxia became more severe, individuals significantly increased their activity and the surface area they visited, regardless of their size. This led them quite synchronously to a refuge zone where they aggregated or stayed in close vicinity, rarely moving, over one and a half days during the overall anoxia of the lake. This zone, located very close to the well oxygenated water inflow, was much more oxygenated and probably one of the most oxygenated zones that was accessible. During this aggregation, the smallest individuals were more active than the largest ones. When temporarily forced to share very limited space and resources, competition between individuals likely increased, especially in this active season. Catfish aggregation can be compared to a school and led to locally high oxygen consumption. According to the position in this school, in front of the inflow current or in the rear of the school, DOC can be highly variable. Thus, some individuals need to change position leading to a reshuffle. The largest dominant catfish could occupy the most suitable positions, and the smallest individuals the least favorable ones. The smallest individuals would then move more often to change position towards better-oxygenated areas in the aggregation.

In the future, the ability of catfish to withstand very low DOC, along with its high optimal temperature range, could give it a competitive advantage over other predatory species in the context of global change.

IV.C Impact of hypoxic conditions on the habitat niche of a population of freshwater predators

2. *Synthesis (French)*

Comportement du silure glane (*Silurus glanis*) en réponse à une hypoxie estivale sévère dans un lac peu profond.

Le cycle saisonnier et les changements associés de température impactent fortement la niche d'habitat des poissons. Un autre facteur clé de la distribution spatiale des poissons est la concentration en oxygène dissous (COD), chaque espèce ayant ses propres valeurs optimales. En fonction des différents processus biologiques (photosynthèse, respiration, décomposition), COD peut varier rapidement et atteindre des valeurs non compatibles avec les exigences physiologiques de certaines espèces dans certaines zones du lac, limitant ainsi l'habitat disponible. Dans cette étude, nous avons analysé les mouvements de 40 silures subadultes et adultes (tailles comprises entre 727 et 2150 mm) dans l'étang des Aulnes durant une hypoxie estivale sévère. Cette hypoxie a engendré une mortalité de masse de la faune piscicole, incluant des espèces pourtant très résistantes aux faibles COD telles que la carpe et l'anguille. Nous avons mis en évidence que le silure pouvait résister à de très faibles COD, jusqu'à 1.3 mg/L dans la moitié supérieure de la colonne d'eau (soit une saturation en oxygène de 16%), alors que ses habitats benthiques préférés étaient anoxiques. Quand l'hypoxie est devenue plus sévère, les individus de toute taille confondue ont significativement accru leur activité ainsi que l'étendue des zones qu'ils parcouraient. Cette agitation les a menés de manière relativement synchrone dans une zone refuge où ils se sont agrégés ou sont restés à proximité, peu mobiles, un jour et demi durant pendant l'anoxie du lac. Cette zone, très proche du flux d'eau bien oxygéné alimentant le lac, était bien mieux oxygénée et probablement une des plus oxygénées disponibles dans le lac. Lors de cette agrégation, les plus petits individus étaient plus actifs que les plus grands. Temporairement contraints à utiliser un espace et des ressources réduits, la compétition entre les individus s'est potentiellement accrue en cette saison de forte activité. L'agrégation des silures s'apparente à un banc de poissons et a localement conduit à une consommation élevée d'oxygène. Selon la position dans le banc, face au courant d'eau entrant ou à l'arrière du banc, COD peut varier considérablement. Certains individus peuvent ainsi avoir besoin de changer de position. Les plus grands individus, dominants, occuperaient les places les plus favorables, et les plus petits contraints d'occuper les moins adéquates. Ces derniers bougeraient alors plus souvent pour rejoindre des zones mieux oxygénées dans

IV.C Impact of hypoxic conditions on the habitat niche of a population of freshwater predators

l'agrégation. Dans le futur, et notamment avec le changement global, cette capacité du silure à supporter de très faibles COD ainsi que son optimaum thermique chaud pourraient lui conférer un avantage compétitif substantiel sur les autres prédateurs.

3. Core paper

Samuel Westrelin, Stéphanie Boulêtreau & Frédéric Santoul (2022) European catfish *Silurus glanis* behaviour in response to a strong summer hypoxic event in a shallow lake. Aquatic Ecology. <https://link.springer.com/article/10.1007/s10452-022-09952-y>

Abstract

Hypoxic events have always naturally occurred in freshwater ecosystems but are worsening due to anthropogenic activities. Hypoxia tolerance greatly varies among fish species and is difficult to quantify in nature in large fish species. We analysed the movements of 40 subadult and adult European catfish *Silurus glanis* ([727; 2150] mm) exposed to a natural summer hypoxic event in a shallow lake of southeastern France. Catfish could withstand very low dissolved oxygen concentrations (DOC), down to 1.3 mg/L in the upper half of the water column (corresponding to a mean dissolved oxygen saturation rate of 16%), when their preferred benthic habitats were anoxic. While hypoxia was becoming more severe, individuals significantly increased their activity and the surface area they visited, whatever their size. This led them to a refuge zone where they aggregated or stayed in close vicinity, very little mobile, over one and a half day during the overall anoxia of the lake. This zone, located very close to the well oxygenated water inflow, was probably one of the most oxygenated accessible zone. During this aggregation, the smallest individuals were however more active than the largest ones. This was probably because they more often needed to move to better oxygenated places within the gathering area, compared to larger dominant fish that occupied the best places. The ability of catfish to withstand very low DOC, along with its high optimum temperature range, could give it a competitive advantage over other predatory species in the context of global change.

Keywords: Aggregation, escape response, fish, hypoxia, lake

Introduction

Low dissolved oxygen conditions, so called hypoxic events, occur in a wide range of marine and freshwater ecosystems (Diaz & Rosenberg, 2011). They happen when oxygen consumption, primarily by decomposing organic matter, exceeds oxygen supply by photosynthetic production and diffusion from the atmosphere. Hypoxic events have always naturally occurred in aquatic ecosystems but the gradual rise in nutrient and organic enrichment due to human activities (sewage, industrial and land runoff) has resulted in the increase in their frequency and seriousness, sometimes leading to anoxia (Druon et al., 2004; Hagy et al., 2004). Increasing hypoxia is now recognized as an environmental issue of global importance for fresh, coastal and oceanic waters (Breitburg et al., 2009; Diaz & Rosenberg, 2011; Jenny et al., 2016). In lentic and lotic freshwater systems, hypoxia varies in seasonality, frequency and persistence, depending on many factors, including eutrophication, inflow of industrial waste, reduced mixing due to depth or wind conditions, thermal variations and ice cover (Poff et al., 2002; Ficke et al., 2007).

Compared with most birds and mammals, ectothermic vertebrates (fish, amphibian, and reptile) are tolerant of variable oxygen availability (Bickler & Buck, 2007). In fish, hypoxia tolerance greatly varies among the 20,000 species. Species such as trout (*Oncorhynchus mykiss*) and tuna (*Katsuwonus pelamis*, *Thunnus albacares*, *Thunnus obesus*), that extensively depend on aerobic metabolism for rapid and sustained swimming, are moderately to extremely sensitive to hypoxia (Gesser, 1977; Bushnell et al., 1990; Gamperl & Driedzic, 2009). Carp (*Cyprinus carpio*), eel (*Anguilla anguilla*), catfish (*Silurus glanis*) and hagfish (*Myxine glutinosa*) can manage with low oxygen concentrations (Weber et al., 1976; Gesser, 1977; Axelsson et al., 1990; Massabuau & Forgue, 1995). At the extreme, the crucian carp (*Carassius carassius*) is able to endure months of hypoxia at low temperature (Nilsson & Renshaw, 2004; Stecyk et al., 2004). Such hypoxia tolerance involves metabolic adjustments, including metabolism depression, tolerance of metabolic products during anaerobiosis, and strategies for avoiding or repairing cellular injuries during reoxygenation (Brauner et al., 2004; Wells, 2009).

Behavioural responses can provide additional flexibility to mitigate exposure to hypoxic stress. Changes in spontaneous swimming activity have been described in a wide range of fish species when exposed to hypoxia (Schurmann & Steffensen, 1994; Chapman & McKenzie, 2009). Domenici et al. (2000) found that the lower was the spontaneous speed in Atlantic herring

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(*Clupeus harengus*) in normoxia, the greater was the increase in speed in hypoxia. Some fish up-regulate their speed, performing an escape response, defined as a type of fast start characterized by a brief and sudden acceleration (Domenici & Blake, 1997). Alternatively, others down-regulate their speed, they show freezing behaviour by adopting a fixed and immobile posture through which they become less susceptible to detection by predators. It has also been suggested that species that reduce their activity in hypoxia tend to be demersal or benthic/pelagic, with a relatively sedentary lifestyle during which they may often encounter hypoxia in their habitat; whereas species that increase activity in case of hypoxia tend to be active pelagic schooling fishes (Domenici et al., 2000; Herbert & Steffensen, 2005; Herbert & Steffensen, 2006). Therefore, changes in swimming activity as behavioural responses to mitigate exposure to hypoxia are difficult to predict since they largely depend on fish species and context (Chapman & McKenzie, 2009). Moreover, such behaviours are difficult to describe and quantify in nature, and also in laboratory conditions for very large species.

The European catfish (*Silurus glanis*) is the largest fish species inhabiting European freshwaters (up to 2.7 m in body length and 130 kg of weight, Boulêtreau & Santoul, 2016). The species is native from Eastern Europe and has been introduced in Southwestern Europe during the 19th Century for sport fishing and aquaculture (Copp et al., 2009). It has successfully established in most of the large Southwest European watersheds (Boulêtreau et al., 2020). Several features could explain its colonization and expansion success. The range of temperatures within which adults do not show any sign of abnormal behaviour is quite large and falls between 12 °C and 28 °C, but reproduction optimally occurs above 20 °C (Souchon & Tissot, 2012). It is also tolerant to water pollution, partly due to low oxygen requirements as little as 1-1.5 mg/L depending on the temperature (Massabuau & Forgue, 1995). The species is considered to use oxygen very efficiently, partly thanks to a high haematocrit (35-38%, Mihalik, 1995). Nevertheless, such physiological capacities have only been measured on young individuals in laboratory conditions. In natural conditions, one study has reported the displacements of 19 juvenile catfish (total length less than 400 mm) in response to a winter hypoxia in one oxbow lake of the river Elbe (Czech Republic). Fish were shown to exhibit unexpected high activity and displacements (Daněk et al., 2014). But no behavioural response to hypoxia has ever been studied on adult European catfish in natural conditions.

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In an experiment set up to assess the space use and activity cycles of the European catfish, 40 large individuals (subadults and adults whose body length ranged in 727 - 2150 mm) have been tracked by acoustic telemetry for three years in a 104-ha shallow eutrophic lake located in South-Eastern France. Within this period, the lake experienced a severe hypoxia, leading to the mortality of many fish from different species, including carp, eel and some small European catfish. However, fourteen months later, our telemetry tracking data revealed that all the 40 tagged catfish were still alive. Therefore, we aimed to analyse how large European catfish individuals could have resisted to hypoxia in natural conditions. More specifically, we examined how telemetry data could provide valuable information to highlight catfish individual tolerance and behaviour changes in response to hypoxia depending on catfish body size.

Materials and methods

Study site

“Etang des Aulnes” is a shallow natural lake, mean depth 3.8 m, maximum depth 6 m, 104 ha area, located in South-Eastern France in a protected natural area. A primary canal and a secondary one collect irrigation waters that feed the lake. The lake then outflows in another canal (Figure IV.C.1). The lake water residence time is 300 days. The outflow is regulated to get high water levels in winter and low water levels in summer (maximal difference of 0.6 m).

The fish assemblage, determined by fyke nets, fishing traps and electro fishing in October 2017, 2018 and 2019 was composed of 16 species. The most dominant species were bream (*Abramis brama*, relative abundance 65%), European perch (*Perca fluviatilis*, 13%), pumpkinseed (*Lepomis gibbosus*, 8%), tench (*Tinca tinca*, 4%), pikeperch (*Sander lucioperca*, 4%), European catfish (*Silurus glanis*, 3%) and Northern pike (*Esox lucius*, 2%). In addition, two crayfishes were present: *Procambarus clarkii* and *Faxonius limosus*. Fishing is allowed but only during daytime from the eastern bank of the lake and no other activity is authorised.

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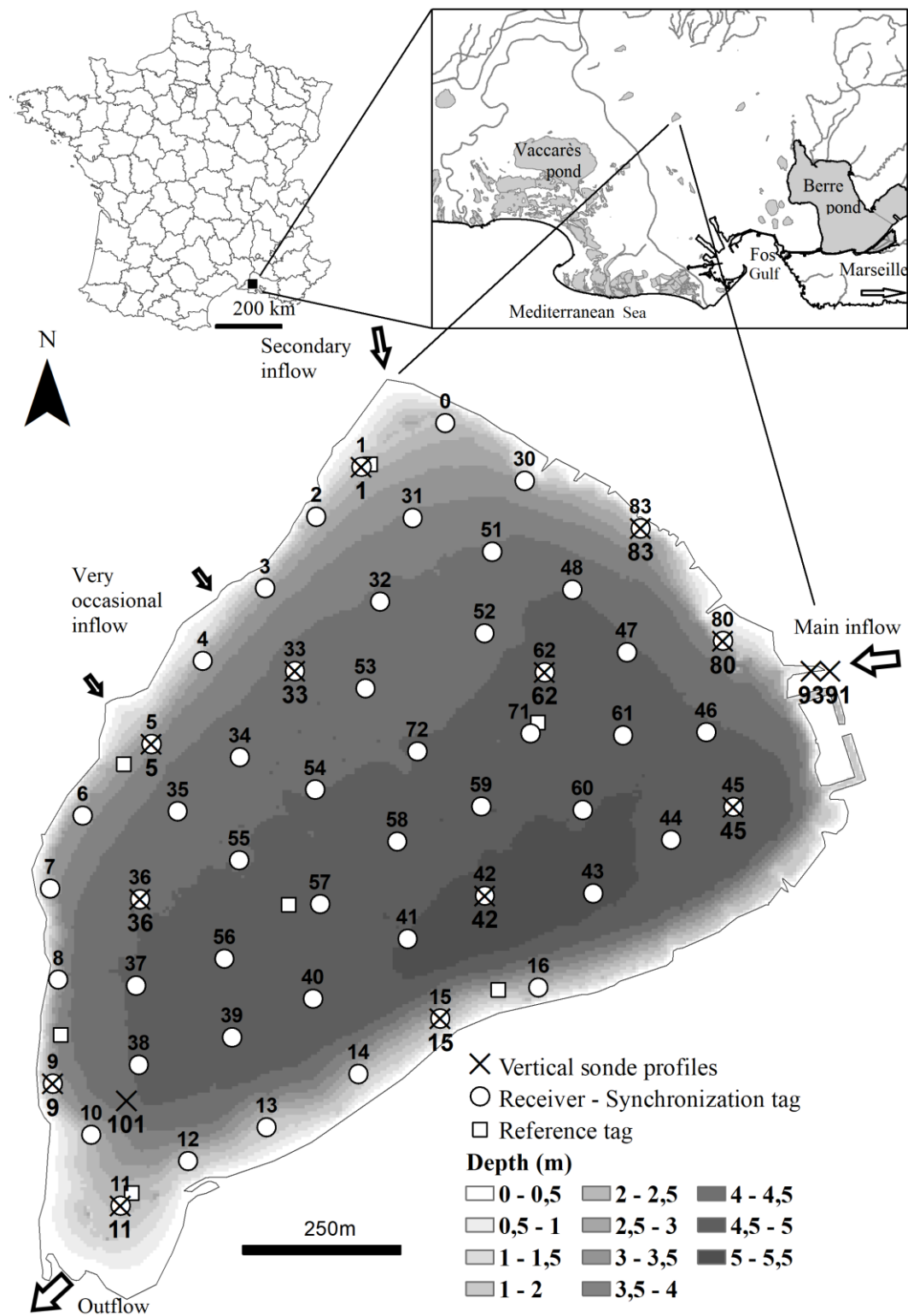


Fig IV.C.1 Bathymetric map of “Etang des Aulnes” at the water level of 11.14 m above sea level and experimental setup. Acoustic receivers and their associated synchronising tags are represented by white dots. Reference tags are symbolised by white squares. Monthly (and also

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hourly for location 42) temperature and dissolved oxygen concentration profiles are located by crosses; location 42 is the deepest in the lake. One primary canal flows into the lake on the eastern bank at location 91 and a secondary one on the northern bank close to location 0. The lake outflows in a canal at its extreme south-west

Physical and chemical lake conditions

Hourly vertical profiles of water temperature (0.5, 3 and 5 m above the bottom) and dissolved oxygen concentration (DOC) (0.5, 1.5, 2.5 and 3.5 m above the bottom) were recorded at the deepest point in the lake (location 42 on Figure IV.C.1). HOBO data loggers U22 were used for temperature and U26 for DOC. The dissolved oxygen saturation rate (DOS) was calculated from DOC and temperature values. At 0.5 m above the bottom, there were no records from 09-02 03:00 to 09-04 12:00, because of a sensor failure. 0.5-1.5 m, 2.5-3 m and 3.5-5 m heights of measurements above the bottom are named bottom, middle and surface, respectively, in the following text. In addition, vertical profiles of temperature and DOC were recorded on 09-04 with a YSI Exo2 multiparameter sonde at different locations in the lake to get a spatial picture of what happened all over the lake at different depths (Figure IV.C.1).

The mean hourly wind speed at a standard height of 10 meters above ground (10-m wind) was measured at the meteorological station of Salon-de-Provence, located 24 km east of the lake and representative of the weather conditions on the lake. The meteorological data were provided by Météo-France, the French meteorological institute, and available from the INRAE CLIMATIK platform (<https://intranet.inrae.fr/climatik/>, in French) managed by the AgroClim laboratory of Avignon, France.

Fish tagging

A total of 40 European catfish were caught by fyke nets, angling or electrofishing over two sampling campaigns: 10 in October 2017 and 30 in October 2018. Different techniques were used to sample the whole range of sizes among subadults and adults and individual behaviours (Harkonen et al., 2016). Once captured, catfish were stocked for a few hours in large aerated basins (2x1.25x0.5 m³) filled with regularly changed lake water to check their condition. Fish were then individually anaesthetised, which took 5-6 minutes, by immersion in a smooth and

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smaller tank $1.8 \times 0.5 \times 0.7 \text{ m}^3$ containing an aerated solution of benzocaine (80 mg/L). Once the fish had lost its balance (ventral side up), did not respond to stimuli anymore and had a very slow and steady operculum rate, it was weighed, measured and placed ventral side up in an identical tank containing an aerated solution of benzocaine (40 mg/L) to irrigate the gills during surgery. A 15 to 20 mm long incision was made with a scalpel in the middle of an imaginary line that would join the basis of the pectoral fin to the pelvic fin. An acoustic transmitter sterilised in surgical spirit and rinsed with physiological liquid was inserted into the peritoneal cavity. Vemco V13-1L acoustic transmitters (30.5 mm long, 9.2 g in the air, mean battery life 1825 days, 180 s - range 120-240s - mean burst interval for the 12 used in 2017 and 320 s - range 260-380s - in 2018) were used. The transmitter weight in the air did not exceed 2% of the fish body weight (Winter, 1996; Snobl et al., 2015). The incision was closed using 2 to 3 simple surgical sutures (3-0 Polydioxanon resorbable monofilament) placed 5 mm apart. An antiseptic and antibiotic dressing was applied on the incision wound to help healing and limit the risk of infection. Two surgeons took turn every four fish to operate, one fish surgery taking 5-6 min. Fish were then put in large, aerated recovery basins ($2 \times 1.25 \times 0.5 \text{ m}^3$), where they were continually observed until they recovered normal opercular activity, swimming ability, balance and behavioural response to stimuli, usually after 10 min. Fish spent 3 to 6 hours in this recovery basin before being released to their capture site. All individuals could be released in good shape. At the time they were tagged, total length of the 40 tracked European catfish ranged in [727; 2 150] mm (mean 1 033 mm) and weight in [2 301; 64 380] g (mean 9 658 g) (Table IV.C.1).

Fish tracking

An array of 52 underwater omnidirectional Vemco acoustic receivers (20 VR2W 69kHz and 32 VR2Tx 69kHz) with their associated synchronisation tag (additional V16-1L transmitter for VR2W and built in V16-like transmitter for VR2Tx, 500-700 s, used to correct for receiver internal clock drift) were anchored to the bottom throughout the lake from December 2017 (Figure IV.C.1). Seven reference tags (V13-1L, 840-960s) were added to detect anomalies in the tracking system. On average, neighbouring receivers were positioned 155 m from each other (range, 100-209 m), in 3.9 m water depth (range, 1.5 - 6 m), 0.5 m above the bottom. Receivers were removed roughly every 6 months to download fish detections. From these detections, fish

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Table IV.C.1 Total length (in mm, mean, sd in italics and range) and weight (in g, mean, sd in italics and range) of all 40 tracked catfish, 9 smallest, 24 medium and 7 largest ones.

	Total length (mm)	Weight (g)
All 40 individuals	1 033 (<i>328</i>) [727 ; 2 150]	9 658 (<i>13 389</i>) [2 301 ; 64 380]
9 smallest individuals	812 (<i>41</i>) [727 ; 847]	3 370 (<i>688</i>) [2 301 ; 4 180]
24 medium individuals	944 (<i>63</i>) [855 ; 1 060]	5 563 (<i>1 065</i>) [3 760 ; 7 680]
7 largest individuals	1 623 (<i>423</i>) [1 100 ; 2 150]	31 786 (<i>22 494</i>) [8 380 ; 64 380]

2D positions were calculated with the Vemco Positioning System (VPS) (Smith, 2013). The horizontal position error, a dimensionless parameter calculated by the VPS for each position, gives information on the quality of the position estimate, and was used to filter the data set (Espinoza et al., 2011b). Here, we retained only positions with horizontal position error not exceeding 100; this limit represented a good compromise between the mean position error (7.4 m) and the percentage of positions kept (87%).

Space use metrics

Fish have been continuously tracked from December 2017 but, here, we focused on ten days throughout August-September of 2019, when a severe hypoxic event occurred. Individual raw positions were interpolated using the R package *trajr* (McLean & Skowron Volponi, 2018) for each quarter hour between the first and the last position to get synchronised individual tracks. Interpolated positions from gaps in raw positions longer than 1 hour were discarded. These

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tracks were all together plotted on the lake map to create a video of the catfish displacements, useful to get insights on catfish space use (Suppl. Mat. IV.C.1). Distances between consecutive positions were computed and set to zero if less than the telemetry system mean position error (7.4 m). To represent fish swimming activity, for each individual and each hour, the mean speed (m/h) was calculated. A mean daily speed (m/h) was calculated for each individual if at least seven hourly mean speeds were available in a day. The mean distance of each individual to all others was calculated using the R package *spatstat* (Baddeley et al., 2015). The distance to shore of each individual was calculated using the R package *rgeos* (Bivand & Rundel, 2019). These distances were calculated for every quarter hour and averaged over every hour and every day. The individual daily home ranges were estimated with an Epanechnikov kernel as the utilization distribution with probability levels of 95% and 50%; the home range 50% is often referred to as the core area (Powell, 2000). These both metrics were also estimated for all pooled individuals over different periods of the ten days to map the areas used by the fish. These spatial analyses were conducted using the R package *adehabitatHR* (Calenge, 2006).

The video (Suppl. Mat. IV.C.1) showed an attractive location where individuals gathered. To identify possible differences in individual behaviours during the aggregation dynamics, we analysed input-output movements of every fish when they could be identified on video recording. We could extract the time when the fish reached the aggregation and stayed inside for 34 among 40 fish and the time when it definitively left (i.e. it did never swim back to the aggregation location) for 30 among 40 fish.

Statistical analyses

We applied an algorithm to detect possible breakpoints corresponding to structural changes in the 2-month time series of DOC and of the average hourly speed of all 40 individuals (Zeileis et al., 2003). This was done with the *strucchange* R package (Zeileis et al., 2002). Then, we compared the statistically detected breakpoints in each time series to identify potential concomitance between changes in fish swimming activity and DOC dynamics. Among these periods bounded by the breakpoints, one comprised the severe hypoxia. The same algorithm was re-run on the mean hourly speed within this period to detect possible different levels of catfish activity depending on the hypoxia severity. DOC was compared among these different

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periods of activity by Kruskal-Wallis tests and pairwise comparisons by Fisher's least significant difference (R package *agricolae*, de Mendiburu, 2020).

To assess relationships between fish behaviour (characterised by speed, distance to shore, distance to others and home ranges) and DOC, generalized linear mixed-effects models (Zuur et al., 2009) were used by focusing on this hypoxic period. To get rid of temporal correlation that impeded the model robustness, daily means of the different variables were used. After preliminary trials, fish size class and day gave from far the best model adjustments compared to size in mm and DOC, very probably because of threshold effects of DOC on the behaviour. Fish size was defined from body length measured during fish tagging, i.e. up to 22 months before the anoxic period, and was classified into three classes: “small”, “large” and “medium” corresponding to total length < 850 mm, ≥1100 mm and in-between, respectively (Table IV.C.1). The two extreme classes were considered in order to maximise the chances that the size of individuals from these both classes still differed in August-September 2019. The fish identity was considered as a random effect to explicitly account for individual variability. To take into account the skewed distribution of mean individual daily speed or distance to shore towards zero, a Tweedie family function with a log-link was used (Gilman et al., 2012).

The model could be written as follows:

$$\log(\overline{\text{METRICS}_{\text{ind}}}) = \alpha + \text{SIZE} * \text{DAY} + s(\text{ind}) + \varepsilon$$

where $\overline{\text{METRICS}_{\text{ind}}}$ is the expected daily mean individual speed, distance to the shore or home range, α is the overall intercept, SIZE is the size class (Table IV.C.1), $s(\text{ind})$ is a smoothing function modeling the individual effects (Wood, 2008), and ε is the error term following a normal distribution with zero mean. Means among days and among sizes by day were pairwise compared by using the *emmeans* R package (Lenth, 2016). The model fitting was assessed with regards to the homogeneity and normality of the residuals (Zuur et al., 2009) and to the percentage of explained variance (Hastie & Tibshirani, 1990). For mean individual distance to others, as we could not find a reliable model, we compared the distributions between days and between size classes among days by using Kruskal-Wallis tests and, if significantly different, we made pairwise comparisons by Fisher's least significant difference (R package *agricolae*, de Mendiburu, 2020).

All statistical analyses were made with R version 3.6.3 (R Core Team, 2020).

Results

DOC dynamics

The surface DOC showed large variations over August-September 2019 (Figure IV.C.2). A striking event occurred at the end of August when the surface DOC collapsed and, during several days, reached very low values (mean surface DOC was 1.2 mg/L over 08-29 – 09-04), even becoming null for 52 hours. This corresponded to a full anoxia which first appeared at the bottom on 08-26 and propagated at the surface to make the whole water column anoxic on 08-30 03:00 (Suppl. Mat. IV.C.2). At this time, water temperatures were stratified and ranged from 22.8 °C at the bottom to 26.7 °C at the surface (Suppl. Mat. IV.C.2). The anoxia ended on 09-02 16:00 when surface DOC raised up to 1.6 mg/L and the oxygenation was homogeneous over the whole water column (middle and bottom DOC respectively at 1.6, mg/L and 1.5 mg/L). One hour before, DOC was 0, 0.2 and 0.2 mg/L, at the surface, in the middle and at the bottom respectively. In parallel, water temperatures started to homogenize from 09-01 14:00 to be mixed on 09-02 04:00 (24.7 °C at the bottom and 24.8 °C at the surface). This was very linked to the wind that strengthened from 09-01 09:00 (greater than 3 m/s, Suppl. Mat. IV.C.2).

DOC dynamics and fish activity

Several structural change points were found in the hourly mean speed and DOC time series (Figure IV.C.2). The corresponding dates for 2-month speed time series matched well those of surface DOC. Worthy of note, they did not match with dates of changes of deeper DOC (Suppl. Mat. IV.C.3). In the next, we focus on surface DOC.

The 08-27 23:00 to 09-06 06:00 period, that comprises the full anoxia, shows very large variations of hourly speed that appear different from the diel cycle that could be observed outside of this period (Figure IV.C.2b). Within this period, four subperiods were detected: at the beginning, fish activity appeared quite similar to the previous period; then, speed sharply increased for 32 hours before fish suddenly stopped and performed very few movements during one and a half day, after which they started to progressively move again. The surface DOC was different between all four speed subperiods (Kruskal-Wallis test, $\chi^2=94.010$, 3 d.f., $p<0.001$): the surface DOC was 1.1 mg/L in average (DOS 13%) during the highest activity subperiod

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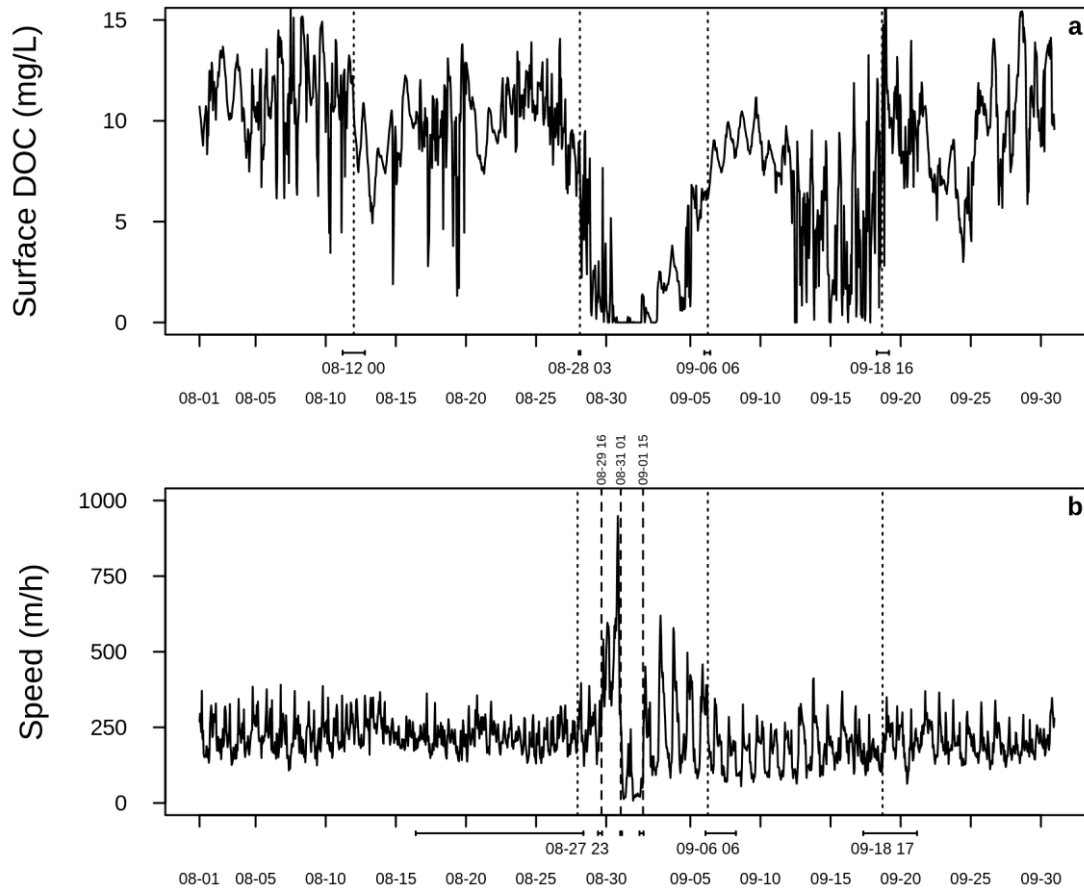


Fig IV.C.2 Catfish mean speed and surface DOC during the summer period (from 1st August to 30 September 2019). Panel a: hourly surface DOC (in mg/L at 3.5 m above the bottom at the deepest point of the lake, 5.5 m depth). Panel b: mean hourly speed over all individuals (in m/h). The dates of structural changes over the 2-month time series and their 95% confidence interval are labelled on the x-axis and represented by vertical dotted lines and interval at their basis. Hereafter, dates are given in the format mm-dd hh. These dates and associated 95% confidence interval are 08-27 23 [08-16 10 ; 08-28 09], 09-06 06 [09-06 02 ; 09-08 06] and 09-18 17 [09-17 08 ; 09-21 04] for mean speed, and 08-12 00 [08-11 05 ; 08-12 19], 08-28 03 [08-28 01 ; 08-28 04], 09-06 06 [09-06 00 ; 09-06 10], 09-18 16 [09-18 07 ; 09-19 04] for surface DOC. In addition, the dates of structural changes of mean speed time series within the period 08-27 23 to 09-06 06, comprising the anoxia, are labelled above the panel and represented by dashed vertical lines and associated 95% confidence interval at their basis

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and 0.1 mg/L (DOS 1%) during the lowest. The daily analysis also showed that the speed increase (on 08-30) and decrease (on 08-31 and 09-01) were significant (Table IV.C.2a, Figure IV.C.3b). This enhanced activity corresponded to higher individual home ranges (Tables IV.C.2c, IV.C.2d, Figures IV.C.3e, IV.C.3f) and to larger areas visited by the pool of individuals (Figure IV.C.4b). Conversely, the home range 95% as well as the core area were considerably reduced when the activity was the lowest (Figures IV.C.3e, IV.C.3f) and most of individuals gathered in a tiny area (Figure IV.C.4c) where they aggregated (Figure IV.C.3d). On 09-02, when fish recovered their activity, the areas they travelled over were still reduced (Figure IV.C.3f) and nearby the area where they had aggregated (Figure IV.C.4d).

The highest activity subperiod started when surface DOC dropped down to 1.3 mg/L (DOS 16%) and ceased when the whole water column became anoxic. After the reduced activity subperiod, fish started to progressively move again when surface DOC raised up to 0.7 mg/L (DOS 8%) whereas the half lower of the water column was still anoxic (Suppl. Mat. IV.C.2).

Table IV.C.2 Numeric results from the Generalized Linear Mixed-Effects Model that tested the fixed effects of fish size, day and their interactions on mean individual daily speed (panel a), mean individual distance to shore (panel b), individual home ranges 95% (panel c) and individual core areas (panel d). Fish identity was used as a random effect.

	Daily speed		a
	d.f.	F	p-value
Size	2	1.301	0.274
Day	9	12.083	< 0.001
Size: Day	18	3.897	< 0.001
Individual	16.26	0.79	0.004
Explained variance (%)	56.6		

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	Distance to shore		b
	d.f.	F	p-value
Size	2	3.163	0.043
Day	9	29.599	< 0.001
Size: Day	18	1.199	0.260
Individual	24.1	1.88	< 0.001
Explained variance (%)	59.6		
	Home range 95%		c
	d.f.	F	p-value
Size	2	4.689	0.010
Day	9	11.069	< 0.001
Size: Day	18	2.517	< 0.001
Individual	6.887	1.88	0.207
Explained variance (%)	53.7		

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	Core area	d	
	d.f.	F	p-value
Size	2	2.824	0.061
Day	9	11.984	< 0.001
Size: Day	18	2.963	< 0.001
Individual	15.67	0.712	0.001
Explained variance (%)	49.9		

Aggregation location and dynamics

From 08-31 to 09-01, catfish were almost inactive, closer to each other, closer to the bank and gathered in a same tiny area (Figures IV.C.3b, IV.C.3c, IV.C.3d, IV.C.4c). They aggregated where the main tributary flows into the pond. This was among the places that exhibited the highest DOC values recorded on 09-04 in the whole lake, a few days after the full anoxia (Figure IV.C.5). At the main inflow location (points 91 and 93), 1-m deep, DOC was near 8 mg/L (DOS 85%) and temperatures much cooler, 18°C against 23 - 24°C everywhere else (not shown).

The time span between the first fish to join the aggregation location and the last one was 26 hours 15 min (from 08-30 16:45 to 08-31 19:00), but 27 individuals joined the location in a short time, 4 hours 45 min (from 08-30 20:30 to 08-31 01:15). The dates at which individuals definitively left the aggregation location spanned over a much longer period: 3 days 6 hours 45 min (from 09-01 14:15 to 09-04 21:00). 26 individuals left it in 1 day 17 hours 45 min (from 09-02 02:15 to 09-03 20:00).

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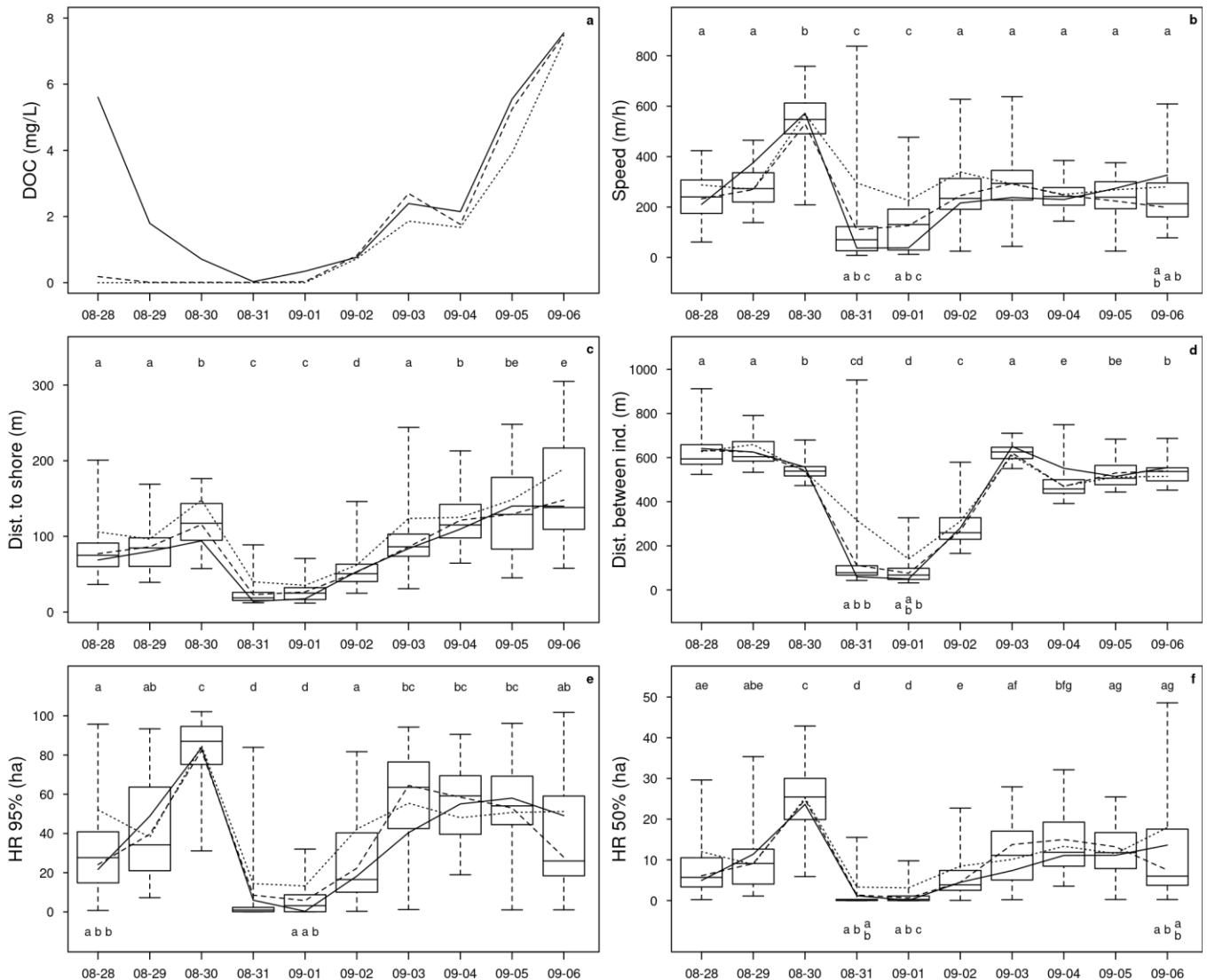


Fig IV.C.3 Catfish daily space use during the hypoxic period (from 28 August to 6 September 2019). Panel a: mean daily DOC (at 1.5, 2.5 and 3.5 m above the bottom in dotted, dashed and solid line respectively) at the deepest point in the lake, 5.5 m deep. In panels b, c and d, the boxplots represent the minimum, the first quartile, the median, the third quartile and the maximum of the distribution. In panels b, c and d, the dotted, dashed and solid lines represent the daily means over small, medium and large catfish respectively. Panel b: distribution of mean daily individual speeds (m/h). Panel c: distribution of mean individual daily distances to all others. Panel d: distribution of mean individual daily distances to shore (m). Panel e: distribution of individual home ranges 95% (hectares). Panel f: distribution of individual home ranges 50% (hectares). Letters above the boxplots stand for post-hoc comparisons between days: days which share a same letter have distributions which do not significantly differ (at the

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5% significance level). Letters below the boxplots stand for comparisons between sizes within a day; no letter means the three sizes do not differ; sizes that share the same letter do not significantly differ (within a day, letters from left to right correspond to small, medium and large catfish, respectively). As the interaction between size and day was not significant for distance to shore, the comparison between sizes within a day has not been performed

Fish behaviour and size dependence

The swimming activity, proxied by the mean daily speed, was significantly different among the days during the hypoxic event, and, some days, size class behave differently (Table IV.C.2a). The distance to shore was dependent on fish size and also different among days (Table IV.C.2b). In details on Figure IV.C.3b, whatever their size, all fish significantly increased their activity on 08-30 when the bottom anoxia was propagating to the surface. This corresponded to higher individual core areas for all fish whatever their size and, to a lesser extent, home ranges 95% (Figures IV.C.3e, IV.C.3f). On both following days, when the whole water column was anoxic and fish swimming activity the lowest, the larger individuals were even less active than the smaller ones (Table IV.C.2a, Figure IV.C.3b) and occupied a more reduced area on 09-01 (Tables IV.C.2c, IV.C.2d, Figures IV.C.3e, IV.C.3f); the smaller individuals were further to others than the larger ones (Figure IV.C.3d). In general, the smaller fish were further to the shore (Table IV.C.2b, Figure IV.C.3c, p-values of pairwise comparisons between Small and Large and Small and Medium <0.001) and had larger home ranges 95% (Table IV.C.2c, Figure IV.C.3e, p-values of pairwise comparisons between Small and Large and Small and Medium <0.05).

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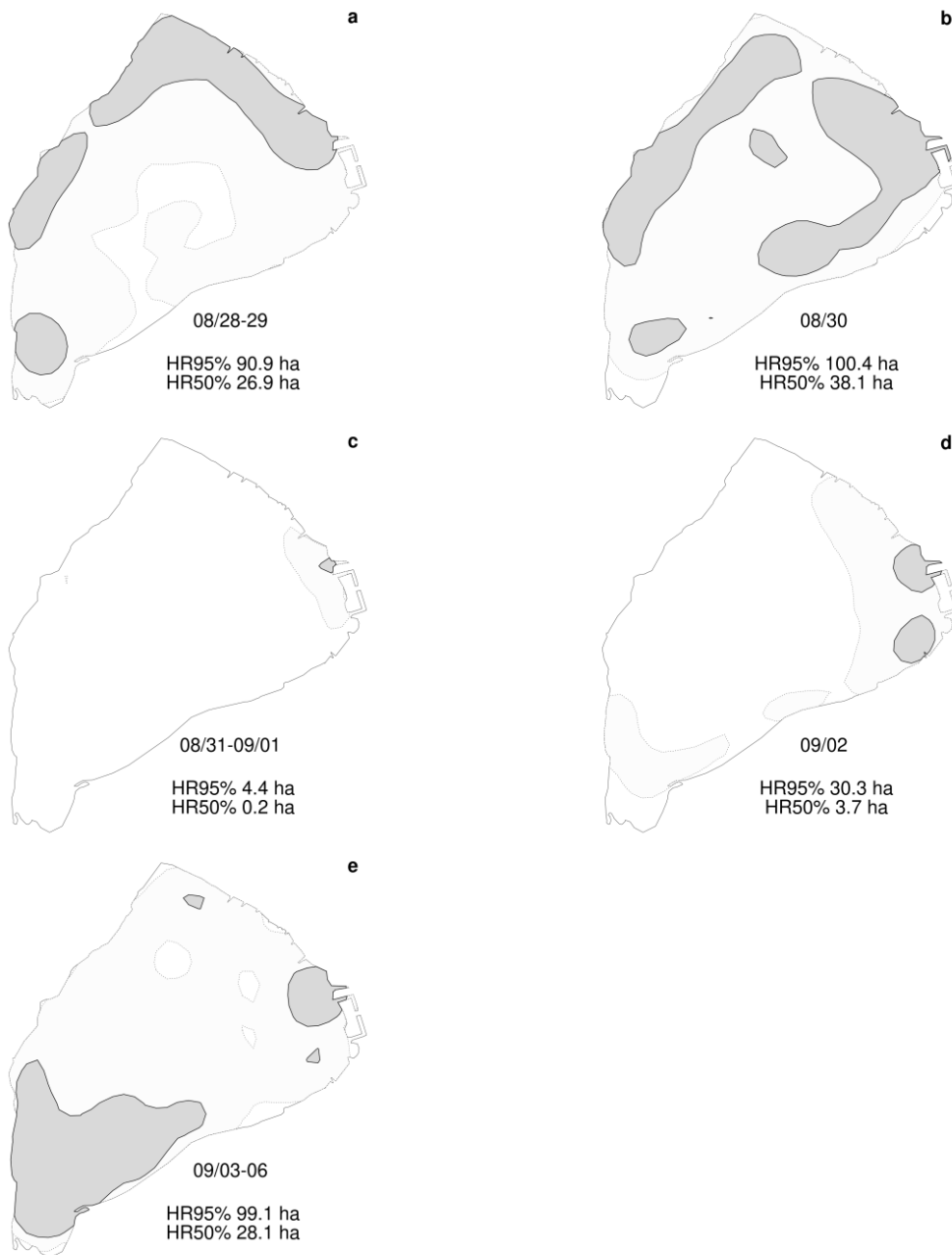


Fig IV.C.4 Catfish home ranges during the hypoxic period (from 28 August to 6 September 2019). The home range 95% and the core area (home range 50%) are mapped in pale grey with a dotted contour and in grey with a solid contour, respectively. They have been calculated with all pooled individuals over different grouping days brought out from figures IV.C.3e and IV.C.3f. Panel a stands for days 08-28 and 08-29, b for day 08-30 when the activity was the highest, c for days 08-31 and 09-01 when the activity was the lowest, d for day 09-02 when fish recovered their activity and e for days 09-03 to 09-06. The corresponding areas (in hectares) are given in each panel

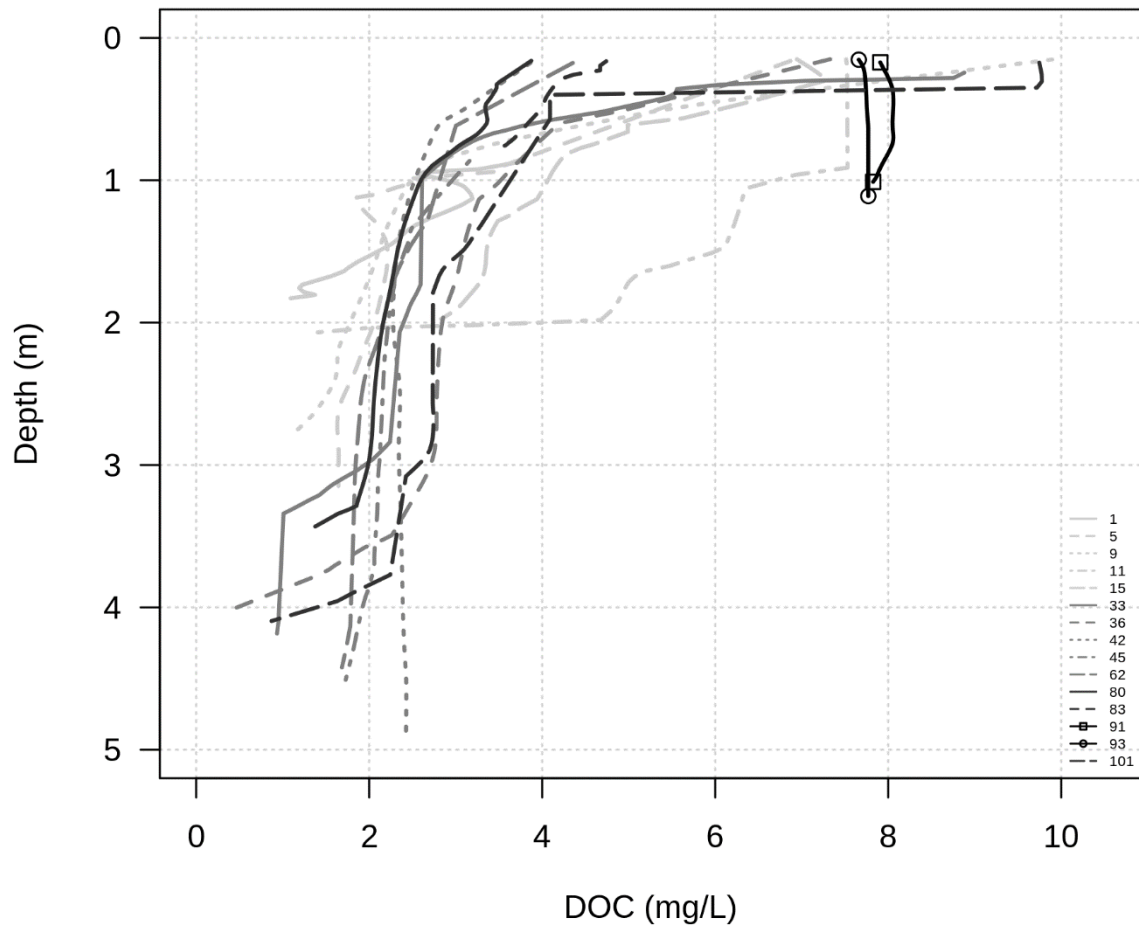


Fig IV.C.5 Vertical profile of DOC at different locations in the pond on 09-04. The labels of the legend correspond to the different locations labelled on the lake map and symbolised by a cross. Data go from the surface to approximately 0.5 m above the bottom. Points 91 and 93 are located near the main inflow and point 11 is the closest to the outflow

Discussion

Our dataset gave an excellent context to analyse the *in situ* response of a species to an environmental stress. The high resolution and high frequency of the positions collected by telemetry and the number of tagged individuals allowed to detect changes in behaviour at individual level and at timesteps suitable to be confronted with DOC variations (Bauer & Schlott, 2006; Daněk et al., 2014).

Catfish tolerance to low DOC

All the 40 tagged catfish survived the severe hypoxic event that lasted more than two days and led to the death of lots of other fish, including species known to manage very well with low oxygen conditions such as carp and eel (Weber et al., 1976; Gesser, 1977). Subadult and adult European catfish could go through very low oxygen conditions during the summer when water temperatures ranged in 23-27 °C. Their behaviour was impacted only when, at the deepest point in the lake, the lower half of the water column was anoxic and when DOC dropped down to 1.3 mg/L (corresponding to a mean DOS of 16%) in the upper half. This DOC value was in the lower range of what Daněk et al. (2014) found on juvenile catfish, 1.3-2.4 mg/L in winter conditions (water temperature around 5 °C). It was in the range of Massabuau & Forgue (1995) laboratory results which concluded that very young catfish (weighing 100-150 g) could maintain dioxygen homeostasis in 1-1.5 mg/L DOC range at 13°C and even very probably in a 10-23 °C temperature range. However, increased temperature lessens oxygen solubility and thus reduces oxygen supply for ichthyofauna; it also elevates basal oxygen demand (Rogers et al., 2016). With comparable critical DOC but higher temperature, we can thus reasonably hypothesise that oxygen supply was more critical in our study. The possible lower critical oxygen threshold in our study could be explained by large differences in catfish body weights between studies. Large fish could have an advantage thanks to their lower mass-specific metabolic rate (Nilsson & Östlund-Nilsson, 2008). These tolerance values were in all cases much lower than the limit of 3-3.5 mg/L reported by Mihalik (1995).

Catfish behaviour in response to the hypoxia extent

Horizontal catfish movements were not altered when anoxia was limited to the half lower part of the lake. However, these extreme conditions are likely to considerably reduce the suitable habitats regarding oxygen conditions in this shallow lake, by the way compressing fish habitat (Kraus et al., 2015). The tags did not record the pressure and thus could not provide information on fish depth. Nevertheless, we could suppose that catfish rose to the surface layer to find tolerable DOC, while they are known to mainly occupy benthic habitats (Bruton, 1996; Cucherousset et al., 2018). This remains questioning. One day before complete anoxia at the deepest point of the lake, catfish exhibited a sudden higher level of activity and unusual large displacements over greater areas for about one day, all fish sizes alike. Many fish species change

IV.C Impact of hypoxic conditions on the habitat niche of a population of freshwater predators

their spontaneous swimming activity when exposed to hypoxia, reducing or increasing their activity (Chapman & McKenzie, 2009). Usually, sedentary species decrease their swimming speed to save energy (Domenici et al., 2013). Crucian carp (*Carassius carassius*) that can endure anoxia for several hours and even days (at 9 °C) reduces its activity by 50% (Nilsson et al., 1993). The increased activity observed in the tagged catfish was unexpected for such a large species that tries to reduce its energy costs (Slavík et al., 2014) and usually performs few movements (Carol et al., 2007; Capra et al., 2018). The stress caused by the resource unavailability can significantly increase catfish movement activity (Slavík et al., 2016). Intense agitation of fish in deep hypoxia could also be interpreted as an avoidance response that helps to find a more suitable place (Domenici et al., 2000; Herbert & Steffensen, 2006; Chapman & McKenzie, 2009) as catfish not only became faster but also explored extended areas. Such an increase in activity was also observed on juvenile catfish facing dissolved oxygen deficiency before they found a refuge (Daněk et al., 2014) or on school of Atlantic herrings (*Clupeus harengus*) whose speed peaked during severe hypoxia before decreasing until the school disrupted (Domenici et al., 2000). The reasons for such an agitation need further investigations.

Aggregation and refuge location

Most of catfish finally converged and gathered where the main canal flows into the lake. They stayed there or in close vicinity by considerably reducing their swimming activity for one and a half day. With the inflow canal, this gathering place was likely the most oxygenated in the lake, able to fulfill their oxygen requirements. In this summer period, irrigation led to quite a strong current in the main canal that continuously brought cool and well oxygenated water flowing through the gathering place. This place and places very close to the bank outside the receiver network were in general at the edge of the telemetry coverage area so that individuals were less often located during the anoxia (Smith, 2013), which could sometimes be visible on the video (Suppl. Mat. IV.C.1). Overall unsuitable environmental conditions temporarily forced catfish to share very limited space and resources. As a consequence, competition between individuals likely increased. European catfish have been reported to actively defend their access to resources (Cucherousset et al., 2018) and have been shown to expend more energy when in contact with conspecifics in preferred areas of habitat (Slavík & Horký, 2009). This could give advantage to the biggest individuals. High body mass was also shown to decrease stress from

IV.C Impact of hypoxic conditions on the habitat niche of a population of freshwater predators

limited availability of resources (Slavík et al., 2016) which could explain why the smallest individuals were more active and further from the shore than the biggest during the anoxic event. Catfish aggregation, that can be compared to a school, led to a high oxygen consumption. According to the position in this school, in front of the inflow current or in the rear of the school, DOC can vary a lot so that some individuals need to change position leading to a reshuffle (Domenici et al., 2002; Herbert & Steffensen, 2006). The largest catfish, dominant, could occupy the most suitable positions, while the smallest individuals would be left with the least favourable ones and would then move much more often to change position toward better-oxygenated areas in the aggregation.

Remarkably, the synchronisation they showed to join the refuge place contrasted with the time needed for all individuals to definitively leave the location. This would also need further investigations.

Hypoxic conditions are likely to become more frequent and severe with temperature rising and increasing eutrophication of ecosystems due to human activities. Aside temperature, DOC is a key environmental parameter driving space use by fish population. The ability of catfish to withstand very low DOC, along with its high optimum temperature range, could lead to an extent of the suitable geographical range for this species in the future. This is important to account for when engaged in conservation or fisheries management.

Acknowledgements

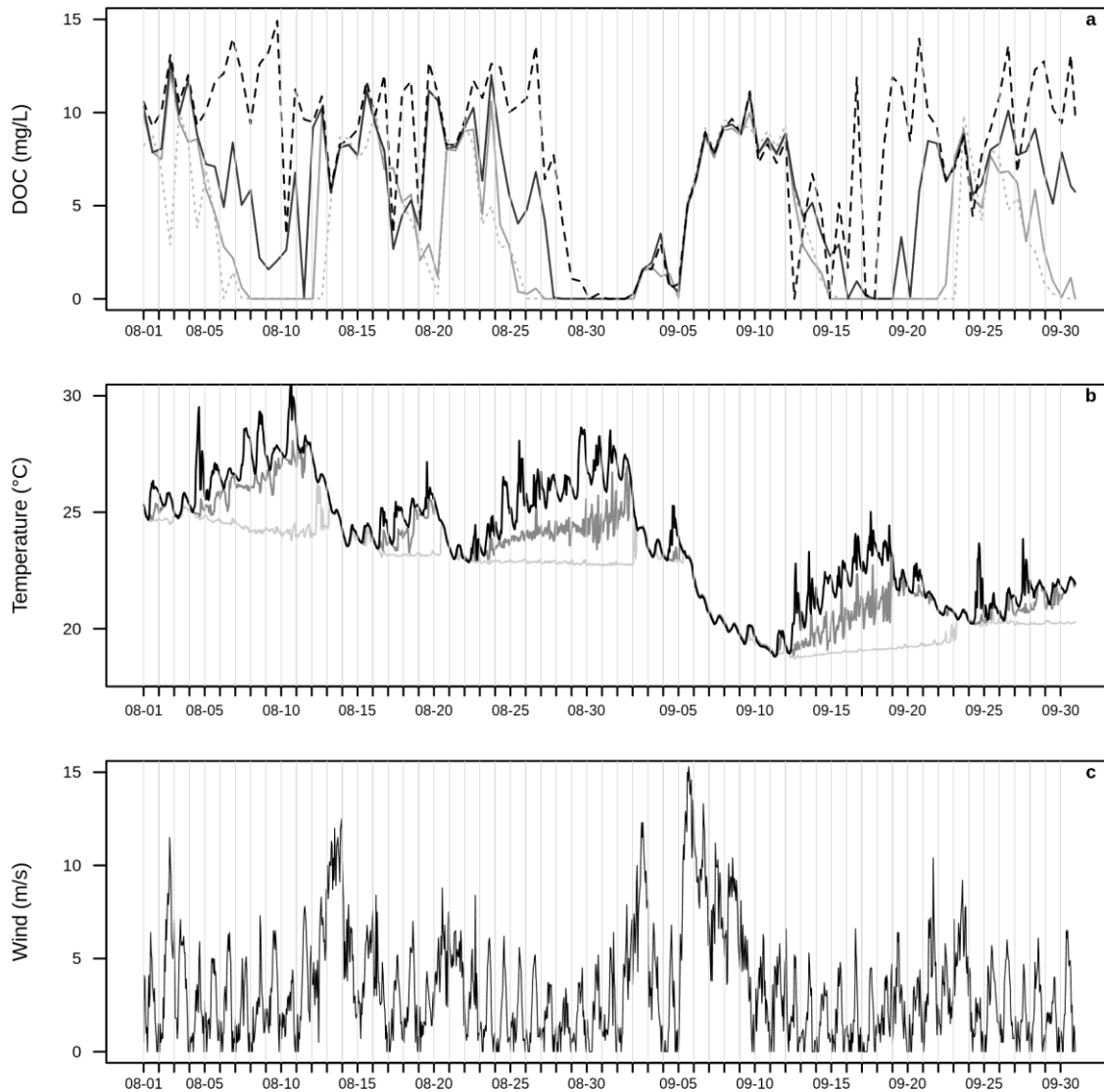
We are very grateful to Virginie Diouloufet, Julien Dublon, Dorian Milesi and Ange Molina for their investment in the field work and data entry and to Yann Le Coarer and Nathalie Reynaud for dGPS treatments including fieldwork support. We would like to thank Maïlove Benoliel, Léa Voisin and numerous other people who occasionally helped in the field as well as Coralie Garron for English correction of this manuscript. We also thank Lionel Allègre, Stéphanie Bertrand and Dominique Ghione for their warm welcome and logistical support on the study site. Finally, we appreciated the positive and relevant comments of the two reviewers, Johann Mourier and an anonymous reader, that significantly improved the finished document. This project was in part funded by the “Département des Bouches-du-Rhône”.

4. *Supplementary materials*

Suppl. Mat. IV.C.1 Video of catfish movements over 25 August - 6 September 2019. Top panel: hourly DOC (at 0.5, 1.5, 2.5 and 3.5 m above the bottom in dark green, light green, orange and red line respectively, on the left axis) and hourly temperature (at 0.5, 3 and 5 m above the bottom in blue, violet and cyan line, respectively, on the right axis) at the deepest point in the lake, 5.5 m deep. Bottom panel: tracks of the 40 catfish, each represented by a different colour, at each quarter hour. A dot symbolizes the position of a catfish at the indicated date. If available, it is joined to the previous position by a segment, itself joined to the position corresponding to half an hour before. A circle corresponds to the position at the previous quarter hour joined to the position at the previous half of an hour by a segment; a single circle locates the position at the previous half of an hour. The lake background colour symbolizes the bathymetry from 0 to 5.5 m by 0.5 m, the deeper is the blue the deeper is the zone.

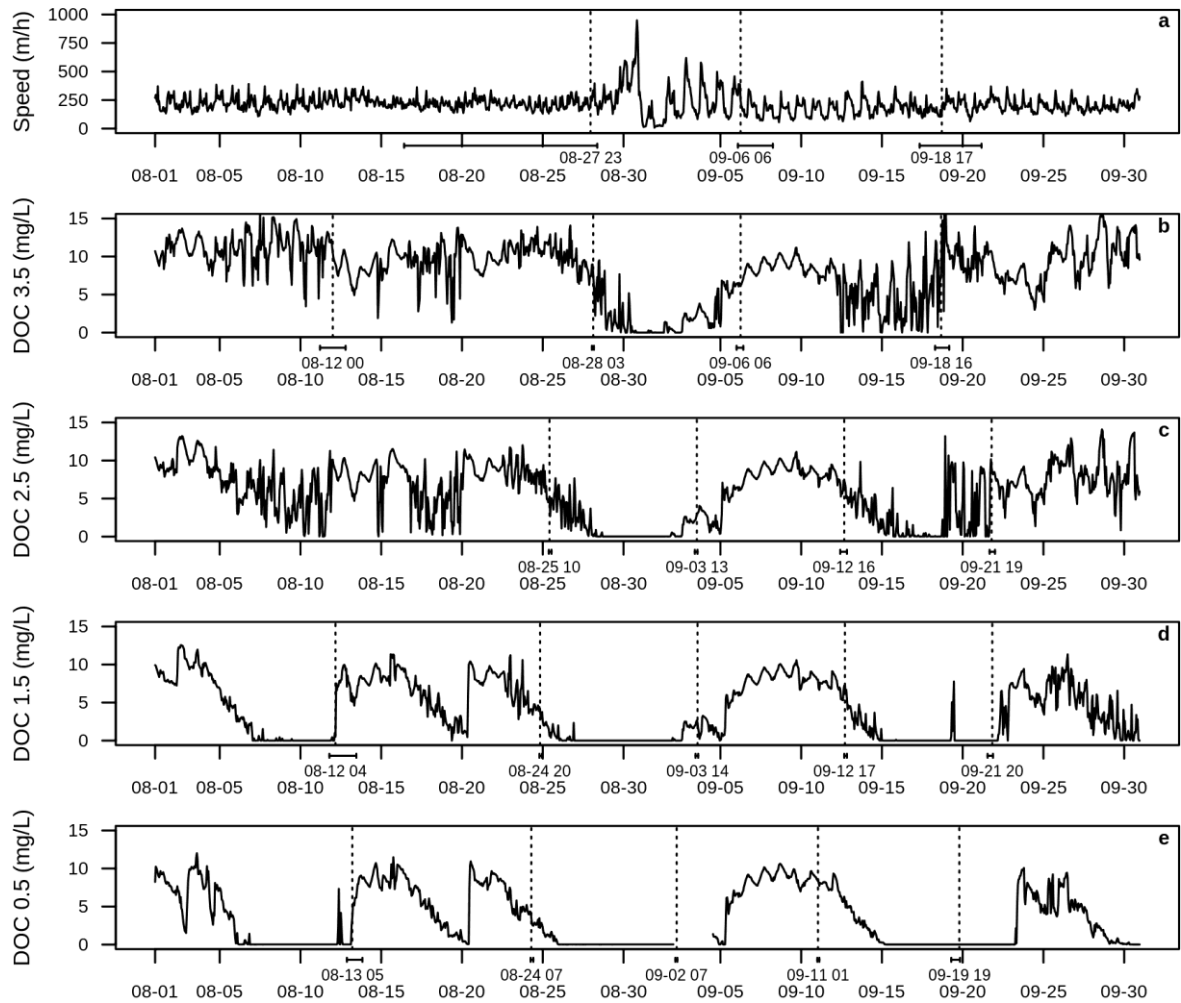
<https://link.springer.com/article/10.1007/s10452-022-09952-y#Sec18>

IV.C Impact of hypoxic conditions on the habitat niche of a population of freshwater predators



Suppl. Mat. IV.C.2 Environmental conditions during the summer period (from 1st August to 30 September 2019). Panel a: hourly DOC (in mg/L at 0.5, 1.5, 2.5 and 3.5 m above the bottom in light grey dotted line, medium grey solid line, dark grey solid line and black dashed line respectively. Data have been smoothed over 3-hour window for a better readability) at the deepest point in the lake, 5.5 m deep. Panel b: hourly temperature (in °C at 0.5, 3 and 5 m above the bottom in light grey, medium grey and black solid line, respectively, on the left axis) at the deepest point in the lake. Panel c: mean hourly 10m wind speed (m/s)

IV.C Impact of hypoxic conditions on the habitat niche of a population of freshwater predators



Suppl. Mat. IV.C.3 Catfish mean speed and DOC vertical profile during the summer period (from 1st August to 30th September 2019). Panel a: mean hourly speed over all individuals (m/h). Panel b: hourly DOC 3.5 m above the bottom (mg/L). Panel c: hourly DOC 2.5 m above the bottom (mg/L). Panel d: hourly DOC 1.5 m above the bottom (mg/L). Panel e: hourly DOC 0.5 m above the bottom (mg/L). The dates of structural changes over the 2-month time series are represented by vertical dotted lines. Their 95% confidence interval are represented by line segments below the x-axis

V.

Discussion and perspectives

V. Discussion and perspectives

A. Synthesis of results

My research gave evidence of habitat and trophic niche partitioning among species in freshwater predator communities, probably as a way to limit interspecific competition and thus stabilize species coexistence, in accordance with ecological theory (Chesson, 2000). Yet, in both these niche components, the variation among individuals or intraspecific variation was often very large. Environmental conditions have been shown to drive species niche; in particular, they could impact species abundance and, in turn, species' trophic niche. Seasons impacted species' habitat niches that overlapped more in low activity seasons (autumn, winter). In some specific environmental conditions, at seasonal or daily timescales, habitat niche shifts could be extreme, such as winter aggregation of catfish or grouping of catfish in a refuge area during hypoxic event. This very probably impacted within-species interactions.

B. Habitat and trophic partitioning

In the Bariousses reservoir, pike, perch and pikeperch segregated their habitat, even if this partitioning was buffered in cold season. An important question that remains unanswered relates to the respective importance of the 'fundamental niche' and the 'realized niche' in this partitioning. Indeed, these three predators differ in terms of their ecological traits (see II.B.1), which could drive differences in their fundamental habitat niches (Violle, 2009). In a lake inhabited only by pike and perch, large perch were exclusively pelagic during daytime (Hölker et al. 2007). In a manipulative experiment that consisted of introducing pikeperch in this lake, perch shifted their habitat use towards the littoral while pike was hardly affected (Schulze et al., 2006). Following pikeperch introduction, perch shifted to partially occupying both pelagic and littoral habitats (Hölker et al., 2007). Perch modified their habitat niche to minimize the interaction with pike and pikeperch. The fundamental habitat niche of pike and pikeperch appears very complementary, and we can reasonably suppose they could coexist without strong competitive interactions for habitat. Pike is an ambush predator that is mainly littoral and diurnal (Eklov 1992, Craig 1996) while pikeperch usually frequents the pelagic zone and is highly active during the night (Vehanen & Lahti, 2003; Huuskonen et al., 2019). The habitat niche of large perch was situated between these two extremes, in agreement with our observations in the Bariousses reservoir. The plastic behavior of perch very probably facilitated

this coexistence (Craig 2000, Olsson 2007). The evaluation of the habitat niche of these predatory species in different sites with different assemblages would provide useful information and would shed light on how much species modify their preferred niche to coexist, depending on the piscivorous guild composition.

Regarding the trophic niche, we examined how this assemblage with catfish shared resources in “Etang des Aulnes”. Likewise, trophic niche partitioning was observed between the four species. Greater abundance of a species generally led to an enlargement of its trophic niche and a greater trophic diversity among individuals, probably as a way to buffer intraspecific competition by expanding its niche to less valuable resources (Svanbäck & Bolnick, 2007; Araújo et al., 2011). This mechanism contributed to the preservation of body condition of fishes, and strengthened the food web resilience to ecosystem changes (Wellard Kelly et al., 2021). Remarkably, our results illustrate how stabilizing mechanisms that were originally developed in niche theory promote coexistence in wild ecosystems. Perch had the most variable trophic niche size, which correlates with its plasticity in habitat use. Surprisingly, YOY catfish, a generalist predator that feeds on a large range of resources at least when adult (Vejřík et al., 2017; Vagnon et al., 2022), had a narrower niche than specialist species like pikeperch or pike, and did not widen its trophic niche even when more abundant, contrary to pikeperch or pike. At first, this could appear contradictory to what is expected from a generalist (Araújo et al., 2011; Cicala et al., 2020; De Santis et al., 2022), but it could in fact underscore an alternative generalist behavior: instead of individually focusing on more or less specific resources via individual partitioning (Bolnick et al., 2007; Svanbäck & Bolnick, 2007; Araújo et al., 2011; Sheppard et al., 2018), catfish individuals may feed on the same wide spectrum of resources, which in turn results in the same average isotopic signature among individuals (Bolnick et al., 2003; Stewart et al., 2021) (Fig V.B.1). Furthermore, the recent successful invasion of introduced catfish in western Europe (Copp et al., 2009) might have been facilitated by its trophic generalism (Gozlan et al., 2010; Volta et al., 2013; Jackson et al., 2016; Cathcart et al., 2019; Cicala et al., 2020). The coexistence of these four species was probably favored by the assemblage of more specialized species like pike and pikeperch (Schulze et al., 2012) and more generalists like perch and catfish (Craig, 2000; Vagnon et al., 2022). Again, it would be worth performing such studies in different sites with different assemblages to estimate the sensitivity of species’ trophic niche to the predatory assemblage.

Although YOY have to deal with a significant predation pressure (Hölker et al., 2007; Wellard Kelly et al., 2021), here we did not consider the predation risk from piscivorous adults, which

could however impact juvenile habitat use and consequently their trophic niche (Svanback & Eklov, 2002; Araújo et al., 2011). We actually hypothesized that competition within the same YOY predatory guild was the dominant pressure as piscivorous adults can prey upon a much more abundant cyprinid community in “Etang des Aulnes”. Evaluating the predation pressure, that could act as an equalizing mechanism between species, would bring useful additional information to interpret the observed patterns.

C. Environmental conditions and niche variation

Among the causes of population niche variation, environmental changes stand as a major driver (Chesson & Huntly, 1997; MacDougall et al., 2018; Liu et al., 2021; Stewart et al., 2021). Environmental fluctuations influence organisms not only directly, but also indirectly by driving species interactions (Chesson, 1988; Liu et al., 2021). The different case studies exposed in this research strengthen the close links between ecological niche and environmental conditions.

Perch shifted its habitat niche between seasons and habitat partitioning seemed to be relaxed among predators in winter. Periodic seasonal variation creates temporal niches (e.g. cold or warm season) that could promote partitioning of food resources and thus stabilize the coexistence; species with low preferred temperature like pike, and perch to a lesser extent, could continue being relatively active in winter compared to species from warm guild like pikeperch (Shuter et al., 2012; Speers-Roesch et al., 2018). Species from warm guild reduce activity to save energy in the cold season (Speers-Roesch et al., 2018). This was observed in catfish during their long-lasting seasonal grouping, with individuals making few excursions outside the aggregation. Even if this likely enhanced competition among individual catfish, competition was limited by the reduced feeding activity during this period (Cucherousset et al., 2018). In this way, the concentration of catfish at the same place over a long period could have contributed to the availability of resources and habitats for species from colder guilds.

Unsuitable dissolved oxygen concentrations temporarily forced catfish to share very limited space. However, this occurred over very short periods (~ 2 days) and the consequences on the catfish population itself were probably very limited. Indeed, afterward, we showed that catfish could resist these extreme oxygen conditions; moreover, catfish do not need to feed daily (Vejřík et al., 2017). This forced inactivity period for about 2 days was probably not damaging.

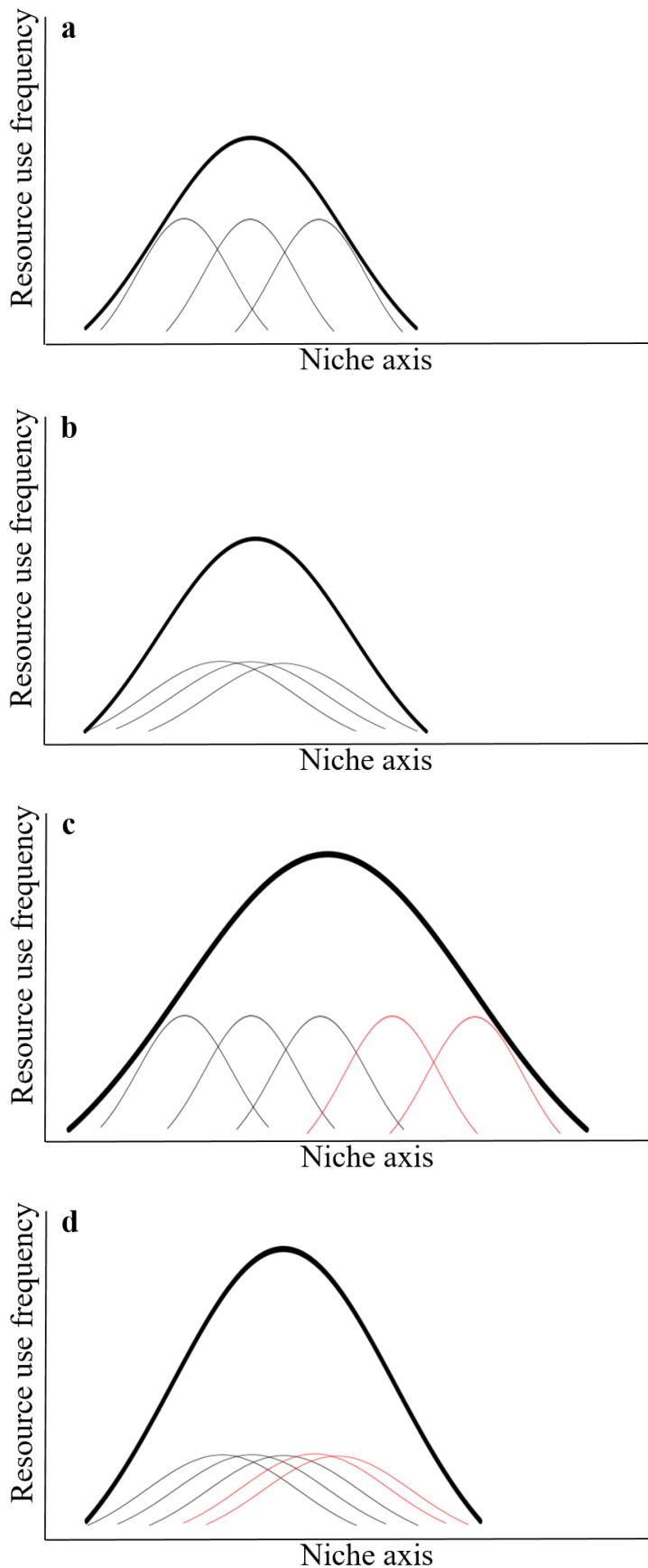


Fig V.B.1 : Figure inspired from Bolnick et al. (2003). Schematic diagram of how individuals (thin curves) can contribute to the population's niche (thick curve). Here are cases wherein a population is composed of individual specialists (a) and of generalist individuals (b). In (a), the intraspecific variability is higher than in (b). In the case of individual specialists, the increase in population abundance (red curves in addition to black ones) leads to an enlargement of the population niche (c). In the case of individual generalists, the increase in the population niche does not greatly impact the population's niche (d). Wild populations are likely much more complex and could contain both generalized and specialized individuals, unlike the schematic diagrams shown here.

But, this anoxia in “Etang des Aulnes” in 2019 very likely led to the collapse of the YOY pikeperch cohort (mass mortality was observed after this event), pikeperch being particularly sensitive to low DOC (Dolinin, 1974). Conversely, the YOY catfish cohort, that can withstand low DOC (Daněk et al., 2014; Westrelin et al., 2022), was unusually abundant. The YOY predator community was very different from other years, consequently affecting species interactions. In 2020, the YOY pikeperch cohort was substantially larger than other years. This temporal variability in species abundance illustrates the storage effect as a coexistence mechanism (Chesson & Warner, 1981; Chesson, 1994): species benefit differently from changes in year-to-year environmental patterns, some years being beneficial for some species others being advantageous for others. Good years allow species to survive bad years and to coexist in the long-term. In the end, these environmental fluctuations did not impact fish body condition in “Etang des Aulnes”, contrary to what Olin et al. (2017) observed on roach *Rutilus rutilus*. This might be explained by relatively abundant resources in the eutrophic “Etang des Aulnes”, including the use of a wider range of resources if preferred resources became scarce which would fit the resource diversity hypothesis (Costa-Pereira et al., 2019).

When environmental stochasticity is so strong that it leads to conditions that overwhelm the repertoire of species survival strategies, we can reasonably hypothesize that it becomes detrimental (Kim & Ohr, 2020). This is the case for anoxia on YOY pikeperch. In a way, this is also the case for water level fluctuations in reservoirs that can have deleterious impacts, for example by preventing access to critical habitats (e.g. littoral vegetated spawning habitat for pike, that is often stocked in reservoirs), by dewatering spawning grounds and desiccating eggs or even by damaging habitats irreversibly (Winfield, 2004; Hudon et al., 2005; Evtimova & Donohue, 2016). Unexpectedly, perch habitat use was not impacted by WLF but mainly by seasonal changes. Here, the plastic behavior of perch is probably key. Moreover, we expect that the history of WLF probably shaped current population and selected individuals with the most adapted traits (Olsson et al., 2007; Kelley et al., 2018; Shuai et al., 2018), thus buffering the expected impacts of WLF on perch habitat use.

D. Habitat structure and niche

From our personal observations, the shallow lake “Etang des Aulnes” experience year-to-year variations in macrophyte coverage (in spring and summer) with a shift from a macrophyte-dominated state to phytoplankton-dominated state, that can significantly modify basal resources

and impact the whole food web (Sagrario et al., 2018; Xu et al., 2019; Mao et al., 2021; Stewart et al., 2021). In the macrophyte-dominated state, food webs were ^{13}C -enriched compared to algae dominated food webs that were ^{13}C -depleted and ^{15}N -enriched (Sagrario et al., 2018; Xu et al., 2019; Mao et al., 2021). Interestingly, in our isotope data, we found years when the ^{13}C enrichment of the food web was higher (2018, 2019) compared to years when the food web was ^{13}C -depleted and ^{15}N -enriched (2020, see Suppl. Mat. III.B.4). The macrophyte coverage can be approximately proxied by the yield of the telemetry system (typically, the ratio of the theoretical number of emissions to the recorded number of detections for reference tags) as macrophytes stand as a physical barrier to acoustic signal propagation (Thiemer et al., 2022): the more dense macrophytes are, the lower the yield is. Our field observations in “Etang des Aulnes” reported a high macrophyte coverage in 2018, average coverage in 2019 and much lower coverage in 2020 which correlated with year-to-year variation in the telemetry yield. Importantly, these observations were particularly correlated with ^{13}C enrichment of the food web in 2018 and to a lesser extent in 2019 and ^{13}C depletion and ^{15}N enrichment in 2020 (see Suppl. Mat. III.B.4). Though, this requires further research which would further illuminate the ecological processes related to predator activity and space-use. Getting an accurate estimate of the macrophyte coverage would provide an interesting feature of the lake (e.g. Winfield et al., 2007). Indeed, habitat structure, here macrophyte density, can shape predator-prey interactions by impacting foraging (e.g. Skov et al., 2002; Skov & Koed, 2004; Lund et al., 2010), which consequently affects the strength of resource partitioning among predators (Hughes & Grabowski, 2006).

E. Limitations, improvements

Throughout this research, the sex of individuals was mostly unknown, and, consequently, sexual variability was not evaluated. Indeed, some differences in behavior or diet can originate from sex (e.g. Bulté et al., 2008; Bell et al., 2009; Radabaugh et al., 2010; Mourier et al., 2012; Jacoby et al., 2016; French et al., 2018) even if phenotypes unrelated to sex exist (e.g. Kobler et al., 2009; Radabaugh et al., 2010; Pérez-Bote & Roso, 2012; Colborne et al., 2019; Djait et al., 2019). In the future, it would be interesting to test the importance of sexual variation, implying the acquisition of sufficiently large sample sizes.

Particularly in the “Etang des Aulnes” experiment, it would have been worth tracking other species in addition to catfish, to gain insights into their interactions. However, in our acoustic

telemetry experiments, the number of tagged and tracked animals was already a compromise between the burst interval and signal collisions to get enough positions for a significant pool of individuals. Signal collisions occur when a hydrophone simultaneously receives emissions from several neighboring fish, meaning that it is not able to record all of them (Orrell & Hussey, 2022). This limitation is specific from our telemetry system and is now less likely to happen with new generation equipment (Orrell & Hussey, 2022), but it is an unaffordable investment to replace as many as fifty receivers.

In addition to their use for positioning, tags can contain sensors that record information on the physiological status, activity of fish and also their environment (e.g. acceleration, heart rate, tilt angle, temperature) (Hussey et al., 2015; Whitford & Klimley, 2019; Nathan et al., 2022). These tags could provide useful additional information to complement habitat and trophic niches.

Even if reality mining is a powerful tool for measuring underwater activity, it is restricted to tagged fish and the local context in which they arose remains uncertain. Typically, in the case of winter aggregation of catfish, high-valued complementary metadata would answer the following questions: how many individuals gather? What are their sizes? Do other species participate? What assemblage? What are they doing, do they interact? To respond to some of these questions, we used an acoustic camera (sonar 2D Oculus, 1.2 MHz) on 12 February 2020 (Martignac et al., 2015), and could see a few isolated individuals but could not detect any aggregation patterns. The a posteriori analysis of telemetry data revealed that catfish were not aggregated at this time. Unfortunately, we did not get another opportunity to use this camera but we are confident this will allow us to make valuable additional observations in the future. We also tried using a hydro-acoustics technique that uses echosounding of fish (Rudstam et al., 2012), with an equipment similar to Godlewska et al. (2016) but operating at 120 kHz (SIMRAD EK80) instead. Echosounding results were however not relevant, and moreover fish were not aggregated in January neither. The hydro-acoustic technique described in Goulon et al. (2021) is very likely more suitable for such a lake and would worth being tested in the future. In the end, we tried direct visual observations by scuba diving, but the typical low transparency of the lake (mean Secchi depth = 2.5 m in winter) prevents us from observing anything.

Our isotope sampling was mainly dedicated to reconstructing the food web and focused on the trophic niche of predatory species. As such, baselines of the fish community were based on a large sampling effort while the macroinvertebrate community was based on a few samples. The analysis of trophic niche would have been enhanced by sampling the stomach contents in

addition to stable isotopes (e.g. Zhang et al., 2018; Garcia et al., 2020) allowing us to estimate diet composition (Parnell et al., 2010). Most individuals were caught by fyke nets in which they easily preyed upon trapped fish, making the contents of their stomach not relevant at that time. We thus did not analyze the stomach contents, except for a few large individuals angled or caught with hook lines. These observations, in addition with literature on the diet of adult catfish, will be used in the future to estimate catfish diet composition. However, for young individuals, this will not be possible because the macroinvertebrate community was not sampled and their stomach content was not analyzed, but this information would for sure be valuable to provide on to the interactions we have highlighted in their trophic niches.

In regards to stable isotope analysis, muscle is the most commonly analyzed tissue, but often requires the animals to be sacrificed (Hayden et al., 2015). Favoring non-lethal sampling, as a surrogate of muscle, we used fin tissue (e.g. Winter et al., 2019b), but fin isotopic ratios can be different from that of muscle. A lot of studies have highlighted the importance of acquiring species-specific relationships between stable isotope values of muscle and fin when using fin tissue as a surrogate for muscle. In fact, this relationship can even vary between seasons and fish size (Willis et al., 2013; Busst et al., 2015; Winter et al., 2019b; Roberts et al., 2021). Although we did not sample muscle by favoring a non-lethal sampling, we followed the recommendations of Hayden et al. (2015) by standardizing sampling and only selecting tissue from the extreme tip of a fin and homogenizing fins prior to analysis. In the future, the best practice would be to calibrate a relationship between muscle and fin ratios on a subsample of sacrificed individuals from which both muscle and fin would be sampled (Hayden et al., 2015); this would preserve all other individuals from which only fin tips would be sampled.

F. Perspectives

1. Behavioral types and personality

Species coexistence and related levels of intra- and interspecific competition govern the magnitude of among-individual trophic niche variations (Bolnick et al., 2003; Araújo et al., 2011). This variability helps to cope with environmental fluctuations. For example, adaptive plasticity in traits such as behavior and morphology is a common response to environmental fluctuations (West-Eberhard, 1989; Olsson et al., 2007; Nakayama et al., 2016). Plasticity in traits can have genetic and environmental sources because most traits exhibit intermediate heritability (Lynch & Walsh, 1998). Klauschies et al. (2016) showed that a significant and fast

trait adaptation in a predator-prey community was necessary to promote species coexistence, with the selection pressure governing the speed of trait adjustments. Spatial behavioral types (mobile and resident individuals) in burbot *Lota lota* played a key role in shaping individual space-use (Harrison et al., 2015) and their use of resources by cascade effect. In perch, Olsson et al. (2007) and Mustamaki et al. (2014) demonstrated a resource polymorphism between individuals with different morphologies regardless of whether they foraged in littoral or pelagic zone. Similarly, Senegal et al. (2021) identified a close link between diet and morphology in yellow perch *Perca flavescens*. Kobler et al. (2009) highlighted the coexistence of three behavioural types in pike, that ultimately reduced intraspecific competition in preferred littoral habitats. Differences between individuals have been shown to be often consistent over time; they are termed animal personality when related to behavior and individual specialization when related to food resources (Toscano et al., 2016). Over ecological timescales (contemporary evolution, Post & Palkovacs, 2009), studying individual variation can help to shed light on links between ecological and evolutionary processes (Bolnick et al., 2011; Dall et al., 2012).

The dataset collected on individual pike, perch, pikeperch and catfish movements over several years appears as an excellent opportunity to tackle the question of fish personality by studying individual activity, home ranges and habitat-use across years and seasons, paying great attention to the possible repeatability of individual patterns and coexistence of different behavioral types (e.g. Taylor & Cooke, 2014). Unfortunately, this will not be possible for the diet as too few individuals were recaptured. Yet, obtaining a high-resolution quantification of individual diet over a long period appears key to understand how intrapopulation diet structure drives population niche (Sheppard et al., 2018; Stewart et al., 2021), for example in response to environmental impacts.

2. *Linking behavior and diet*

The availability of resources is one of the most important factors governing habitat selection (Stephens et al., 2007). Coupling stable isotope and telemetry techniques can thus help decipher movement (Hussey et al., 2015). In this way, Eggenberger et al. (2019) related the level of activity of common snook *Centropomus undecimalis* to the nutrient enrichment of the hosting lake. Harrison et al. (2017) showed that variation in individual trophic niche of burbot *Lota lota* arose due to a differential littoral/pelagic prey reliance and was linked to variation in activity. More mobile juvenile pike have been shown to grow faster and reach higher trophic positions

by acquiring more resources (Nygqvist et al., 2018). By examining spatial and dietary overlap between two coexisting reef fish, Matley et al. (2017) showed that both species had similar trophic niches but different space-use, probably to decrease competition. Repeated individual sampling of diet and space-use helps to improve our understanding of how animals select habitats under variable environmental conditions or to highlight connections between behavioral inter-individual variations and dietary specialization (Cunjak et al., 2005; Harrison et al., 2017; Eggenberger et al., 2019; Stewart et al., 2021). In our experiment, we sampled isotopic data when tagging catfish. We can thus estimate their isotopic niche over the three months preceding the first records of their movements. Even if the time coverage of trophic and movement data do not overlap, it would be worth looking for potential links between activity, space use and diet, at least during the weeks following the isotope sampling.

G. Contribution to lake evidence-based management

This type of research provides valuable insights for lake managers about how habitat- and resource-use of species varies over time (Crossin et al., 2017; Rous et al., 2017). It thus helps to identify potential bottlenecks and can provide guidance on which critical habitat or resources to preserve for species conservation (e.g. Ebner & Thiem, 2009). Moreover, it also provides information on interactions between species (e.g. Vanovac et al., 2021). As such, it can enlighten species management by evaluating the strength of competitive interactions, and, for example, the need for species regulation, especially when the lake hosts invasive exotic species that can be harmful for native fishes. Importantly, this work stresses the value of collecting time-integrated information on ecosystems (timescale of several years) to draw robust conclusions, as a single year may not be representative of the observed patterns.

VI.

References

VI. References

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VII.

List of figures, tables and supplementary
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where \overline{SR}_{ind} is the expected mean individual selection ratio of pikeperch, strictly positive; α is the overall intercept; origin discriminates wild from farmed pikeperch, $s(ind)$ is a smoothing function modelling the individual effects (Wood, 2008) and ε is the error term following a normal distribution with zero mean. To take into account the skewed distribution of individual selection ratios towards zero, a Tweedie family function with a log-link was used (Gilman et al., 2012). This model tested the fixed effects of water depth, season, pikeperch origin and some of their interactions, as well as the individual effects, on selection ratios. The percentage of explained variance quantified the data variability represented by this model. Results demonstrated that there was no effect of pikeperch origin.....60

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