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Réponses des poissons et des macroinvertébrés aux variations rapides des conditions hydrauliques à l'aval des centrales hydroélectriques gérées par éclusées

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RÉSUMÉ

Les éclusées sont des variations artificielles, fréquentes et rapides du débit permettant de répondre à des pics infra-journaliers de la demande d'électricité. Les variations hydrauliques qu'elles génèrent peuvent provoquer l'échouage-piégeage ou la dérive forcée des organismes ce qui peut entraîner des changements dans la structure des communautés aquatiques. Jusqu'à maintenant, que ce soit à l'échelle de tronçon (~ 100 m) ou du microhabitat (~ m²), peu d'études ont mis en évidence des liens transférables entre les variables liées aux éclusées (p.ex. gradient de hausse de vitesse) et les réponses biologiques (p.ex. densité des espèces, sélection de l'habitat). Il est souvent difficile (1) de traduire les débits en conditions hydrauliques proximales et (2) de tester l'influence relative des éclusées par rapport aux autres déterminants environnementaux. Afin de combler ces lacunes de la littérature, dans notre premier article, nous avons évalué les effets des variations hydrauliques provoquées par les éclusées sur les populations de poissons en réalisant une combinaison originale d'analyses spatiales (sur 45 tronçons de rivières dont six groupes de tronçons géographiquement proches) et temporelles (sur 3 à 17 ans). Nous avons montré que l'influence des éclusées était secondaire par rapport à la structuration le long des gradients longitudinaux et aux influences négatives des crues sur les densités annuelles. Cependant, les analyses spatiales et temporelles ont suggéré que les éclusées défavorisent les espèces de poissons typiques des rivières de taille moyenne au profit des espèces typiques des petites rivières (truite, vairon, chabot). Pour mieux comprendre les effets des éclusées, dans notre second article, nous avons étudié la sélection de l'habitat des poissons et des macroinvertébrés dans une rivière de taille moyenne (la rivière d'Ain) à l'échelle du microhabitat. Pour ce faire, nous avons utilisé des observations des abondances de poissons dans 1180 microhabitats (507 échantillonnés par pêche électrique, 673 par observations subaquatiques) et des abondances de macroinvertébrés dans 36 microhabitats (hyporhéiques et benthiques) ainsi qu'un modèle hydraulique 2D pour estimer l'hydraulique passée des microhabitats (pendant les 15 jours avant l'échantillonnage). Globalement, l'hydraulique passée a influencé la sélection des microhabitats, avec un effet plus fort sur les macroinvertébrés que sur les poissons et une influence directe plus forte de l'assèchement (3-15 fois moins de macroinvertébrés dans les microhabitats qui s'assèchent) que des fortes vitesses passées. Les poissons suivent leurs conditions d'habitat favorables et évitent donc les fortes vitesses tandis que les macroinvertébrés restent et se cachent. A partir des résultats de ces deux analyses, des perspectives opérationnelles sont proposées, notamment pour intégrer les résultats dans les modes de gestion.

ABSTRACT

Hydropeaking is the frequent and rapid artificial variations in flow to meet sub-daily peaks in electricity demand. The hydraulic variations it generates can cause the stranding or forced drift of organisms, which can lead to changes in aquatic community structure. To date, at either the reach (100 m) or microhabitat (~ m²) scale, few studies have demonstrated transferable links between hydropeaking variables (e.g. upramping rate of current velocity) and biological responses (e.g. species density, habitat selection). It is often difficult (1) to translate flow into proximal hydraulic conditions and (2) to test the relative influence of hydropeaking versus other environmental drivers. To address this knowledge gap, in our first paper, we evaluated the effects of hydraulic variations from hydropeaking on fish communities. In particular, we conducted an original combination of spatial (over 45 river reaches including six groups of nearby reaches) and temporal (over 3 to 17 years) analyses. We found that the influence of hydropeaking was secondary compared to well-known spatial variations in fish assemblage structure along longitudinal gradients, and negative influences of floods on annual densities. However, spatial and temporal analyses suggested that hydropeaking may disfavour fish species from medium-sized rivers compared to species from small rivers (trout, minnow and sculpin). To better understand the effects of hydropeaking, in our second paper, we investigated habitat selection by fish and macroinvertebrates in a medium-sized river (Ain River) at the microhabitat scale (~ m²). To do so, we used observations of fish abundances in 1180 microhabitats (507 sampled by electrofishing, 673 by snorkeling) and macroinvertebrates abundances in 36 microhabitats (hyporheic and benthic) as well as a 2D hydraulic model to estimate the past hydraulics of microhabitats (for the 15 days before sampling). Overall, past hydraulics influenced microhabitat selection, with a stronger effect on macroinvertebrates than fish and a stronger direct influence of dewatering (3-15 times fewer macroinvertebrates in microhabitats that were dewatered) than high velocities. Fish follow their suitable habitat conditions and thus avoid high velocities while macroinvertebrates stay and hide. Based on these two analyses, operational perspectives are proposed, in particular to integrate the results into management models.

ARTICLES

Judes et al. (A) :

Consistent but secondary influence of hydropeaking on stream fish assemblages in space and time.

Judes, C, Gouraud, V, Capra, H, Maire, A, Barillier, A, Lamouroux, N.

Article accepté par *Journal of Ecohydraulics*

Judes et al. (B) :

Past hydraulics influence microhabitat selection by macroinvertebrates and fish in hydropeaking rivers.

Judes, C, Capra, H, Gouraud, V, Pella, H, Lamouroux, N.

Article soumis à *River Research and Applications*

Batz et al. (Soumis) :

Habitat dynamics in hydropeaking rivers: the impact of flow frequency and duration on patch-scale habitat dynamics.

Batz, N.*, Judes, C.*, Weber, C.

Article soumis à *River Research and applications*

**Les auteurs ont contribué à parts égales*

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


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Première partie

Synthèse

INTRODUCTION : LES ECLUSEES, UNE PERTURBATION A PLUSIEURS ECHELLES SPATIALES, TEMPORELLES, ET A PLUSIEURS NIVEAUX BIOLOGIQUES

Le mode de gestion des ouvrages hydroélectriques par éclusées consiste à lâcher les eaux retenues dans un réservoir afin d'adapter la production d'énergie aux fluctuations de la consommation d'électricité ou de compenser les variations de production des énergies intermittentes. La production d'hydroélectricité est, ainsi, la seule énergie décarbonée permettant de suivre la demande en électricité et de soutenir le réseau. En France, la production par éclusées vient compléter l'électricité produite par les centrales thermiques et nucléaires qui fournissent 80% de la production (RTE 2019), mais qui ne peuvent pas répondre rapidement aux fluctuations de la demande. Les centrales d'éclusées sont au nombre de 140 pour 4 000 MW de puissance et 14 TWh de production annuelle moyenne (UFE 2017).

Le mode de gestion par éclusées génère des fluctuations de débit infra journalières rapides et fréquentes (Bruder et al. 2016). Leur fréquence quotidienne est de deux ordres de grandeur plus élevés que dans les systèmes naturels (Archer et al. 2002, Greimel et al. 2016) et le débit de pointe peut-être jusqu'à dix fois plus élevé que le débit de base quotidien (Figure I.1) et ainsi provoquer des variations de hauteur d'eau de plus de 3m (Moog 1993, McManamay et al. 2016).

Chaque espèce est adaptée pour survivre et exploiter le régime hydrologique naturel (c.-à-d. durée, fréquence, timing, intensité des variations de débit) d'où elle a évolué. Leurs cycles de vie, leurs morphologies ou leurs comportements leur permettent de résister aux crues, aux étiages ou aux variations saisonnières du débit lorsqu'elles sont dans les gammes de débit naturel et qu'elles arrivent de manière prévisible à une période précise de l'année (Encadré 1). Les éclusées étant plus rapides, plus fréquentes et plus intenses que les variations journalières naturelles, elles peuvent agir comme une "perturbation" sur les écosystèmes de rivière, c'est-à-dire qu'elles agissent comme "une force, un agent ou un processus physique, abiotique ou biotique, provoquant une perturbation dans une composante ou un système écologique" (Rykiel

1985). Cette perturbation sur le système écologique peut être visible à différents niveaux biologiques (ou résolutions) (Figure I.2). L'impact écologique de ce mode de gestion doit donc être quantifié pour pouvoir mettre en place des mesures d'atténuation adaptées à son intensité. Cela est d'autant plus urgent que la proportion de linéaires de rivières subissant des éclusées pourrait augmenter à l'échelle mondiale pour pallier l'intermittence de production des énergies vertes (Kougiaris et al. 2019).

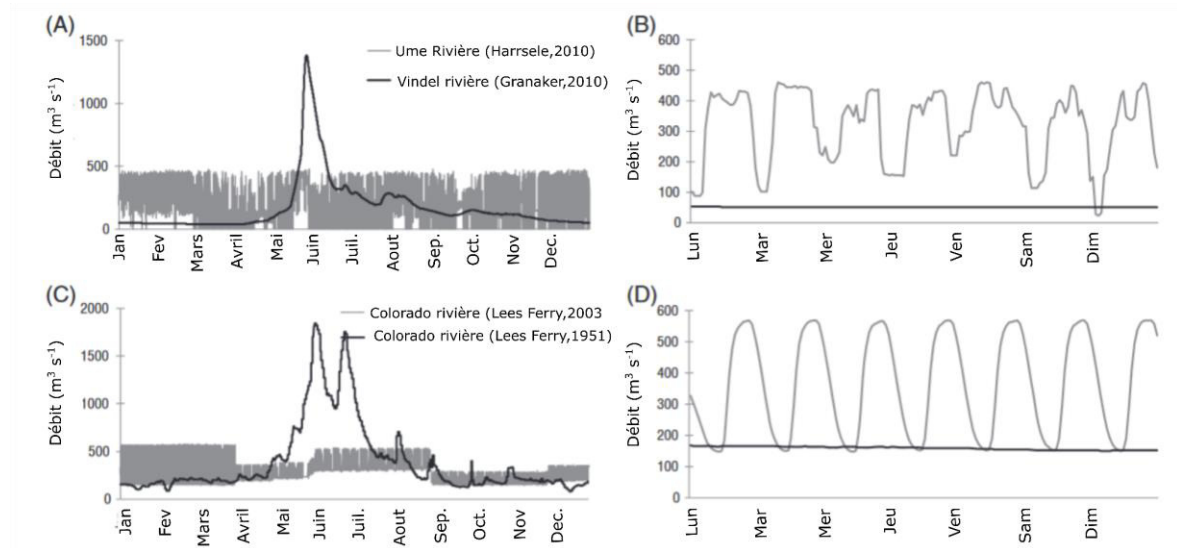


Figure I.1. Débits horaires enregistrés dans différents tronçons de rivière soumis à éclusées. (A, B) la rivière Ume au niveau de la centrale hydroélectrique de Harrsele et la rivière Vindel (à écoulement libre) au niveau de Granåker près de Vindeln dans le nord de la Suède. (C, D) la rivière Colorado à Lees Ferry avant et après la fermeture de la centrale hydroélectrique gérée par éclusées de Glen Canyon dans l'Utah, USA. Les graphiques (A) (B) sont sur une année tandis que (B) et (D) sont sur une semaine. Tiré de Bejarano et al. (2018).

Encadré 1. Sélection naturelle et régime hydrologique

Le régime hydrologique agit comme un filtrage environnemental, il sélectionne au fil des générations des comportements et/ou une morphologie permettant aux organismes de survivre et exploiter les variations de débit. Généralement, cela implique une synchronisation des événements du cycle de vie, tels que la reproduction et la croissance avec les variations temporelles du débit naturel. Par exemple, la perche dorée (*Plectroplites ambiguus*) originaire des rivières arides d'Australie a besoin des crues pour frayer, sinon, les œufs en développement se résorbent dans le tissu somatique (Mackay 1973).

Tous les régimes hydrologiques ne favorisent pas la sélection des traits permettant de survivre aux variations de débit. La théorie des traits d'histoire de vie prédit que l'amplitude, la fréquence et la prévisibilité des événements extrêmes, peuvent affecter la façon dont les organismes évoluent ou non (Lytle & Poff, 2004). Lorsque les débits extrêmes sont fréquents, importants et prévisibles, la sélection naturelle favorise les cycles de vie qui sont synchronisés pour éviter ou exploiter les événements de débit extrême. En revanche, si les débits extrêmes sont fréquents, de grande intensité mais imprévisibles, la force de sélection est faible et cela même s'ils peuvent engendrer des fortes mortalités. Dans ce cas, c'est plutôt une stratégie de minimisation des risques (ou "bet hedging" en anglais) qui est adoptée, les parents produisent différents types de descendance qui correspondent à différents futurs possibles (Cohen 1966, Lytle et al. 2004).

Les effets des éclusées sur une espèce donnée dépendent donc du régime hydrologique historique auquel l'espèce a dû faire face et pour laquelle elle a été sélectionnée au cours des générations (Biggs et al. 2005).

A une échelle plus locale, les variations de débit induisent des variations des conditions hydrauliques locales sur quelques mètres carrés (ci-après, échelle du "microhabitat"). L'habitat hydraulique des organismes aquatiques varie dans l'espace à chaque variation de débit. Batz et al. (Soumis) ont montré sur la rivière Aare en Suisse que dans une parcelle de quelques mètres carrés de rivière la vitesse peut changer de classe huit fois par jour (une classe tous les 0.25 m s^{-1}) dans le cas d'un régime soumis à des éclusées contre seulement 0.2 fois par jour si l'hydrologie avait été naturelle. Dans cette même rivière, ils ont aussi montré qu'un habitat hydraulique donné peut se déplacer de 15 mètres en moyenne par jour dans une rivière à éclusées contre seulement 0.4 mètre par jour en moyenne en hydrologie naturelle (Batz et al. soumis). Ainsi, il peut y avoir une sélection des espèces et des stades de vie qui sont capables soit de bouger ou de se cacher rapidement lors des variations de débit soit de résister à des conditions hydrauliques locales extrêmes (assèchement ou forte vitesse). Les organismes qui n'en sont pas capables peuvent mourir par échouage-piégeage lorsque la lame d'eau se retire

trop rapidement (Figure I.2), ou être entraînés de force par dérive lors des augmentations de vitesse. Dans la rivière de Alta (Ukraine), Jensen et al. (1992) ont trouvé environ 1,5 poissons (toutes espèces confondues) échoués par m² après une seule baisse des débits. Dans la rivière Kootenai (USA), Perry & Perry (1986) ont montré que le nombre de macroinvertébrés en dérive était huit fois plus élevé lors de l'augmentation des débits par éclusées (de 4,1 à 283 m³ s⁻¹) que lors du débit de base. La modification des conditions d'habitat local agit aussi sur le comportement de frai et peut compromettre l'éclosion des œufs par décapage ou générer l'assèchement des nids. Par ailleurs, les variations hydrauliques peuvent induire des variations de température modifiant les cycles de vie des organismes, la date d'émergence et la dérive des macroinvertébrés (Hogg et al. 1996, Céréghino et al. 1997).



Figure I.2. Exemple de perturbations générées par les éclusées : échouage de poissons sur la rivière d'Ain (Photo N. Lamouroux, 2018).

Puisque ces processus peuvent entraîner la mort (dérive ou échouage-piégeage) ou perturber la reproduction, les éclusées peuvent affecter la fitness (survie x reproduction) des organismes ce qui peut induire des changements à l'échelle des populations (Figure I.3). Ainsi, souvent dans les tronçons à éclusées, il y a une perte de diversité, d'abondance et de biomasse (Bain et al. 1988, Bain 2007). Par exemple, Hayes et al. (2021) ont montré que la biomasse en ombres (*Thymallus thymallus*) était environ huit fois plus élevée dans les tronçons sans éclusées que dans les tronçons soumis aux éclusées. Cependant, les processus agissant à l'échelle de l'individu ne se traduisent pas toujours par des effets sur la population. Par exemple, Hedger et al. (2018) et Sauterleute et al. (2016) ont montré par modélisation que l'influence de

l'échouage-piégeage des juvéniles de saumons atlantiques pouvait être compensée partiellement par l'effet de la densité dépendance (agissant comme un mécanisme de rétroaction négative qui atténue les changements d'abondance à l'échelle de la population).

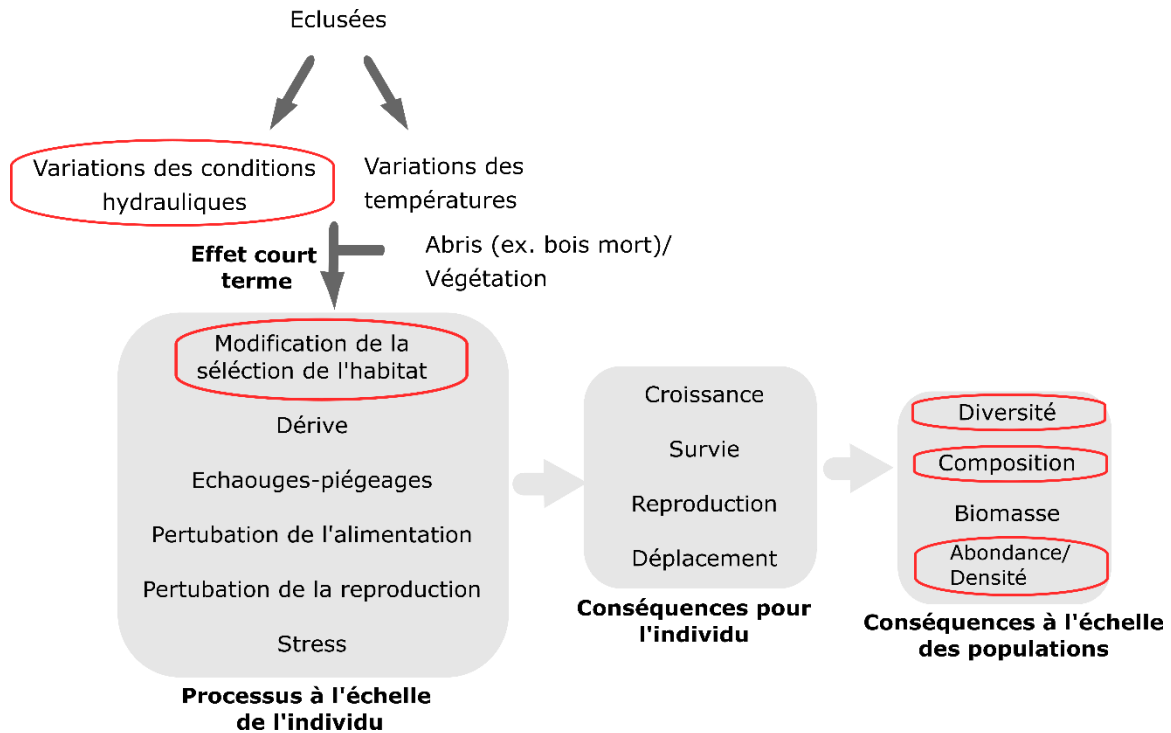


Figure I.3. Cascade d'influences des effets des éclusées de l'individu à la population. La thèse traite uniquement ce qui est entouré en rouge. L'influence des températures ou les interactions avec d'autres éléments du paysage tels que la présence d'abris, ou de confluences n'ont pas pu être traitées. Repris de Barillier et al. (in press).

Des lacunes de la littérature empêchent de développer des mesures d'atténuation des éclusées transférables d'une rivière à l'autre et adaptées aux communautés en place. D'un point de vue méthodologique jusqu'à présent la plupart des études décrit les éclusées par des descripteurs hydrologiques. Les descripteurs hydrologiques ne permettent pas de tenir compte de la morphologie et empêche la transférabilité des liens entre éclusées et réponses biologiques. D'un point de vue écologique, il manque des connaissances (1) sur la sensibilité des espèces ou groupe d'espèce en fonction de leurs préférence d'habitat ou de leurs trait d'histoire de vie, (2) sur l'influence des autres déterminants environnementaux sur le lien entre éclusées et les réponses biologiques et (3) sur les mécanismes, c'est-à-dire sur la compréhension des phénomènes à l'échelle du microhabitat pour expliquer et comprendre les résultats observés à plus large échelle spatiale.

L'objectif de ma thèse est de répondre à ces lacunes de la littérature pour mieux comprendre l'influence des variations hydrauliques induites par les éclusées sur les poissons et les macroinvertébrés. Pour cela, à l'échelle de la population (échelle du tronçon), les liens entre les éclusées et les densités de poissons ont été étudiés par une analyse multisites (45 tronçons) à l'échelle de la France sur plusieurs années (Judes et al. A). Ensuite, pour s'affranchir des effets confondants multiples des analyses multi-sites et obtenir une compréhension plus mécanique des effets des éclusées sur les populations, la sélection du microhabitat par les organismes a été étudiée. Pour cela, 1180 microhabitats de poissons et 72 pour les macroinvertébrés ont été échantillonnés dans un secteur de 6 km de la basse rivière d'Ain (rivière de taille moyenne, affluent du Rhône) (Judes et al. B). Concrètement à ces deux échelles spatiales, la variabilité des conditions hydrauliques vécue par les populations où les individus avant l'échantillonnage (Judes et al. (A): 1 an avant, Judes et al. (B): 15 jours avant) a été liée à l'abondance des taxa du tronçon ou du microhabitat (Figure I.4). Pour obtenir des relations les plus transférables possibles, l'influence relative des variations hydrauliques induites par les éclusées a été étudiée par rapport aux autres déterminants environnementaux principaux. Ces autres déterminants environnementaux sont les conditions hydrauliques extrêmes et la structuration longitudinale (de la source à l'embouche) des peuplements de poissons dans Judes et al. (A) et les conditions hydrauliques présentes (ou actuelles) dans Judes et al. (B). Les interactions avec des éléments du paysage comme la présence d'abris ou de confluence n'ont pas pu être considérées.

Les deux premières parties de cette synthèse de thèse résument les apports des études de Judes et al. (A) et Judes et al. (B) pour la littérature et abordent les perspectives scientifiques. La troisième partie s'appuie en partie sur un troisième article dont je suis coauteur, Batz et al. (Soumis), et aborde les perspectives opérationnelles à tirer des résultats majeurs de la thèse. Cette partie aborde en particulier comment à partir des connaissances acquises à l'échelle du microhabitat on peut estimer l'impact des éclusées sur les populations de poissons.

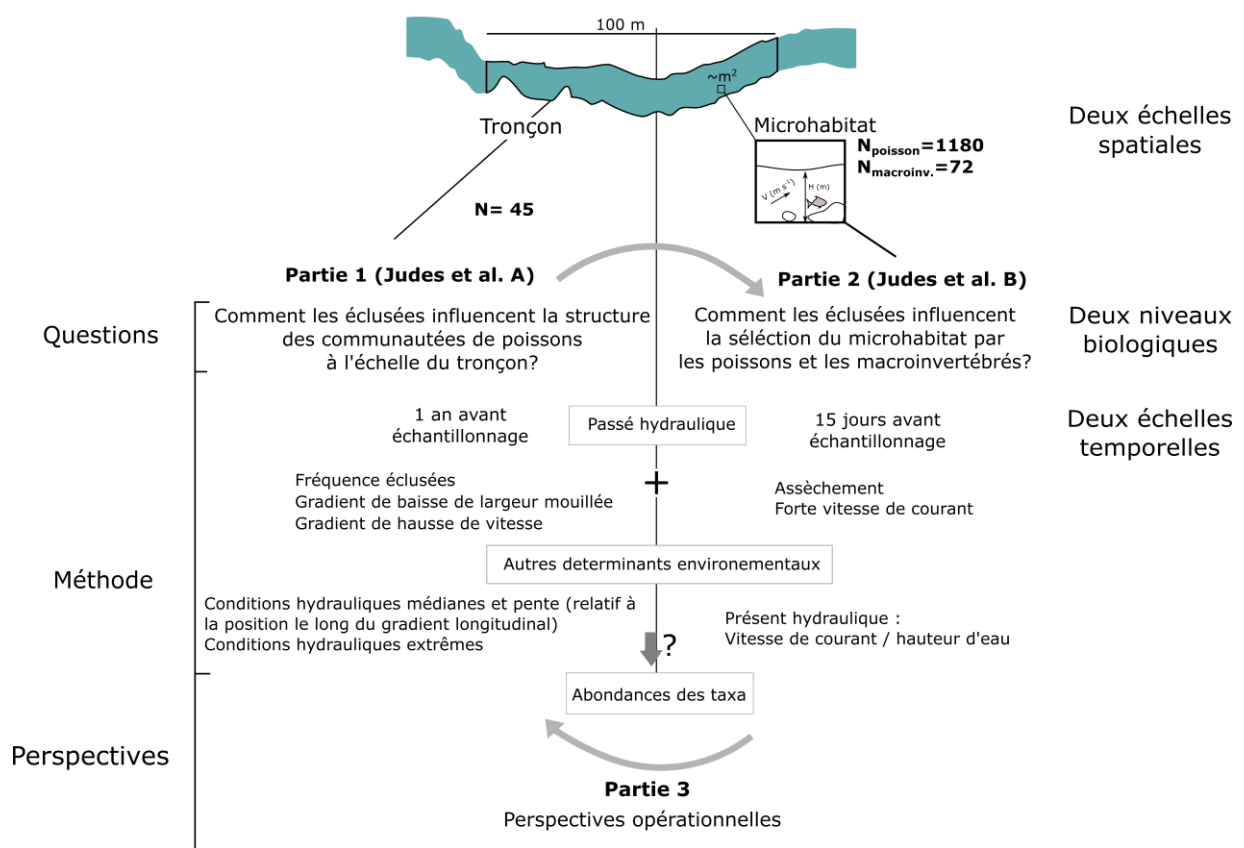


Figure I.4. Résumé et liens entre les articles de la thèse. La synthèse de thèse est organisée de la manière suivante : Partie 1 : recherche l'influence des éclusées sur les communautés de poissons (densité des espèces), Partie 2 : recherche des mécanismes par lesquels les éclusées peuvent affecter les communautés de poissons en s'intéressant à l'influence des éclusées sur la sélection du microhabitat, Partie 3 : résumé des perspectives opérationnelles et zoom sur les façons dont on peut extrapoler les connaissances acquises à l'échelle du microhabitat pour estimer les perturbations à l'échelle du tronçon (échelle utilisée pour la gestion).

1. INFLUENCES DES ECLUSEES SUR LES DENSITES DE POISSONS (ECHELLE DES POPULATIONS)

1.1 Etat de l'art : un manque d'analyse multisites décrivant des processus communs

Les effets mesurés à l'échelle de la population sont souvent jugés préoccupants pour la gestion car ils se traduisent par une hausse de mortalité pour un ou plusieurs stades de développement (recrutement, juvénile ou adulte) qui sont les paramètres démographiques déterminant de la viabilité des populations. Ainsi, déterminer les causes de variation des densités de poissons est un objectif essentiel pour le développement des connaissances aussi bien que pour la gestion des ressources (p. ex. Lobón-Cerviá, 2009).

La grande majorité des études sur l'impact des éclusées sur les populations de poissons sont faites autour d'un seul aménagement par une comparaison : amont/aval, référence/influencé (Crips et al. 1983, Travnicek et al. 1994, Connor et al. 2004, Enders et al. 2017), ou avant/après changement du mode de gestion (protocole BACI Before-After-Control-Impact, p. ex. Conquest, 2000). Le problème de ce genre d'études comparatives sur peu de tronçons est que les résultats sont peu transférables et les conclusions sont parfois différentes. La majorité des études montrent une diminution de l'abondance (Parasiewicz et al. 1998, Macnaughton et al. 2015, Mihalicz et al. 2019) ou de la diversité (Schmutz et al. 2015) en poissons et en macroinvertébrés dans les tronçons soumis aux éclusées. Cependant, Smokorowski et al. (2011) ont trouvé que la composition, l'abondance des macroinvertébrés et la biomasse des poissons étaient égales ou supérieures dans un tronçon de rivière soumis à éclusées par rapport à un tronçon de rivière sans éclusées. De façon similaire, il y a aussi des incertitudes concernant les espèces les plus sensibles. Par exemple, Garcia De Jalon et al. (1994) ont constaté qu'après la construction d'une centrale hydroélectrique à éclusées sur la rivière Tera (Espagne), les populations de presque toutes les espèces de cyprinidés ont diminué alors que la population de truite a persisté. Cependant, sur le Rio Duraton (Espagne), Camargo & Garcia de Jalon (1990) ont constaté l'effet inverse : les populations de cyprinidés ont persisté ou même augmenté alors que la truite a disparu. Ces différences sont difficiles à expliquer et dépendent probablement de la gestion des éclusées, de la période d'échantillonnage (p. ex. la saison, après

une crue), de leur emplacement le long du gradient longitudinal et/ou des caractéristiques morphologiques des tronçons. Enfin, l'analyse d'une seule rivière ne permet pas d'isoler les influences des différents paramètres de gestion des éclusées, tels que les gradients de hausse/baisse de débit ou la valeur du débit de base.

Il est donc nécessaire de faire des études à large échelle, sur plusieurs rivières et suivies pendant plusieurs années pour avoir des relations générales et transférables d'une rivière à une autre. Cependant ces études sont rares puisque qu'il est difficile (1) de réunir des données hydrologiques, biologiques et des traductions hydrauliques sur de nombreux tronçons suivis pendant plusieurs années, et (2) de démêler l'influence des éclusées par rapport aux autres déterminants environnementaux structurant les communautés de poissons. En effet, la structuration des communautés de poissons longitudinale de la source à l'embouchure (Encadré 2) et les événements extrêmes tels que les crues et les étiages (Huet 1949, Verneaux 1973, Nicola et al. 2009, Alonso et al. 2011, Bret et al. 2015) sont parfois difficiles à considérer puisque cela nécessite de réaliser à la fois une étude spatiale et temporelle.

Il existe quand même quelques rares études multi-tronçons (Hayes et al. 2021 ($N_{\text{tronçons}}=74$), Schmutz et al. 2015 ($N_{\text{tronçons}}=69$), en Autriche). Ils ont permis d'identifier des gradients de baisse de hauteur d'eau à partir desquels les communautés piscicoles étaient fortement dégradées (12-24 cm h⁻¹ pour les ombres (Hayes et al. 2021) et 15 cm h⁻¹ (Schmutz et al. 2015)). Cependant, ces études ont leurs limites : (1) elles n'impliquent pas de variables hydrauliques proximales, comme le gradient de diminution de la largeur mouillée (lié directement au risque d'échouage) ou le gradient de hausse de la vitesse de courant (lié directement au risque de dérive) (Moreira et al. 2019), (2) en utilisant une variable représentant la communauté biologique dans son ensemble ou uniquement sur les densités d'ombre, ces études ne permettent pas de savoir quelle espèce est la plus impactée, (3) elles n'ont pas étudié l'importance relative des éclusées par rapport aux autres déterminants environnementaux.

Encadré 2. La structuration des communautés le long du gradient longitudinal

De nombreux concepts expliquent la distribution des espèces le long du réseau hydrographique. Ces concepts se basent sur les changements physiques et énergétiques (Huet 1949, Illies et al. 1963, Verneaux 1973, Vannote et al. 1980, Statzner et al. 1986). De l'amont vers l'aval la pente diminue, la largeur de la rivière et la hauteur d'eau augmentent.

Huet (1949) postule que les deux principaux déterminants de la distribution des poissons dans les eaux vives sont la vitesse du courant et la température de l'eau (effet majoritaire), tous deux dépendant de la pente. Ainsi Huet a fait correspondre quatre zones piscicoles à

des gammes de pente. Les limites de pente d'une zone piscicole dépendent de la largeur des rivières : plus la rivière est petite, plus la pente tolérée par une espèce de poisson donnée est grande. La typologie de Verneaux (1973) augmente le nombre de zones afin d'adapter la zonation aux rivières françaises.

Vannote (1980) introduit l'influence de l'énergie disponible pour expliquer les successions biologiques le long du gradient longitudinal des milieux tempérés (le concept de la continuité fluviale). La taille des particules organiques diminue vers l'aval, du fait que chaque espèce est adaptée pour exploiter un certain type de matière organique, cela conditionne leur répartition longitudinale.

D'autres concepts sont venus après compléter celui de la continuité fluviale. Parmi eux, on peut citer le concept du régime de crue ou le concept de la discontinuité. Ce dernier intègre l'effet des grands barrages et des réservoirs (Ward et al. 1983). En effet, de par les modifications anthropiques les rivières ne sont pas des entités continues. Les discontinuités modifient les composantes physico-chimiques et changent la structure des communautés biologiques. Le concept du régime de crue ("flood pulse") ajoute au concept de continuité fluviale l'importance de considérer les crues. Ces dernières permettent un apport en particules organiques et jouent donc un rôle important dans la structuration des communautés biologiques (Junk et al. 1989).

1.2 Influence cohérente mais secondaire des éclusées sur les communautés de poissons des rivières dans l'espace et le temps (Judes et al. A)

Grâce à un large jeu de données piscicoles (45 tronçons suivis de 3-17 ans), Judes et al. (A) ont testé l'influence relative des variations hydrauliques induites par les éclusées par rapport à la structuration le long du gradient longitudinal des communautés et aux événements extrêmes de forts et faibles débits (Figure I.5) sur les densités de plusieurs espèces de poissons communes en France. Pour cela, à l'aide d'analyses multivariées (de type Co-inertie (Doledec et al. 1994, Méricoux et al. 1999)) ils ont combiné trois approches : (1) une analyse spatiale des effets des éclusées sur les communautés de poissons entre tronçons (pour peser l'influence relative des éclusées par rapport à la structuration amont-aval des peuplements), (2) une analyse temporelle de ces effets au sein des tronçons (permet de s'affranchir de l'influence spatiale pour peser l'influence relative des éclusées par rapport aux événements extrêmes), et (3) une comparaison impliquant six groupes de tronçons voisins soumis à différentes intensités d'éclusées (permet de s'affranchir à la fois des effets spatiaux et temporels). Chaque variation de débit a été traduite en variation des conditions hydrauliques grâce à des modèles de géométrie hydraulique (Morel et al. 2020). Ces modèles permettent de décrire les variations des conditions hydrauliques

(hauteur d'eau, largeur mouillée, vitesse du courant) en fonction du débit dans l'espace et le temps. Ils fournissent les meilleures estimations de l'hydraulique des tronçons pour un débit donné en l'absence de mesures hydrauliques détaillées sur le terrain (Morel et al. 2020).

L'analyse spatiale a montré que la structuration longitudinale des communautés de poissons masque l'influence des éclusées. Sur un site donné, le suivi de la composition du peuplement sur plusieurs années a montré que les événements extrêmes de fort débit sont plus structurants que les variations hydrauliques liées aux éclusées. Ainsi, la prise en compte des événements de fort débit est importante à intégrer dans les études d'impacts des éclusées afin d'aboutir à des diagnostics fiables de l'état des peuplements. De façon secondaire à ces événements extrêmes de fort débit, l'analyse temporelle de Judes et al. (A) a montré que les éclusées pourraient favoriser les espèces typiques des petites rivières (truite fario, vairon, chabot). Le caractère secondaire des effets des éclusées peut être lié aux gradients hydrauliques subjournaliers modérés au sein des tronçons du jeu de données. Enfin, la comparaison des tronçons voisins a montré que, pour les tronçons situés dans des rivières de taille moyenne, une plus forte intensité d'éclusées était associée à des densités plus élevées d'espèces de poissons typiques des petites rivières et à des densités plus faibles d'espèces typiques des rivières de taille moyenne (gardon, barbeau, chevesne, hotu) (Figure I.5). Ainsi ces résultats sont cohérents avec ceux de l'analyse temporelle et Judes et al. (A) qui concluent que de façon secondaire par rapport à la structuration longitudinale des peuplements et aux événements extrêmes de fort débit, les éclusées pourraient défavoriser les espèces de poissons typiques des rivières de taille moyenne par rapport aux espèces typiques des petites rivières.

Comment les éclusées influencent la structure des communautés de poissons?

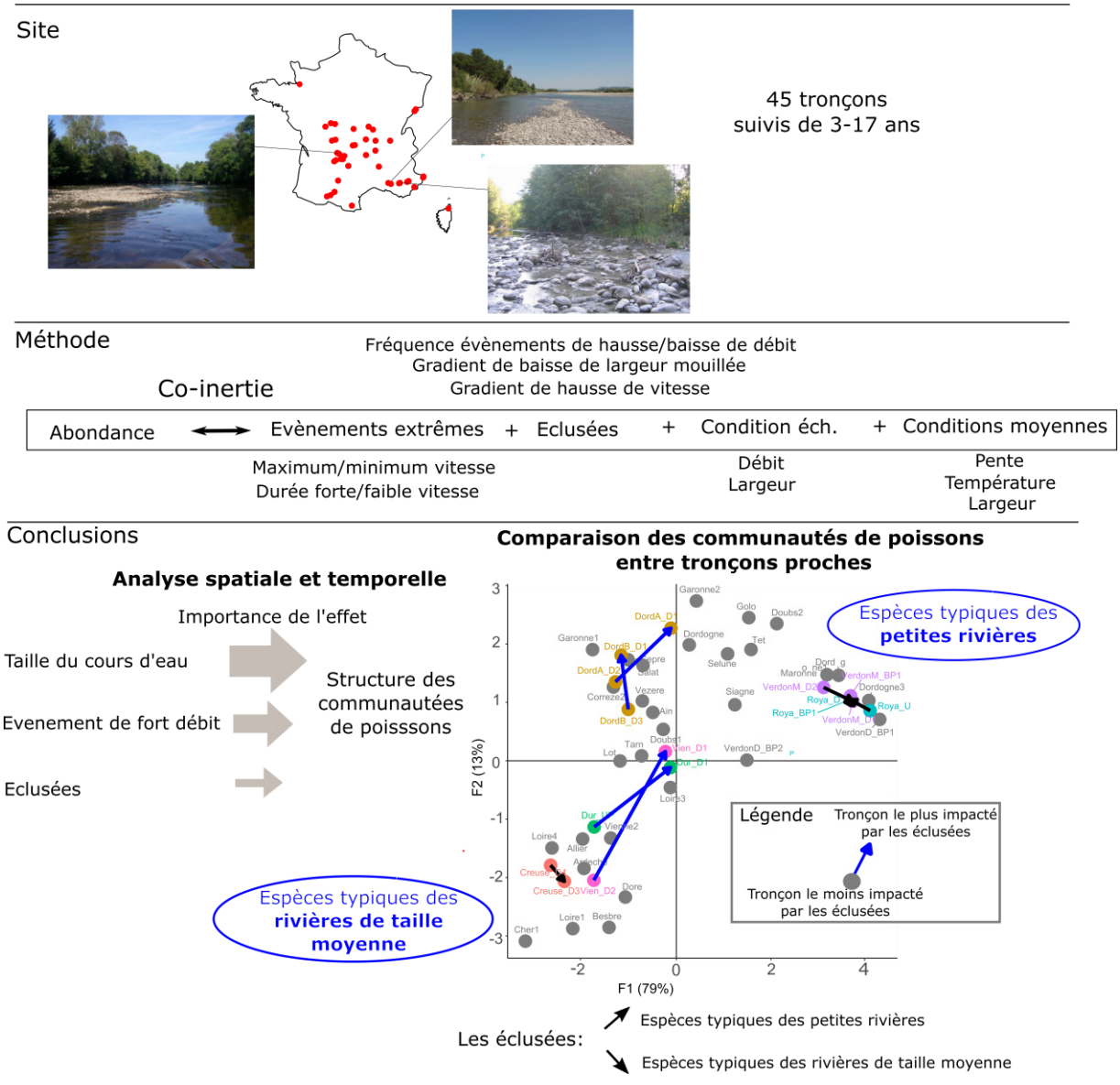


Figure I.5. Résumé de l'article de Judes et al. (A). La figure en bas à droite représente les scores des tronçons sur le premier et le deuxième axe de l'analyse spatiale de coinertie entre tronçons. Les flèches indiquent la position des paires de tronçons proches, les flèches vont du tronçon le moins influencé par les éclusées au tronçon le plus influencé. Les flèches bleues montrent les paires pour lesquels le tronçon le plus influencé présente des densités plus élevées d'espèces typiques des petites rivières et des densités moins élevées des espèces typiques des rivières de taille moyenne que le tronçon le moins influencé.

1.3 Perspectives scientifiques

A l'avenir, les liens entre la gestion des éclusées et la structure des peuplements piscicoles pourraient être approfondis par les actions suivantes :

- Couvrir un gradient d'intensité de gestion des éclusées plus important (en termes de fréquence d'éclusées et de gradient de hausse et de baisse de débit). Judes et al. (A) ont considéré principalement des tronçons avec une intensité de gestion des éclusées qui était relativement faible par rapport à ce que l'on peut trouver ailleurs en Europe (Schmutz et al. 2015). Ainsi, par la suite il faudrait compléter leurs analyses avec des tronçons issus des autres pays européens subissant des intensités de gestion des éclusées plus importantes.
- Augmenter le nombre de tronçons proches mais subissant différentes intensités de gestion des éclusées. Cela permettra de réaliser une étude quantitative mettant en lien les différences d'intensité des gestions des éclusées avec les différences de peuplement piscicole dans des contextes d'événements hydrologiques extrêmes similaires.
- Développer des modèles d'atténuation des gradients de vitesse et de largeur mouillée avec la distance d'évolution. Ces modèles devront considérer la géomorphologie moyenne du linéaire comme la largeur mouillée, la hauteur d'eau au module et la pente. Cela permettrait de considérer des tronçons de pêche plus éloignés des stations de mesure de débit et donc de pouvoir augmenter drastiquement la taille du jeu de données. Judes et al. (B) avait imposé une distance <25 km et l'absence d'obstacles majeurs ou d'affluents entre le jaugeage et la station de pêche poissons.
- Considérer les variations de température ou des éléments du paysage comme la présence d'abris ou de confluence. Il y a généralement un compromis à faire entre précision des données et quantité pour réaliser une analyse multisites. Judes et al. (B) par exemple ont décidé de ne pas considérer les variations de températures car elles étaient disponibles sur une proportion trop faible de tronçon. A l'avenir, l'idéal serait d'avoir un large jeu de données avec des

descriptions précises de l'environnement, du paysage et des poissons (taille, poids) sur le long terme.

2. INFLUENCES DES ECLUSEES SUR LA SELECTION DU MICROHABITAT (ECHELLE DE L'INDIVIDU)

2.1 Etat de l'art : des connaissances parcellaires et contradictoires

Pour être en mesure de comprendre les mécanismes qui expliquent la structure des communautés aquatiques (poissons, macroinvertébrés), il est nécessaire de descendre au niveau des réponses individuelles. La sélection du microhabitat fait partie des réponses individuelles qu'il est intéressant d'étudier pour comprendre comment les éclusées affectent le quotidien des organismes et les risques associés. Ce genre d'étude peut permettre de répondre à des questions telles que : Est-ce que les organismes se déplacent pour suivre leurs conditions d'habitat favorables (induisant des pertes énergétiques) ? Est-ce qu'ils utilisent ou évitent des habitats à risques (dérive et échouage) ? Est-ce qu'ils restent et subissent des conditions hydrauliques défavorables (ex. diminution de l'efficacité de nourrissage) ?

A l'échelle du microhabitat, il a déjà été montré que les conditions hydrauliques (hauteur d'eau, vitesse du courant) peuvent expliquer les effets des éclusées. Par exemple, Halleraker et al. (2003) ont montré que l'échouage de truites brunes (*Salmo trutta*) juvéniles se produit lorsque les gradients verticaux de hauteur d'eau sont supérieurs à $0,10 \text{ m h}^{-1}$. En revanche, on sait peu de choses sur la façon dont le processus de sélection du microhabitat est influencé par les variations des conditions hydrauliques à cette échelle.

Concernant les poissons, les conclusions des précédentes études divergent et on ne sait pas bien si lorsque le débit varie, les poissons (1) suivent leurs conditions d'habitat favorables dans l'espace ou (2) restent sur place et subissent des conditions d'habitat pouvant être défavorables. Kemp et al. (2003), en milieu expérimental, et Korman et Campana (2009), par pêche électrique in situ, ont constaté que peu d'individus (*Salmon parr* et *Oncorhynchus mykiss* respectivement) cherchent à se maintenir dans un habitat favorable lorsque le débit varie. Deux à trois fois plus de poissons étaient pêchés proche des berges à bas débit par rapport à haut débit. A l'inverse, Robertson et al. (2004) et Harby et al. (2001) ont montré que les juvéniles de saumons atlantiques se déplaçaient à chaque variation de débit pour suivre leurs conditions d'habitat favorables. Par ailleurs, certains organismes seraient capables de percevoir leur environnement et de sélectionner les habitats les moins variables. C'est ce qu'ont montré Capra

et al (2017) par télémétrie sur le Rhône en France sur trois espèces de poissons (barbeau, chevesne et silure) : les organismes évitaient les zones qui s'assèchent lors des baisses de débit. De même, Geist (2008) a montré en laboratoire que les esturgeons sélectionnent les habitats les moins variables en termes de vitesse.

Concernant les macroinvertébrés, des études ont montré (1) qu'ils étaient moins abondant le long des berges à cause des assèchements fréquents (Fisher et al. 1972, Troelstrup et al. 1990, Blinn et al. 1995) et (2) que la zone hyporhéique (dans le substrat) pourrait jouer un rôle de refuge lors des fortes vitesses ou des assèchements (Dole-Olivier et al. 1997, Stubbington et al. 2019). Cependant, peu d'études ont comparé la réponse des macroinvertébrés benthiques à celle des macroinvertébrés hyporhéiques dans les rivières à éclusées pour confirmer cette dernière hypothèse.

Malgré les études montrant que la dynamique spatio-temporelle des habitats pouvait influencer le comportement de sélection du microhabitat des poissons et des macroinvertébrés, peu d'articles ont étudié de manière quantitative l'influence des assèchements et encore moins celle des fortes vitesses de courants passés sur la sélection du microhabitat des poissons et des macroinvertébrés (Capra et al 2017). Cela est certainement dû à la difficulté de décrire les conditions hydrauliques passées des microhabitats car cela nécessite des modèles hydrodynamiques précis et spatialement explicites, tels que des modèles bidimensionnels (2D) qui permettent de cartographier les hauteurs d'eau et les vitesses du courant (moyennées sur la verticale) à différents débits. L'étalonnage (hauteur d'eau pour un ou des débits donnés) et la validation (hauteur d'eau et en vitesse du courant) des modèles 2D prend beaucoup de temps et sont donc très coûteux. De plus, chercher les liens entre la sélection du microhabitat et les conditions hydrauliques passées nécessite un travail de terrain important, afin d'échantillonner les organismes à plusieurs débits dans un nombre suffisant de microhabitats et avec diverses combinaisons de conditions hydrauliques passées et présentes (p. ex. pour limiter la corrélation négative attendue entre la fréquence d'assèchement et la hauteur d'eau).

2.2 Les variations hydrauliques influencent la sélection du microhabitat des macroinvertébrés et des poissons dans les rivières à éclusées (Judes et al. B)

Judes et al. (B) ont étudié l'effet des éclusées de la basse rivière d'Ain (Encadré 3) sur la sélection du microhabitat des poissons et des macroinvertébrés principalement dans le but de (1) quantifier l'influence de l'hydraulique passée (assèchement et forte vitesse) sur la sélection de l'habitat et (2) de montrer si la sélection du microhabitat dans une rivière à éclusées était différente de la sélection du microhabitat dans des tronçons de rivière non influencés par des éclusées. Pour cela, Judes et al. (B) ont observé l'abondance des taxa de poissons dans 507 microhabitats par pêche électrique et 673 microhabitats par observations subaquatiques et l'abondance des taxa de macroinvertébrés benthiques et hyporhéiques dans 36 microhabitats le long d'un tronçon de 6 km en conditions d'éclusées. L'échantillonnage a été réalisé à différents débits pour réduire la corrélation entre les conditions hydrauliques présentes et passées (p. ex. la corrélation négative attendue entre la fréquence d'assèchement et la hauteur d'eau). Un modèle hydraulique 2D calibré sur le tronçon a permis de simuler l'hydraulique passée des microhabitats. Pour chaque microhabitat le passé hydraulique a été représenté par deux variables : l'assèchement et les vitesses de courant élevées ($>1,3 \text{ m s}^{-1}$) sur les 15 jours précédant l'échantillonnage. Ces deux variables étaient qualitatives : condition rencontrée pendant plus de 10 heures ou moins de 10 heures. L'influence des conditions hydrauliques, a été testée sur des guildes de taxa représentant les préférences d'habitat. Pour les poissons, la guildes "chenal" regroupe les taxa utilisant des habitats à fortes vitesses de courant et profond, et la guildes "berge", les taxa utilisant les habitats peu profonds et des faibles vitesses de courant. Judes et al. (B) ont regroupé les macroinvertébrés préférant les faibles vitesses de courant dans la guildes "limnophile" et ceux ayant une affinité pour les fortes vitesses de courant dans la guildes "rhéophile". Seule la comparaison de la sélection du microhabitat dans l'Ain avec les rivières sans éclusées a été faite sur les taxa individuellement quand des données étaient disponibles dans la littérature. Chaque abondance de guildes a été liée à l'hydraulique passée et présente des microhabitats (mesurée lorsqu'elle est disponible, modélisée sinon) par des GLMs. Pour éviter une surparamétrisation et en raison d'une puissance statistique limitée, Judes et al. (B) ont dû considérer des modèles impliquant des combinaisons d'une seule variable hydraulique présente (hauteur d'eau/vitesse) et d'une seule variable hydraulique passée (assèchement/forte vitesse).

Encadré 3. Zoom sur la rivière d'Ain.

La rivière d'Ain est le plus important affluent du haut Rhône, elle draine un bassin versant de 3630 km² et parcourt 200 kilomètres de sa source sur le plateau de Nozeroy (Jura) à sa confluence avec le Rhône (St Maurice de Gourdans). La rivière d'Ain a un régime pluvial (ou pluvio nival), elle est soumise à des crues rapides et fortes (les crues cinquantennales sont de 2500 m³ s⁻¹). De par son lit constitué de galets et de graviers et ses berges très érosives (galets, sables, limons), elle se transforme à chaque crue.



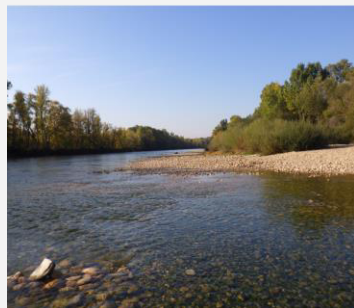
Il existe six centrales hydroélectriques sur la rivière d'Ain, de l'amont vers l'aval : Vouglans, Saut Mortier, Coiselet, Moux Charmines, Cize-Bolozon et le barrage d'Allement. Le tronçon d'étude de Judes et al. (B.) est situé à 20 km à l'aval du barrage de l'Allement dans ce qu'on appelle la Basse Vallée de l'Ain.

Le débit moyen annuel sur ce site d'étude est de 103 m³ s⁻¹ avec un débit moyen journalier compris entre 14 m³ s⁻¹ (dépassé 95% du temps) et 278 m³ s⁻¹ (dépassé 5% du temps). Le tronçon d'étude est soumis à de fréquentes variations de débit infra-journalières, avec un débit de base généralement compris entre 14 m³ s⁻¹ et (occasionnellement) 150 m³ s⁻¹ et un débit de pointe généralement compris entre 40 m³ s⁻¹ et 200 m³ s⁻¹. Le débit est plus stable pendant les week-ends et les périodes de faible débit (juin-septembre).

La Basse Vallée de l'Ain est connue pour sa faune piscicole variée, on y compte de nombreuses espèces de cyprinidés (barbeaux, chevesnes, vairons, hotus...) mais aussi des salmonidés, l'ombre commun et la truite.

Elle était jusqu'en 1994 la seule rivière en France à être classée « principalement peuplée d'ombres communs ». Elle possédait de ce fait une grande renommée au niveau européen pour la pêche. Dès 1939, Vibert évoquait l'impact des éclusées sur les peuplements de poissons et la biodiversité sur l'Ain et exposait la perte économique encourue si l'image halieutique de la rivière d'Ain se dégrade. De 1994 à 2011, la convention « Frayères » passée entre EDF et la fédération de pêche de l'Ain garantissait un débit minimum de 28 m³ s⁻¹ pendant la période de reproduction des salmonidés (01/12 - 01/05), alors qu'il est réglementairement de 12,3 m³ s⁻¹ le reste de l'année, en sortie d'Allement. Le but de cet accord était de limiter l'exondation des zones de fraie après la ponte. Une nouvelle convention (la convention « Salmonidés ») a été signée en janvier 2013. Encore maintenant, les associations de pêche de la basse vallée de l'Ain négocient avec EDF pour limiter au maximum l'impact des éclusées sur les poissons.

Bas débit (14 m³ s⁻¹)



Haut débit (150 m³ s⁻¹)



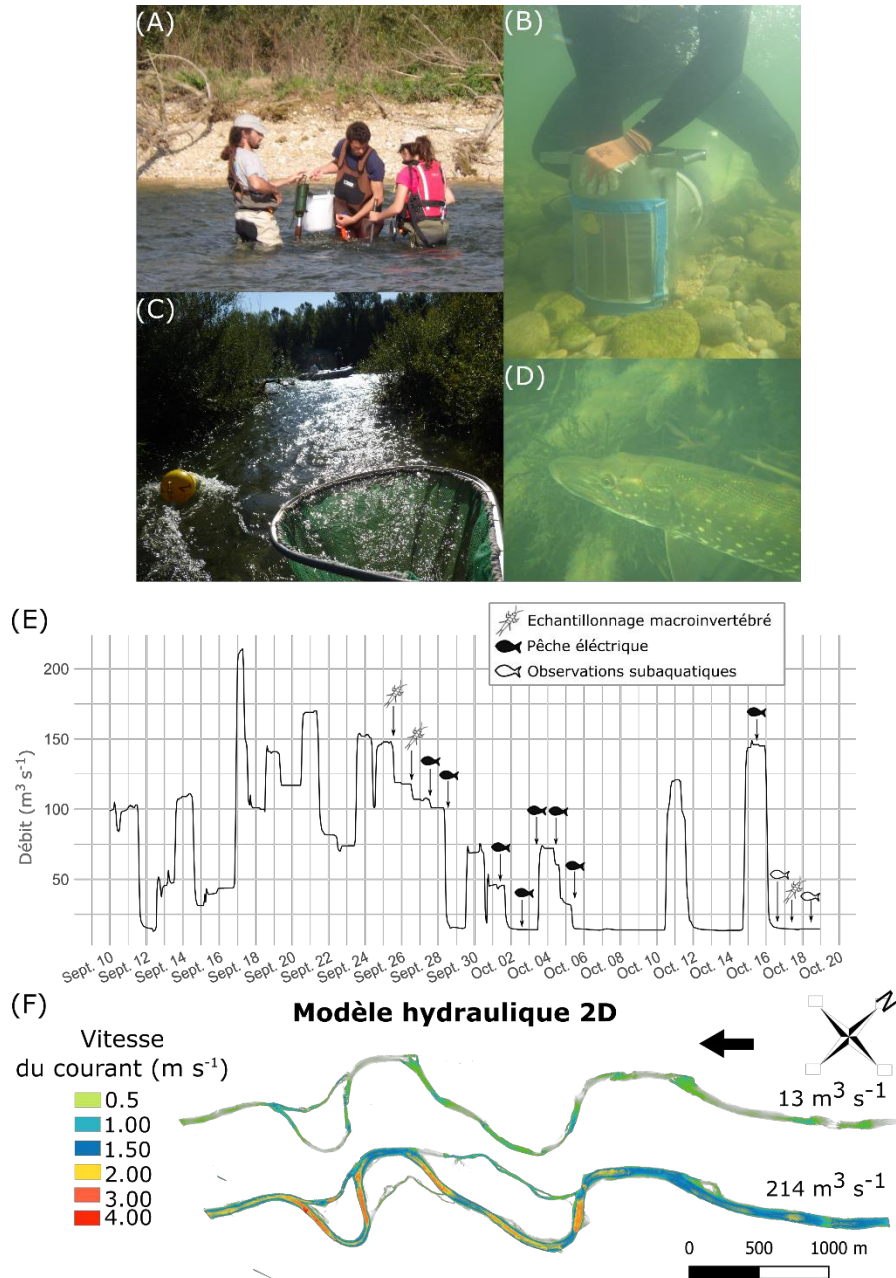


Figure I.6. Échantillonnage des poissons et des macroinvertébrés à plusieurs débits sur l'Ain et carte des vitesses de courant obtenue à partir du modèle hydraulique 2D (Judes et al. B). (A) Échantillonnage de macroinvertébrés hyporhéiques (avec un tube bou-rouch). (B) Échantillonnage de macroinvertébrés benthiques (avec un bethomètre). (C) Échantillonnage de poissons par pêche électrique. (D) Échantillonnage de poissons par observations subaquatiques. (E) Débit horaire à Pont d'Ain (7,5 km en amont du tronçon d'étude) pendant les 15 jours précédant l'échantillonnage et pendant l'échantillonnage (2018). Les flèches indiquent les jours d'échantillonnage à midi. A noter que les forts débits ($\sim 100 \text{ m}^3 \text{ s}^{-1}$) du 17 septembre au 28 septembre sont des lâchers d'eau pour le soutien des centrales nucléaires du Rhône. (F) Cartes de la vitesse de courant pour le débit maximal et le débit minimal rencontrés sur la période d'étude. La flèche indique le sens du courant.

Judes et al. (B) ont montré que l'hydraulique passée, en particulier les assèchements passés, influence grandement la sélection des microhabitats des macroinvertébrés. Les macroinvertébrés étaient 3-15 fois moins abondants dans les microhabitats qui se sont asséchés. Les macroinvertébrés ne semblent pas capables de suivre leurs conditions d'habitat favorables puisque leurs préférences pour l'hydraulique présente étaient différentes de celles observées dans les rivières sans éclusées (Figure I.7). Ces observations amènent à se questionner sur le terme de « sélection du microhabitat » lorsque l'on parle d'organismes à faible mobilité dans des rivières très dynamiques telles que les rivières à éclusées (Encadré 4). Par ailleurs, Judes et al. (B) ont montré que les macroinvertébrés benthiques et hyporhéiques ont répondu de la même manière aux assèchements. Au vu de ce résultat les macroinvertébrés dits « hyporhéiques » ont probablement été échantillonnés encore dans la zone benthique même si les prélèvements se sont faits à 30 cm de profondeur dans le substrat. Il semblerait, en tout cas, qu'à cette profondeur le substrat ne soit pas saturé en eau de façon pérenne. Les futures recherches devront tester s'il existe une zone hyporhéique pérenne sur les bords de la rivière d'Ain, si oui à quelle profondeur elle se trouve et si elle joue un rôle refuge à l'assèchement pour certain taxa de macroinvertébrés (certainement les plus petits).

Encadré 4. La sélection du microhabitat dans les milieux fortement dynamiques.

La sélection de l'habitat est définie comme un choix actif (inné ou appris) d'utiliser un habitat plutôt qu'un autre disponible autour de lui (Krausman 1999). L'abondance est utilisée comme un proxy de la sélection de l'habitat puisque la préférence d'habitat se traduit par l'utilisation disproportionnée de certains habitats par rapport à d'autres (Morrison et al. 1992). Lorsque l'hydrologie est naturelle (moins variable que dans les rivières à éclusées), l'hypothèse d'un choix actif est certainement vraie mais cela peut poser question dans les rivières à éclusées, en particulier pour les taxa ayant de faibles capacités de déplacement (ex. les macroinvertébrés). Dans un milieu fortement variable, la part de processus actif et passif expliquant l'abondance d'un taxon dans un microhabitat dépend de la durée entre le changement de débit et l'échantillonnage par rapport aux capacités de déplacement et de résistance du taxon (à l'assèchement ou aux fortes vitesses de courant). Par exemple, si un organisme a de faibles capacités de déplacement, les abondances observées à l'instant t peuvent refléter un choix actif ayant eu lieu à l'instant t-1 puis une résistance aux conditions de l'instant t (choix passif). Plus les conditions de ce que l'on observe sont là depuis longtemps (durée dépendante du taxon considérée), plus il est probable que les abondances observées soient issues d'un processus actif de sélection de l'habitat.

Judes et al. (B) ont montré que les poissons suivent leurs conditions d'habitat favorables (Figure I.7). Ces résultats s'opposent à certaines études ayant montré que les poissons étaient réticents à se déplacer pour suivre leurs conditions d'habitat favorables avec le débit (Kemp et al. 2003, Korman & Campana, 2009). Les différences de réponses dépendent certainement de

l'équilibre entre le gain/perte associé au fait (1) d'être toujours dans les conditions hydrauliques favorables (gain: optimisation de l'alimentation et du repos ; perte: coût énergétique et risque de prédation associé au déplacement) et (2) de rester au même endroit (gain: garder le territoire et éviter la prédation pendant le déplacement ; perte: difficulté à se nourrir ou à se reposer et coût énergétique lié au fait de subir des conditions hydrauliques défavorables) (Korman et al. 2009). Ces différences sont aussi largement attribuées à des facteurs (1) physiques, par exemple la présence de refuges de vitesse et la dynamique spatio-temporelle des habitats et (2) biologiques, par exemple la variabilité inter et intra-individuelle ou la présence de prédateurs (Krimmer et al. 2011, Taylor et al. 2014).

Judes et al (B) ont montré que l'hydraulique passée avait une influence moins forte sur la sélection de l'habitat des poissons par rapport aux macroinvertébrés. Néanmoins, les poissons de la guildes « berge » sélectionnent positivement les microhabitats qui se sont asséchés et à l'opposé les poissons de la guildes « chenal » les évitent. Ces différences s'expliquent par les préférences d'habitat plus strictes des poissons de la guildes « berge », ils sont obligés d'utiliser les microhabitats qui s'assèchent pour rester dans leurs conditions d'habitat favorables. La relation positive s'explique par le fait que les poissons se réfugient sur les bords lors des augmentations de débits. Les résultats de Judes et al. (B) fournissent donc un aperçu mécanistique permettant en partie d'expliquer comment les espèces de poissons des rivières de taille moyenne sont affectées par les éclusées : les poissons suivent leurs conditions d'habitat favorables et ces déplacements provoquent certainement des pertes énergétiques, de la fatigue et augmentent le risque de prédation. Certaines études ont montré qu'effectivement les poissons se déplacent plus dans les rivières à éclusées que dans les rivières sans éclusées (Harby et al. 2001, Harvey-Lavoie et al. 2016) mais d'autres n'ont pas trouvé de différence (Bunt et al. 1999, Berland et al. 2004). Néanmoins, ces études impliquent des suivis individuels par télémétrie et ignorent généralement les déplacements et mouvements des petits organismes (plutôt guildes « berge ») qui semblent les plus concernés par ces déplacements fréquents.

Judes et al (B) n'ont pas montré d'influence significative des fortes vitesses passées chez les poissons et chez les macroinvertébrés limnophile. Les poissons de la guildes « berge » restent proches des berges et ne subissent donc pas les fortes vitesses alors que les poissons de la guildes « chenal » arrivent certainement à les supporter ou se cachent dans les refuges hydrauliques. Les macroinvertébrés rhéophiles auraient tendance à sélectionner positivement les microhabitats soumis à des fortes vitesses passées. Ils ont certainement la capacité de résister

aux fortes vitesses en raison de leurs adaptations morphologiques ou comportementales aux fortes vitesses de courant. Holomuzki & Biggs (2000) ont étudié la réponse du comportement de quatre espèces de macroinvertébrés de Nouvelle-Zélande (l'escargot *Potamopyrgus antipodarum*, l'éphémère *Deleatidium* spp, et deux espèces de Tricoptère : *Pycnocentroides aeris* et *Hudsonema amabilis*) aux fortes vitesses de courant ($1,4 \text{ m s}^{-1}$). Ils ont montré que ces espèces pouvaient “sentir” l’augmentation des contraintes de cisaillement et y répondre rapidement. L’ensemble des espèces ont réalisé de petits mouvements entre les couches de substrat pour chercher des refuges hydrauliques, en s'enfonçant dans le substrat ou en se repositionnant à la surface du substrat (Lancaster et al. 1997). Par ailleurs, certains taxa ont des adaptations physiologiques pour s'accrocher aux substrats et tenir lors des fortes vitesses de courant. Par exemple, les Trichoptères se fixent aux substrats à l’aide de leurs soies, l'éphémère grâce à ces griffes tarsiennes et l'escargot par son pied.

Les principaux résultats de la thèse sont résumés dans la Figure I.8.

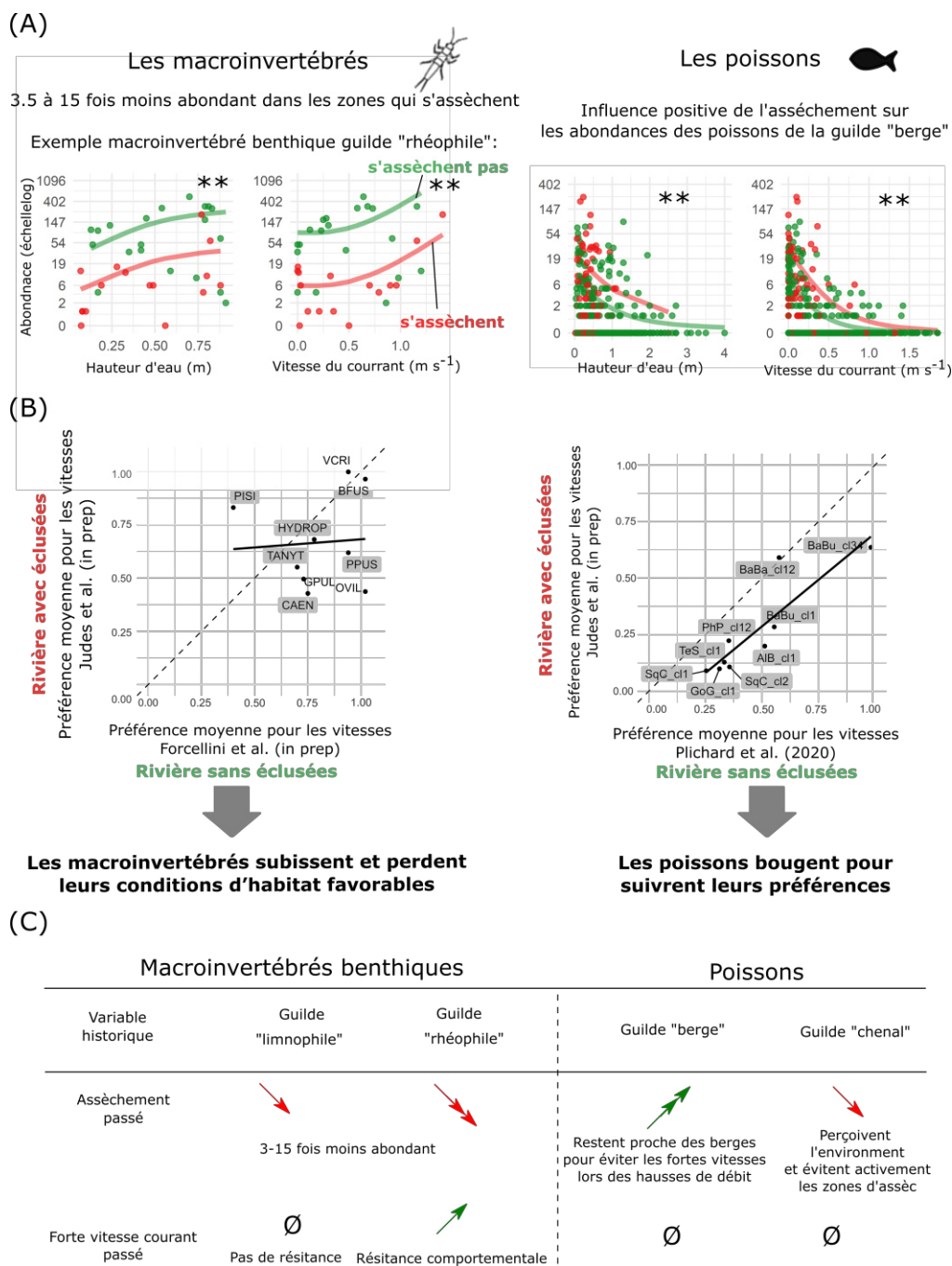


Figure I.7. Résumé des résultats de Judes et al. (B). (A) Ajustements des modèles (ou courbe de préférence d'habitat) reliant l'abondance des guildes à l'hydraulique présente et incluant un effet additif de l'assèchement (courbe rouge). Les étoiles (**) indiquent que l'effet de l'hydraulique passée était significatif $P < 0,01$. (B) Adéquation de la préférence moyenne pour la vitesse obtenue dans Judes et al. (B) avec les données de la littérature sur des rivières majoritairement non-soumises aux éclusées. Les régressions des axes (lignes pleines) sont représentées ainsi que les lignes $y = x$ (lignes pointillées). (C) Tableau des effets des variables de l'hydraulique passée sur l'abondance des guildes de taxa. Les flèches rouges représentent un effet négatif, les flèches bleues un effet positif. Le nombre de flèches représente la significativité des résultats : une flèche pour $P < 0,05$; double flèche pour $P < 0,01$. Les résultats sur les poissons concernent uniquement les données de pêche électrique (les observations subaquatiques n'ont pas révélé d'effets significatifs de l'hydraulique passée).

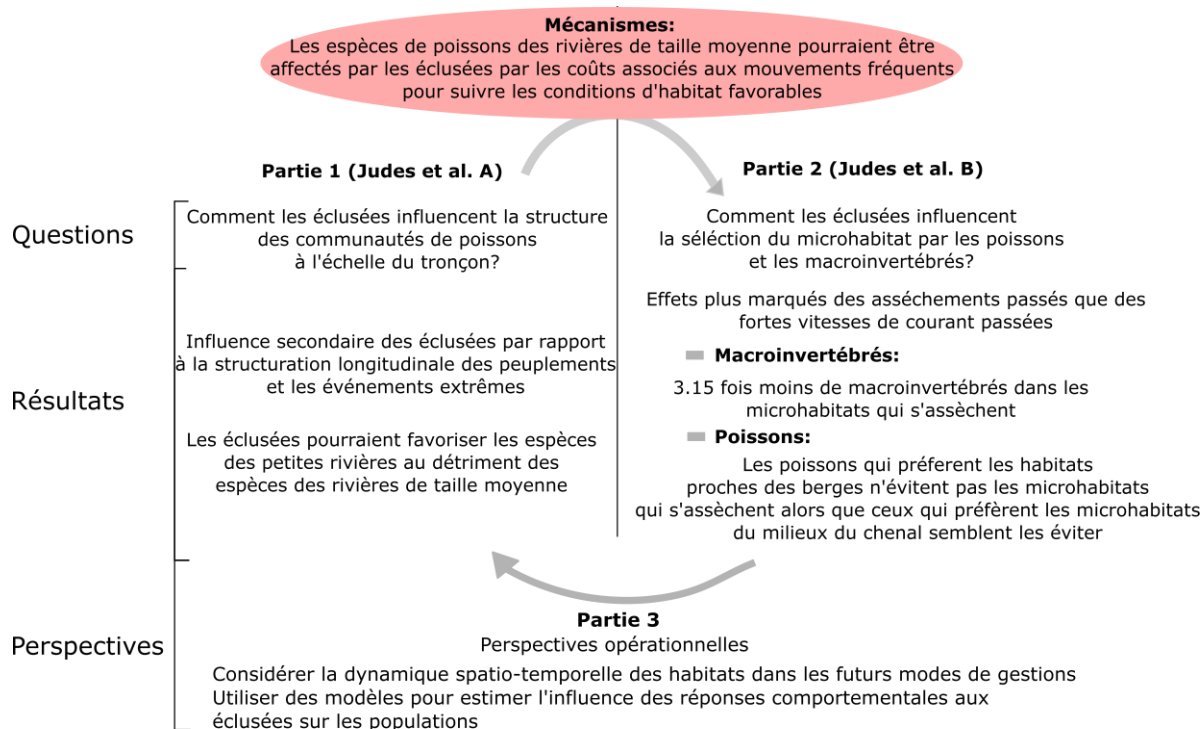


Figure I. 8. Résumé des principaux résultats de la thèse.

2.3 Perspectives scientifiques

Quelles sont les conséquences des mouvements fréquents des poissons sur leurs bilans bioénergétiques ?

Judes et al (B) ont montré que les poissons de la guildes « berge » (globalement des juvéniles) se repositionnent à chaque changement de débit pour suivre leurs conditions d'habitat favorables. Les déplacements fréquents de ces poissons provoquent certainement des pertes énergétiques, de la fatigue et augmentent le risque de prédation.

Plusieurs études ont comparé de manière qualitative le poids par rapport à la taille (condition physique), la masse corporelle, ou le taux de croissance des organismes entre des conditions avec ou sans variations artificielles de débit (en laboratoire ou in situ). Malgré quelques exceptions (Puffer et al. 2015), la majorité des études ne semblent pas avoir montré d'effets des éclusées sur ces paramètres (Enders et al. 2017, Finch et al. 2015, Flodmark et al. 2006, Puffer et al. 2017). Par exemple, Puffer et al. (2017) et Flodmark et al. (2006), dans des

chenaux artificiels, ont montré uniquement des effets mineurs et non significatifs des éclusées sur les performances de croissance des salmonidés (saumons atlantiques et juvéniles de truites brunes). Ainsi cela suggère que le bilan bioénergétique est équilibré (c.-à-d. que l'énergie dépensée est égale à l'énergie gagnée) : il ne semble ne pas y avoir d'augmentation ou de diminution des réserves internes d'énergie en réponse aux éclusées. Cependant, puisque tout comportement utilise du temps et de l'énergie (Cuthill et al. 1997), soit (1) la dérive des macroinvertébrés, plus forte durant les éclusées (Schulting et al. 2016), permet de compenser les pertes énergétiques pour certains taxa, soit (2) pour compenser les poissons sont obligés d'augmenter leur temps à rechercher de la nourriture. Puisque les organismes sont sujets à des plus forts risques de prédation lorsqu'ils sont en recherche de nourriture que lorsqu'ils se reposent (McNamara et al. 1992) cela peut affecter leurs survies. Il est donc important d'étudier si le temps de recherche de nourriture est plus important dans les rivières à éclusées. Pour cela, je suggère deux approches.

Premièrement, une approche empirique visant à comparer le temps à rechercher de la nourriture par les poissons avec ou sans éclusées. Bien qu'aucune ne soit idéale pour le moment, plusieurs méthodes sont possibles. Parmi elles, l'expérimentation ex situ ou in situ via des vidéos (Boisclair, 1992, Enders et al. 2005, Sabo et al. 1996, Shamur et al. 2016). Les approches basées sur la vision fonctionnent bien lorsque l'eau est claire et que les poissons sont dans le champ de vision de la caméra. Lorsque ce n'est pas le cas, il sera peut-être bientôt possible d'utiliser des électrocardiogrammes puisque Shen et al. (2021) ont développé un algorithme permettant de détecter les phases de nourrissage par les changements du rythme cardiaque. Cependant, utiliser le rythme cardiaque en tant qu'indicateur d'activité peut être parfois difficile puisque la fréquence cardiaque est influencée par d'autres variables (température de l'eau, stress etc.). Pour l'instant, il n'est pas possible d'étudier les comportements de recherche de nourriture par des suivis individuels de poissons par télémétrie en rivière car la précision des localisations ne permet pas de les différencier du repos.

Deuxièmement, une approche théorique qui consisterait à convertir les distances entre les deux habitats favorables successifs (Batz et al. soumis) en coût énergétique associé à la nage. La conversion des mouvements des poissons en coûts nécessite des relations entre les caractéristiques des mouvements et les dépenses énergétiques. Les relations sont généralement développées à partir d'expériences de respirométrie réalisées en laboratoire (Enders et al. 2005, Enders et al. 2003, Guensch et al. 2001, Sabo et al. 1996). Une fois les pertes énergétiques

connues, elles pourraient être traduites en temps supplémentaire à rechercher de la nourriture grâce à des modèles de recherche de nourriture. Les modèles de recherche de nourriture sont des simplifications du mode de vie dans lequel les poissons trouvent et consomment leurs nourritures. Ces modèles prennent en considération des facteurs tels que le comportement de recherche de nourriture, la vitesse de nage, la densité et la taille des proies, la distance et l'efficacité de capture des proies (et leur dépendance par rapport à la clarté de l'eau) (Guensch et al. 2001, Hayes et al. 2007).

Comment compléter l'étude de Judes et al. (B) ?

Pour confirmer les hypothèses formulées par Judes et al. (B) il faudrait tout d'abord tester si l'effet de l'hydraulique passée sur la sélection du microhabitat des poissons et des macroinvertébrés est transférable et généralisable à d'autres rivières. Pour cela, il faudrait réaliser la même expérimentation que Judes et al. (B) dans une rivière à l'hydrologie et à l'intensité de gestion des éclusées contrastées par rapport à la rivière d'Ain.

Concernant les macroinvertébrés, plusieurs approches sont possibles pour compléter l'étude de Judes et al. (B). Premièrement, Judes et al. (B) ayant échantillonné uniquement à fort débit ($\sim 100 \text{ m}^3 \text{ s}^{-1}$) et au débit de base ($14 \text{ m}^3 \text{ s}^{-1}$), il faudrait échantillonner à des débits intermédiaires (p. ex. $28/50/70 \text{ m}^3 \text{ s}^{-1}$) afin de tester la réponse des macroinvertébrés à d'autres patterns d'assèchement (p.ex. différentes durées entre deux remises en eau et différentes fréquences d'assèchement). Deuxièmement, il faudrait tester l'influence de la durée depuis la remise en eau puisqu'il s'agit un facteur important pour la recolonisation des microhabitats asséchés (Kjaerstad et al. 2018). Pour cela, il faudrait échantillonner des microhabitats remis en eau depuis différentes durées (p. ex. 15 jours, 1 mois, 2 mois). Sur l'Ain, pour obtenir une longue période de fort débit il faudra échantillonner à la fin du printemps. A priori, Judes et al. (B) ont montré qu'une période de huit à neuf jours de fort débit (lâché prolongé de $100 \text{ m}^3 \text{ s}^{-1}$ pour le fonctionnement des centrales nucléaires du Rhône, Figure I.6) ne suffit pas pour permettre la recolonisation complète des microhabitats souvent asséchés. Troisièmement, il faudra tester l'influence de l'hydraulique passée vécue sur une période plus longue avant l'échantillonnage que les 15 jours testés par Judes et al. (B) (c.-à-d. 1 mois ou 2 mois avant l'échantillonnage). L'été 2018 (juste avant l'échantillonnage de Judes et al. (B)) a été très sec, les débits n'ont pas dépassé $100 \text{ m}^3 \text{ s}^{-1}$ de la mi-juin à la fin août. Cette longue période de faible

débit a pu expliquer en partie la réponse des macroinvertébrés à l'assèchement de Judes et al. (B). Enfin, il faudrait répliquer l'expérimentation de Judes et al. (B) au printemps pour avoir le maximum de taxa échantillonnés et identifiés jusqu'à l'espèce. En effet, Judes et al. (B) ayant échantillonné en automne ils n'ont pas pu étudier l'ensemble des taxa de l'Ain car la plupart émergent au printemps ou été (Brabec et al. 2021, Buffagni et al. 2021, Graf et al. 2021 a, b). Judes et al. (B) avaient dû faire un compromis entre l'hydrologie (avoir des débits contrastés) et la période idéale des échantillonnages biologiques.

Concernant les poissons, pour confirmer que les poissons de la guildes "chenal" évitent les microhabitats qui s'assèchent, il faudra d'abord tester l'influence de la disponibilité des habitats sur la sélection de l'habitat (Encadré 5) (Pert et al. 1994). Cela n'a pas pu être fait par Judes et al. (B) à cause d'un manque de pouvoir statistique lié au fait de devoir diviser le jeu de données en deux (faible et fort débit) pour le tester. Par ailleurs, l'échantillonnage sur des poissons de la guildes "chenal" devra être complété par des observations subaquatiques à fort débit ou des suivis par télémétrie. L'avantage de l'observation subaquatique est qu'elle permet d'apporter de grandes quantités de données rapidement et à faible coût, mais pourrait être limitée par des vitesses de courant trop fortes. La télémétrie est sans doute la seule méthode permettant d'observer les organismes dans les habitats à fortes vitesses de courant, mais elle peut être sensible à la profondeur (radio) ou à la turbulence (acoustique). Cette méthode permettrait cependant de tester si les poissons de la guildes « chenal » utilisent des habitats à plus fortes vitesses de courant lors des forts débits.

Par ailleurs, il serait intéressant de tester l'influence de l'hydraulique passée sur la sélection du microhabitat par les poissons par d'autres méthodes que les modèles corrélatifs développés par Judes et al. (B). Parmi les autres méthodes existantes, il y a l'écologie du mouvement (Nathan et al. 2008) qui vise à étudier les interactions entre les individus et l'environnement dans leurs déplacements par l'analyse des trajectoires observées des organismes (p. ex. vitesse, orientation, changements de direction). Cette approche pourrait être mise en œuvre par télémétrie acoustique (précision dans la localisation des poissons < 5 m) dans un tronçon pour lequel un modèle hydraulique 2D est disponible. La télémétrie acoustique permet de calculer la vitesse et les directions des déplacements des poissons, de détecter les phases d'accélération et les changements de direction à échelle fine quasiment en temps réel. La première étape consistera à proposer des indicateurs de trajectoire (vitesse absolue, vitesse

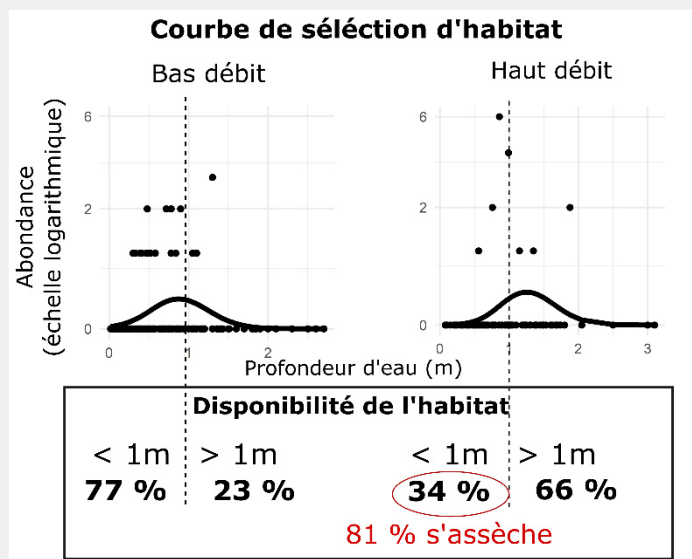
angulaire, accélération, etc.) pour discriminer les différents types de comportements (statique/mouvement). Ensuite, grâce au modèle hydraulique 2D, il s'agira de décrire comment l'hydraulique présente et passée (même variables testées que Judes et al. (B)) influence les changements de comportement. L'hypothèse serait que pour les poissons de la guildes « chenal », la probabilité de rester dans un microhabitat qui s'assèche est plus faible que de rester dans un microhabitat qui ne s'assèche pas alors même que les conditions hydrauliques présentes sont semblables. Concernant les poissons de la guildes « berge », il serait intéressant d'étudier le temps de réaction pour fuir les microhabitats qui vont s'assécher lors des baisses de débit.

Encadré 5. Influence de la disponibilité de l'habitat sur l'interprétation des résultats des études sur la sélection de l'habitat

Lorsque des différences de comportement de sélection de l'habitat sont observées à différents débits, elles peuvent être liées à une différence de disponibilité de l'habitat. En effet, certains organismes peuvent choisir différentes conditions d'habitat en fonction de la gamme de valeurs disponibles autour d'eux (Belaud et al. 1989, Arthur et al. 1996). Si en effet, les organismes suivent la disponibilité des habitats alors il peut y avoir des erreurs dans l'interprétation des résultats, c'est-à-dire de conclure à un évitement des microhabitats qui s'assèchent à tort.

La figure ci-contre illustre les courbes de sélection de la profondeur d'eau à bas débit ($14 \text{ m}^3 \text{ s}^{-1}$) et à haut débit ($214 \text{ m}^3 \text{ s}^{-1}$) pour la guildes « chenal » issues des données de Judes et al. (B). Les valeurs de disponibilité de l'habitat de moins d'un mètre dans le tronçon d'étude de Judes et al. (B) à bas et à haut débit sont aussi représentées (obtenues à partir du modèle hydrodynamique 2D).

Dans cet exemple, à bas débit, 91% des poissons se trouvent dans des habitats de moins d'un mètre alors que ces derniers représentent 77% de l'habitat disponible. Dans ces habitats de moins d'un mètre on ne retrouve plus que 57% des poissons échantillonnés à haut débit mais ces habitats ne représentent plus que 34% de l'habitat disponible. Les habitats de moins d'un mètre à haut débit sont en grande majorité soumis à des assèchements fréquents (81 %). Ainsi si l'on ne considère pas la disponibilité et que l'on met dans une même analyse les données issues des échantillonnages à haut et à bas débit, il est fort probable que la conclusion soit que les poissons évitent les zones d'assec alors qu'en réalité ils les sélectionnent positivement (plus nombreux dans les zones d'assec par rapport à leur disponibilité).



Judes et al. (B) ont étudié l'hydraulique présent par deux variables corrélées, la hauteur d'eau et la vitesse moyenne du courant. A l'avenir, il faudra considérer la hauteur d'eau et la vitesse simultanément dans les modèles statistiques. Mieux encore, pour ne pas surparamétrer les modèles et parce que les organismes perçoivent la hauteur d'eau et la vitesse de courant simultanément (Coarer 2007, Muñoz-Mas et al. 2012, Plichard 2018), il faudrait utiliser une variable qui combine la hauteur d'eau et la vitesse comme le nombre de Froude ($FR=V/[g \times H]^{0.5}$ ou g est l'accélération due à la gravité, sans diminution) (Lamouroux et al. 2002). Par ailleurs, les conditions hydrauliques ne sont pas les seuls paramètres qui décrivent l'habitat des poissons et des macroinvertébrés. Les futures études devront tenir compte de la température et du substrat. D'une part, ces paramètres influencent la sélection du microhabitat par les poissons et les macroinvertébrés (Bradford et al. 1997, Choi et al. 2017) et cela peut possiblement masquer les effets de l'hydraulique passée. D'autre part, ils influencent la susceptibilité à l'échouage-piégeage et à la dérive et ainsi peuvent influencer le choix d'occuper ou non un microhabitat qui s'assèche ou qui est soumis à des fortes vitesses de courant. Par exemple, l'échouage des poissons semble être plus élevé dans les substrats grossiers (>7,6 cm) par rapport à des substrats plus fins (Beck et al. 1989), et durant les basses températures (Bradford et al. 1997).

Y a-t-il une adaptation comportementale aux variations des conditions hydrauliques ?

En général, le processus de sélection du microhabitat est adaptatif car il repose sur des signaux (p. ex. conditions hydrauliques) qui, au cours de l'évolution, ont été corrélés de manière fiable avec la survie et le succès reproducteur. Cependant, si l'environnement change soudainement (p.ex. apparition des éclusées), ces signaux jusqu'alors considérés peuvent ne plus être en corrélation avec le résultat attendu et, par conséquent, la sélection du microhabitat peut ne plus être adaptative (Williams et al. 1984). Dans le cas des rivières à éclusées, par exemple, suivre ses préférences d'habitat n'est plus adaptatif si l'organisme n'est pas capable de fuir à temps les conditions hydrauliques extrêmes pour échapper l'échouage-piégeage ou la dérive forcée. Dans ce cas, le comportement le plus adaptatif serait de sélectionner des habitats certainement moins favorables à l'instant t mais qui ne subissent pas de changements hydrauliques extrêmes (microhabitats qui ne s'assèchent pas ou qui ne sont pas soumis à des fortes vitesses de courant). Un tel changement de comportement pourrait apparaître par

plasticité phénotypique (basé sur l'apprentissage) ou par sélection naturelle (sélection sur la variation génétique existante) (Kokko et al. 2001, Schlaepfer et al. 2002).

Judes et al (B) ont étudié la réponse d'individus de l'Ain subissant des éclusées depuis 1930, il est donc possible que ces individus soient adaptés (sélection naturelle) ou acclimatés (plasticité phénotypique) aux variations rapides des conditions hydrauliques. En particulier, les poissons de la guildes « chenal » sont peut-être adaptés ou acclimatés pour éviter les microhabitats qui s'assèchent et les poissons de la guildes « berge » sont peut-être adaptés ou acclimatés pour changer rapidement de position lors des baisses ou des hausses de débits. Pour tester ces hypothèses, je comparerais en condition expérimentale les réponses comportementales aux variations hydrauliques artificielles d'organismes issues de rivière à éclusées avec ceux issus de rivière non influencée par les éclusées. Concrètement, il s'agirait de regarder le temps de réponse pour fuir les microhabitats qui vont s'assécher en fonction de l'origine des poissons, ou les préférences moyennes pour la vitesse et la hauteur d'eau. A priori, Judes et al. (B) suggèrent que les préférences pour les vitesses moyennes pourraient être plus faibles dans les rivières à éclusées (Figure I.7), il s'agit peut-être d'une adaptation (ou acclimatation) pour éviter de se faire emporter par les fortes vitesses de courant lors des hausses de débit. Une autre manière de faire serait d'étudier génération après génération comment la sélection du microhabitat des taxa évolue dans une rivière récemment soumise aux éclusées.

3. PERSPECTIVES OPERATIONNELLES

3.1 Considérer les connaissances sur la sélection du microhabitat pour mieux quantifier l'influence des éclusées à l'échelle du tronçon

L'échelle du microhabitat est celle qui représente le mieux les conditions d'habitat qui sont perçues et exploitées par les organismes. Il s'agit donc de l'échelle la plus pertinente pour essayer d'identifier les mécanismes expliquant les observations faites à des échelles plus larges. Cependant, les mesures opérationnelles ignorent généralement l'influence des perturbations à l'échelle du microhabitat (Pringle et al. 1988) et concernent principalement l'échelle du tronçon. Il est donc nécessaire de disposer de méthodes qui intègrent les résultats obtenus à l'échelle du microhabitat dans des approches qui permettent d'estimer l'influence des perturbations sur les populations à l'échelle du tronçon (Winemiller et al. 2010).

Quantifier la dynamique spatio-temporelle des habitats

En partant du constat que les poissons et les macroinvertébrés ne répondent pas de la même manière aux éclusées (mouvement ou statique), Batz et al. (Soumis) suggèrent une approche pour quantifier l'influence de dynamique spatio-temporelle des habitats sur les organismes selon un trait d'histoire de vie : la mobilité.

On a vu précédemment que les poissons suivent leurs conditions d'habitat favorables et que ces déplacements peuvent entraîner des pertes énergétiques (dues à la nage) et/ou augmentent le risque de prédation. Ainsi, Batz et al (Soumis) ont proposé des métriques quantifiant les distances de déplacement nécessaires pour se maintenir dans une condition d'habitat particulière à chaque changement de débit (Figure I.9). L'hypothèse étant que les poissons se déplacent dans le nouveau microhabitat favorable le plus proche de lui à chaque changement de débit. Cependant, Shirvell (1994) a montré par télémétrie qu'un poisson se déplaçait en moyenne de 6,8 m à chaque changement de débit alors que les conditions hydrauliques se déplaçaient latéralement en moyenne de 2,0 à 2,9 m. Ce résultat contraste avec les précédentes études montrant que les poissons sont capables de percevoir leur environnement et d'adapter le comportement de sélection de l'habitat le moins contraignant possible (Geist et al. 2005, Capra et al. 2017). De plus, le suivi strict des conditions d'habitat favorables concerne

certainement plus les poissons de petite taille (gilde « berge ») qui ne peuvent pas être suivis par télémétrie. Les futures études devront creuser les liens entre déplacements des organismes et déplacements des conditions d'habitat (Conallin et al. 2014) mais cela risque d'être compliqué à réaliser puisque les poissons se déplacent souvent dans différents habitats selon leurs activités (p. ex. repos, recherche de nourriture).

A l'inverse, les macroinvertébrés, du fait de leurs faibles capacités de déplacement, sont particulièrement affectés par les variations des conditions d'habitat au sein des microhabitats. Pour rendre compte de la perturbation vécue par les macroinvertébrés, Batz et al (Soumis) proposent de délimiter des patchs (zones géographiquement fixes (Pickett et al. 1997) entre 0 et 100m² (Pringle et al. 1988, Winemiller et al. 2010) et d'examiner les variations temporelles des conditions d'habitat au sein de ces patchs. Concrètement, ils ont délimité cinq classes (toutes les 0.25 m s⁻¹) de conditions de vitesse (ou de hauteur d'eau) et ont quantifié le nombre de changements de classe sur une période donnée. Ils proposent aussi de quantifier la persistance temporelle d'une condition d'habitat dans les patchs alors que la persistance était jusqu'alors utilisée pour décrire les tronçons (Freeman et al. 2001). A l'échelle du microhabitat, Judes et al. (B) suggèrent que la persistance de mise en eaux semble importante pour les macroinvertébrés en général et la persistance des faibles vitesses de courant importante pour les macroinvertébrés limnophiles.

La persistance des faibles vitesses pourrait aussi être favorable pour les poissons pour des stades de vie précoces comme les œufs puisque la persistance des conditions de vitesses faibles semble essentielle pour limiter le décapage. Par exemple, Bartoň et al. (2021) ont montré que le site de frai des poissons ne devrait pas dépasser 0,7 m s⁻¹ (sur les œufs de *Leuciscus aspius* sur la rivière de Želivka en République tchèque).

Avant que ces métriques soient utilisées pour la gestion il sera nécessaire de (1) tester leurs pertinences biologiques et (2) de trouver des méthodes pour intégrer les résultats dans des mesures écologiques significatives à l'échelle du tronçon. Cependant, les gestionnaires qui adopteront la perspective des organismes (mobilité) telle que décrite ci-dessus auront l'avantage de permettre une approche spatio-temporelle et de proposer des schémas de gestion affectant la dynamique et la structure de la mosaïque d'habitats (Pringle et al. 1988, Pickett et al. 1997, Hitchman 2017). De plus, une telle approche à l'échelle locale facilitera une comparaison

quantitative et transférable au sein et entre rivières (Pringle, 1988). Bien que les écologistes du paysage aient, une longue expérience de la quantification des formes, des tailles, des configurations, de la diversité, de la densité et de la connectivité des habitats, il manque un ensemble de mesures d'évaluation pertinentes écologiquement pouvant être utilisées par les gestionnaires. L'apprentissage collaboratif (Weber et al. 2017) entre la recherche et la pratique sont nécessaires pour développer des approches de gestion qui tiendront compte de la dynamique spatio-temporelle des habitats.

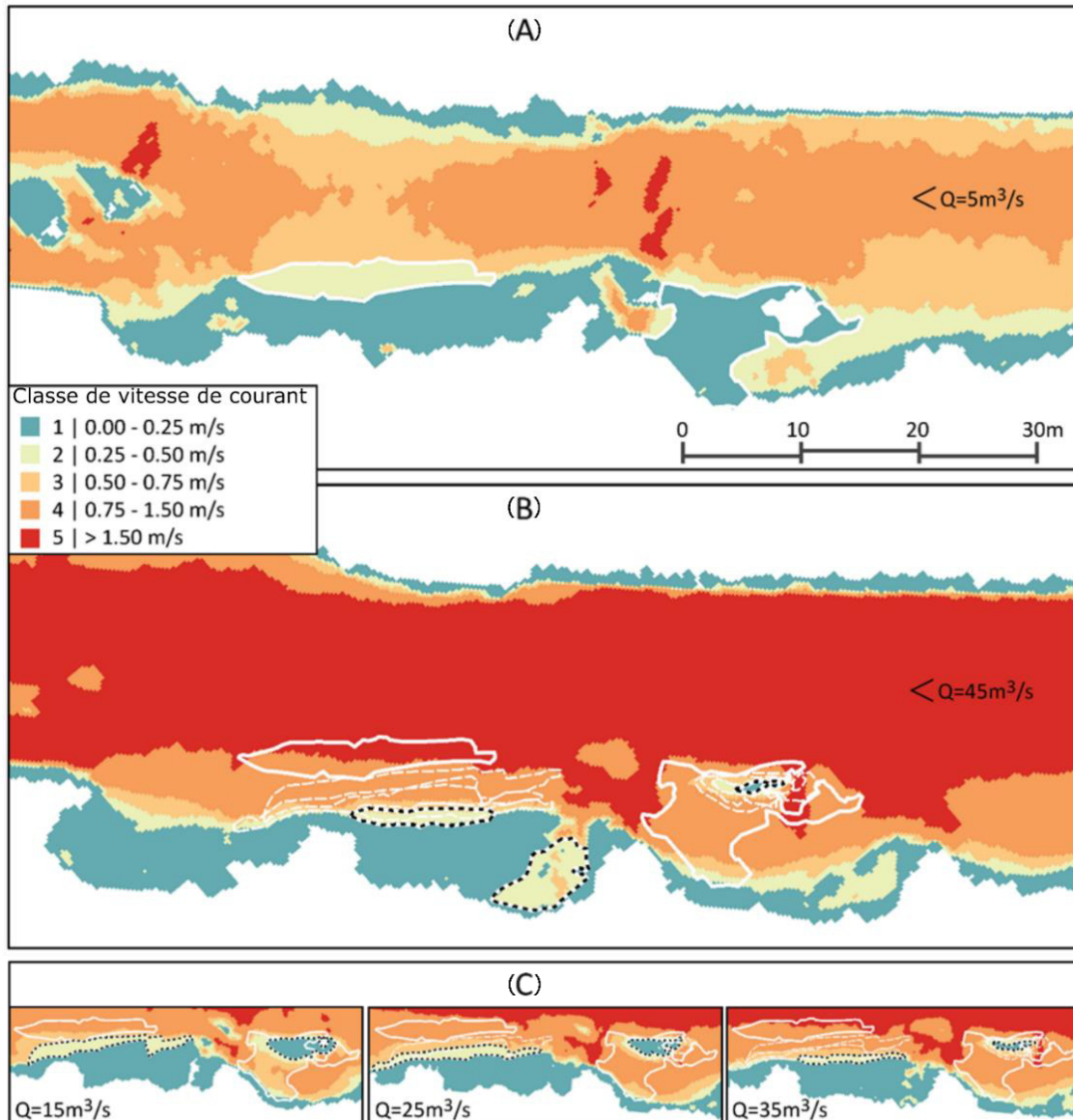


Figure I. 9. Résultats d'un modèle 2D et classification en cinq types d'habitats simples (classes de vitesse du courant) pour un tronçon de la rivière Aare près d'Innertkirchen en Suisse. (A) Distribution des conditions de vitesse au débit de base ($5 \text{ m}^3 \text{ s}^{-1}$), avec deux surfaces d'habitat homogène de référence marquées par des contours blancs (« patch »). (B) Distribution des habitats au débit de pointe ($45 \text{ m}^3 \text{ s}^{-1}$), le déplacement des habitats de références précédent est illustré par les contours en pointillés blanc, et leurs nouvelles positions par des contours pointillés blanc et noir. (C) Etapes intermédiaires entre (A) et (B). Notez qu'avec l'augmentation du débit, le type d'habitat 1 se contracte ; tandis que le type d'habitat 2 s'est déplacé vers les berges. Tiré de Batz et al. (Soumis).

Utiliser les modèles pour lier les connaissances sur la sélection du microhabitat et les effets sur la population

Les modèles d'habitat

Les modèles d'habitat hydrauliques (Lamouroux et al. 2017) sont certainement les plus utilisés pour lier les connaissances sur la sélection du microhabitat des organismes et la perturbation attendue à l'échelle du tronçon. Les modèles d'habitats couplent un modèle hydraulique du tronçon avec les préférences d'habitat connue d'un groupe taxonomique pour fournir une valeur d'habitat potentielle (VH) à chaque microhabitat (compris entre 0 et 1 (bonne qualité)). En sommant le produit des VH par la surface des microhabitats on obtient la « surface pondérée utile » (SPU) du tronçon, interprétée comme une surface d'habitat favorable. Le calcul de la SPU pour plusieurs conditions de débit permet d'obtenir une courbe de SPU. Cette courbe permet d'estimer la réponse de la population selon le débit. Il s'agit d'une méthode très utilisée pour aider à la gestion des débits réservés (débit minimal obligatoire) (Lamouroux et al. 2015), mais jusque-là peu pertinent pour aider à la gestion des débits éclusés. En effet, les modèles de sélection du microhabitat ne considéraient pas jusqu'alors la dynamique temporelle des habitats. Les travaux de Capra et al (2017) et Judes et al (B) sont un premier pas vers le développement de modèles de sélection du microhabitat dynamiques. De tels modèles permettront de mieux estimer l'habitat disponible dans les rivières à éclusées et ainsi d'établir des préconisations de gestion plus pertinentes.

Les modèles bioénergétiques

Les modèles bioénergétiques déterminent les préférences d'habitat en reliant les caractéristiques de l'habitat à des corrélats de la fitness directe, tels que l'apport net énergétique sur la base de connaissances fondamentales de la physiologie ou du comportement du taxon cible (Hayes et al. 2007, Kearney & Porter, 2009). Cette approche utilise comme paramètres d'entrée, les sorties d'un modèle hydraulique (et de température si disponible), les observations sur le terrain des caractéristiques de la populations (p.ex. distribution des tailles et poids), la densité de macroinvertébrés (généralement en dérive) et une connaissance fondamentale de la physiologie ou du comportement du taxon cible (Kearney et al. 2009). De la même façon, que les modèles d'habitat, les modèles bioénergétiques peuvent fournir une valeur d'habitat à

chaque type d'habitat sur une échelle de 0 à 1 reflétant l'apport énergétique net et ainsi obtenir une « surface pondérée utile ».

Ce type de modèle pourrait être adapté pour être applicable aux rivières à éclusées. Pour cela, il faudra lier l'apport énergétique net à l'hydraulique passée. Par exemple, l'assèchement passé réduit l'apport énergétique des organismes se nourrissant de macroinvertébrés benthiques. De plus, il faudrait aussi inclure l'influence des éclusées sur la dérive des macroinvertébrés puisque la dérive augmente avec les hausses de débit éclusées (Schülting et al. 2019).

Il s'agit d'une approche à développer car les modèles biogénétiques établissent un lien plus direct entre la condition physique des organismes et l'habitat biotique (compétition inter- et intra-spécifique et le risque de prédation) et abiotique. Ils sont réputés pour être une approche plus robuste et transférable pour prévoir les réponses biologiques aux changements d'habitat que les modèles d'habitat (Guensch et al. 2001, Cuddington et al. 2013, Naman et al. 2019).

Les modèles individus centrés

La modélisation individu centrée simule l'ensemble des comportements individuels et des relations entre individus pour prédire les réponses à des niveaux biologiques plus grands (Grimm et al. 2016). Elle a donc l'avantage de fournir en sortie l'abondance par classe d'âge ce qui est plus concret pour les gestionnaires que le concept de « surface pondérée utile » (Railsback 2016). La modélisation individu centrée permet aussi d'intégrer une partie de la complexité des systèmes écologiques réels et de comparer les résultats avec des modèles empiriques afin de tester des théories sur l'origine et les motivations des comportements observés (« Pattern-oriented modeling» voir Railsback & Harvey, 2002 et Goto et al. 2015).

Les modèles individus centrés peuvent être utilisés pour modéliser les processus de sélection de l'habitat des organismes en se basant en partie sur la façon dont la probabilité de survie (prédation, échouage piégeage, dérive forcé, famine) et de croissance (disponibilité en nourriture, capacité à attraper la nourriture, compétition, coût énergétique) varie en fonction des habitats disponibles. L'évolution de la population est prédite en intégrant la réponse de l'ensemble des individus de la population (en termes de croissance, de reproduction et de mortalité).

Ce type d'approche pourrait être utile pour la recherche scientifique pour aider à comprendre les origines et motivations des comportements de sélection du microhabitat observés. Ils permettront, entre autres, de tester si les organismes sont adaptés ou acclimatés aux variations spatio-temporelles des habitats dans les rivières à éclusées. Pour cela il faudra réaliser deux modèles, un modèle qui considère que les organismes se basent en partie sur l'hydraulique passée pour choisir le microhabitat qu'ils occupent et à l'inverse un modèle qui considère qu'ils se basent uniquement sur l'hydraulique présente. Enfin, il s'agira de tester lequel des deux modèles reproduit au mieux ce qui est observé sur le terrain (p.ex. les modèles empiriques Judes et al. B). Concernant la gestion, ce type d'approche pourrait être utilisé pour estimer l'abondance des taxa dans les rivières à éclusées en fonction de différents scénarios de dynamique spatio-temporelle d'habitat (p. ex. fréquence et temps d'assèchement ou de forte vitesse de courant, déplacement des conditions hydrauliques). Cela pourrait permettre d'identifier des seuils à partir desquels il y a une diminution nette de la taille des populations et ainsi être un outil précieux pour la gestion.

Cependant, malgré ces nombreux avantages puisqu'il y a énormément de paramètres d'entrée, ces modèles sont souvent extrêmement difficiles à paramétrer et sont compliqués à mettre en œuvre pour la gestion. Souvent les gestionnaires disposent de peu de temps et de ressources et la complexité des calculs, l'étendue et le détail des informations requises pour faire de tels modèles peuvent être un frein à leurs développements.

3.2 Cohérence des résultats de Judes et al. (B) avec les mesures de gestion des éclusées prises sur la basse rivière d'Ain

Les résultats de Judes et al. (B) peuvent être discutés au regard des mesures mises en œuvre par EDF pour réduire l'effet des éclusées sur la basse rivière d'Ain ces dernières années. Ces mesures visent en particulier l'atténuation du risque d'exondation des frayères et du risque d'échouage-piégeage des juvéniles de truites et d'ombre. Concernant l'exondation des frayères, le débit réservé a été élevé à $28 \text{ m}^3 \text{ s}^{-1}$ une partie de l'année (durant la période de reproduction et de croissance larvaire : 01/12 au 01/05) au lieu de $12,3 \text{ m}^3 \text{ s}^{-1}$ le reste de l'année à l'aval immédiat du barrage de l'Allement. La figure I.10 montre la relation entre le débit et la surface immergée : la surface immergée augmente nettement avec le débit de base jusqu'à environ $50 \text{ m}^3 \text{ s}^{-1}$. Puisque Judes et al. (B) ont montré que les macroinvertébrés se trouvent majoritairement

dans les habitats qui restent toujours en eau cette mesure semble pertinente pour augmenter l'abondance des macroinvertébrés dans la basse rivière d'Ain. Concernant les gradients de baisse de débit, pour une baisse de débit compris entre $12 < Q < 80 \text{ m}^3 \text{ s}^{-1}$ le gradient de baisse est limité à $5,8 - 15 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$ en 2016 et pour une baisse de débit comprise entre $12 < Q < 120 \text{ m}^3 \text{ s}^{-1}$ le gradient doit être entre $4 - 15 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$ en 2018-2019. Ces limitations de gradient sont appliquées de mars à fin mai (dates variables). Une proposition a été faite pour 2020 d'appliquer un gradient très atténué ($1 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$) lors des baisses les plus à risque (après 01/05). Judes et al. (B) ont montré que les poissons de la guildes « berge » (majoritairement les juvéniles) utilisent de manière préférentielle les microhabitats qui s'assèchent. Cette proposition semble donc intéressante et mérite d'être suivie si l'on souhaite minimiser l'échouage-piégeage des juvéniles de poissons.

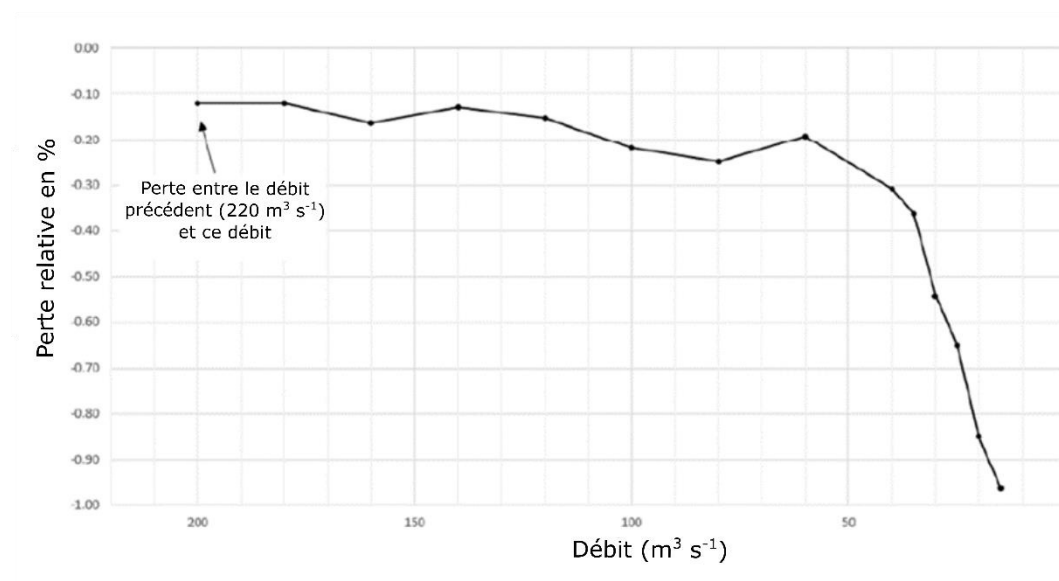


Figure I. 10. Evolution des pertes relatives de surface mouillée par $\text{m}^3 \text{ s}^{-1}$ sur l'ensemble du linéaire étudié à Pont d'Ain sur l'Ain. Tiré de Malavoi (2019).

3.3. Résumé des perspectives opérationnelles de la thèse

Le Tableau I.1 résume les perspectives opérationnelles que l'on peut tirer des résultats de la thèse. Cependant, il faut prendre des précautions quant à leurs mises en œuvre, des analyses supplémentaires devront être réalisées pour confirmer leurs pertinences. Les résultats de Judes et al. (A, B) proviennent de données récoltées in situ, les conditions d'échantillonnage ne sont pas nécessairement représentatives des modes de gestion des éclusées rencontrées sur les tronçons d'études ou de façon plus large à ce qui est rencontré en France ou en Europe. Par exemple, comme on a pu le voir précédemment les échantillonnages de Judes et al (B) sur la

rivière d'Ain se sont fait au cours ou juste après des lâchers d'eau pour le soutien d'étiage des centrales nucléaires du Rhône. Ainsi il y a eu des débits élevés ($\sim 100 \text{ m}^3 \text{ s}^{-1}$) pendant une période inhabituelle, ce qui a pu favoriser l'utilisation des microhabitats souvent asséchés par les organismes (poissons de la guildes « berge »). De même, les modes de gestion des éclusées sur les tronçons étudiés par Judes et al. (A, B) ne sont pas forcément représentatifs des conditions rencontrées de manière générale en France et encore moins en Europe ou dans le monde. Par exemple, dans l'étude de Judes et al. (A) le gradient de baisse de hauteur d'eau moyen était de $3,2 \text{ cm h}^{-1}$ (max = $10,6 \text{ cm h}^{-1}$) alors que Schmutz et al. (2015) en Autriche avait montré un effet négatif des éclusées sur les communautés de poissons à partir d'un gradient de baisse de hauteur d'eau de 15 cm h^{-1} et Hayes et al. (2021) à partir de $12\text{-}24 \text{ cm h}^{-1}$ sur les populations d'ombre (Autriche). Il est donc important de considérer ces mesures au regard du fonctionnement des écosystèmes et de la gestion des éclusées en place.

Tableau I.1. Résumé des perspectives opérationnelles qui découlent des résultats de la thèse.

Articles	Résultats	Perspectives opérationnelles	Études supplémentaires nécessaires
Judes et al. (A)	L'influence des éclusées semble moins importante pour les espèces de poissons typiques des petites rivières par rapport aux espèces de poissons typiques des rivières de taille moyenne.	Être particulièrement vigilant sur l'impact des éclusées dans les rivières de taille moyenne.	Réaliser plus d'études sur les cyprinidés et sur les rivières de taille moyenne
Judes et al. (B)	L'abondance des macroinvertébrés et des poissons de la guild "chenal" est plus faible dans les microhabitats qui s'assèchent. L'assèchement a des effets plus importants sur la sélection de l'habitat des poissons et des macroinvertébrés que les fortes vitesses de courant.	Augmenter le débit de base pour limiter les surfaces d'habitat soumis à des assèchements	Echantillonnage à des débits intermédiaires (entre 14 et 100 m ³ s ⁻¹) pour les macroinvertébrés pour tester d'autres patterns d'assèchement. Résultat qui demande à être confirmé pour les poissons de la guild "chenal" avec plus de données et en considérant la disponibilité en habitat.
Judes et al. (B)	Inclure les conditions hydrauliques extrêmes passées améliore les modèles de sélection du microhabitat des macroinvertébrés et des poissons.	Amélioration de l'estimation de l'habitat disponible si l'on considère l'hydraulique passée dans les futures modèles de sélection du microhabitat.	Validation biologique par la réplication de l'expérimentation Judes et al. (B).

Batz et al.
(Soumis)

Il est nécessaire d'utiliser des métriques qui rendent compte de la perturbation vécue par les organismes selon leurs mobilités. Par exemple, il faut considérer la dynamique spatiale des habitats pour rendre compte de la perturbation vécu par les poissons.

Mieux évaluer la perturbation vécue par les organismes aquatiques. Métriques quantitatives et transférables au sein et entre rivières.

La pertinence des métriques doit être vérifiée par des observations in situ (télémétrie) ou ex situ (caméra).

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Deuxième partie

Articles

1. JUDES ET AL. (A) :

Consistent but secondary influence of hydropeaking on stream fish assemblages in space and time.

Judes C, Gouraud V, Capra H, Maire A, Barillier A, Lamouroux N.

1.1 Abstract

Hydropeaking corresponds to rapid artificial discharge variations, designed to address sub-daily peaks in electricity demand. It generates rapid changes in physical habitat (e.g. flow velocity and water depth) with potential impacts on stream assemblages. For assessing the generality of hydropeaking effects on fish assemblages, we present an original combination of spatial (among 45 reaches, including six groups of nearby reaches) and temporal (over 3-17 years) analyses of these effects. Our analyses involved descriptions of natural and artificial hydraulic variations in reaches, obtained after translating hourly discharge data into hydraulics. We found that the influence of hydropeaking was secondary compared to well-known spatial variations in fish assemblage structure along longitudinal gradients, and negative influences of floods on annual densities. However, the spatial and temporal analyses consistently suggested that hydropeaking may disfavour fish species typical of medium-sized streams relative to species of headwater streams (*Salmo trutta*, *Phoxinus phoxinus*, *Cottus gobio*). The magnitude of hydropeaking effects observed here, as well as an apparent weaker effect of ramping rates than the frequency of hydropeaks, may be due to lower ramping rates in our data set than in other studies.

Keywords: hydropower, flow management, hydraulic habitat, fish community structure, high flow variations

1.2. Introduction

Hydropeaking corresponds to rapid artificial flow fluctuations downstream of hydropower plants, designed to address sub-daily peaks in electricity demand. Hydropeaking management concerns a large number of dams and river reaches (e.g, 144 of about 600 large dams in France and around 800 km of rivers in Austria; Lauters 1995; Metcher et al. 2017), a number expected to increase with the development of renewable energies (IPCC 2011). The flow regime (e.g, flow magnitude, timing and rate of change, frequency and duration of extreme flow events) is strongly modified downstream of hydropeaking power plants, with more rapid and frequent flow variations than occurring naturally. Because many characteristics of the flow regime influence the structure and functioning of river ecosystems (Schlosser 1991; Poff et al. 1997; Humphries et al. 1999; Magoulick and Kobza 2003), an improved understanding of the ecological effects of hydropeaking is needed. This is particularly true for fish assemblages, which can be affected by hydropeaking at several levels: increased drift of individuals during rapid flow velocity increases (Lechner et al. 2016), stranding due to rapid shoreline dewatering (Leclere et al. 2012; Hauer et al. 2014 Sauterleure et al. 2016), and repeated drying and scouring of spawning grounds (McMichael et al. 2005; Malcolm et al. 2012, Casas-Mulet et al. 2014, 2016).

An attractive method for estimating the ecological impacts of hydropeaking on aquatic communities is to perform “pressure-impact” spatial analyses among numerous river reaches (Gehrke and Harris 2001; Schmutz et al. 2015). Their principle is to build correlative models involving descriptors of hydropeaking intensity (e.g. frequency of events, ramping rates: rate of change in water level) and descriptors of fish responses (e.g. species richness or indices of biotic integrity). The work of Schmutz et al. (2015) is to our knowledge the most comprehensive study of this type, analysing the impacts of hydropeaking descriptors in 74 reaches of 16 rivers in Austria, with estimated down-ramping rates typically ranging between 5 and 40 cm h⁻¹. Using the national Austrian fish index, they found that the ecological status of natural-like streams was significantly degraded (the index lost two points on a scale of five) for the largest ramping rates observed. A difficulty with these “pressure-impact” approaches is to appreciate if the variables finally retained in the models, often after removal of several intercorrelated variables, are the actual drivers of observed responses. In other words, intercorrelation between environmental variables along natural and anthropogenic gradients may complicate the interpretation of such spatial analyses. Another difficulty with these large-scale approaches is

that they often lack proximate habitat variables, such as wetted-width ramping rates or rate of changes in flow velocity (Moreira et al. 2019), because these are rarely available across many reaches. Nevertheless, these approaches are extremely useful for identifying thresholds beyond which environmental pressures can become problematic (e.g. hydropeaking ramping rate above 15 cm h^{-1} ; Schmutz et al. 2015).

Interpreting spatial analyses of the ecological effects of hydropeaking among reaches can be facilitated when nearby reaches with contrasting hydropeaking pressures are included in the analyses. Such groups of reaches ideally have similar general characteristics (e.g. morphology, temperature, water quality) and differ only by their hydropeaking regime. These approaches have revealed that hydropeaking can reduce fish biomass and diversity (Liebig et al. 1999; Freeman et al. 2001; Smokorowski et al. 2010; Enders et al. 2017), with different responses among species. For example, Bain et al. (1988) compared two nearby rivers and showed that hydropeaking reduced the abundance of small fish species (and small size classes) living in shallow and slow-flowing habitats (see also Travnichek and Maceina 1994). Nevertheless, these comparisons generally involved one or a few reaches only, limiting the transferability of their results.

Temporal studies (either *in situ* or experimental) of the ecological effects of hydropeaking regime may also contribute to better identify thresholds in hydropeaking characteristics triggering a response of aquatic organisms or assemblages, while limiting problems associated with confounding environmental factors. For example, Saltveit et al. (2001) monitored juvenile fish in a river section during rapid down-ramping events (90 cm h^{-1}) and found that 60% became stranded. Consistently, in artificial channels, Bradford et al. (1995) reported that the proportions of stranded juveniles of rainbow-trout increased from 6% to 30% with down-ramping rates increasing from 5 cm h^{-1} to 60 cm h^{-1} . At the population level, reducing the frequency of hydropeaks may favour the reproduction of several salmonid species (Connor and Pflug 2004). Such experimental studies improve our mechanistic understanding of the ecological effects of the different hydropeak characteristics. However, as for comparisons of nearby reaches, temporal analyses deserve repeated field validations in multiple reaches. Difficulties for gathering hydraulic and fish data in many hydropeaking reaches over several years explain why few or no studies have carried out combined spatial and temporal analyses.

The originality of our study is to combine three approaches: (1) a spatial analysis of the effects of hydropeaking on fish assemblages between stream reaches, (2) a temporal analysis

of these effects within reaches, and (3) a comparison involving groups of nearby reaches subjected to different intensities of hydropeaking (Figure II.1.1.). Our objective was to test whether these different approaches reveal consistent effects of hydropeaking on fish assemblages. For this purpose, we used a unique dataset from 45 reaches of 26 rivers covering 3-17 years. The dataset included six groups of nearby reaches close to hydropower plants, hourly discharge data, hydraulic descriptions of reaches, and electrofishing surveys. We used fish species abundances as response variables to account for differential responses among species (Bain et al. 1988). We expected the spatial analysis to indicate how hydropeaking influences the classical longitudinal organisation of fish assemblages (Vannote et al. 1980). We expected the temporal analysis to better indicate the relative influence of hydropeaking on fish compared to the well-documented influence of high and low flows on fish recruitment (Bischoff and Wolter 2001; Thieme et al. 2001). We expected the comparison between nearby reaches to help disentangle the effect of hydropeaking on fish assemblages from those of other environmental drivers.

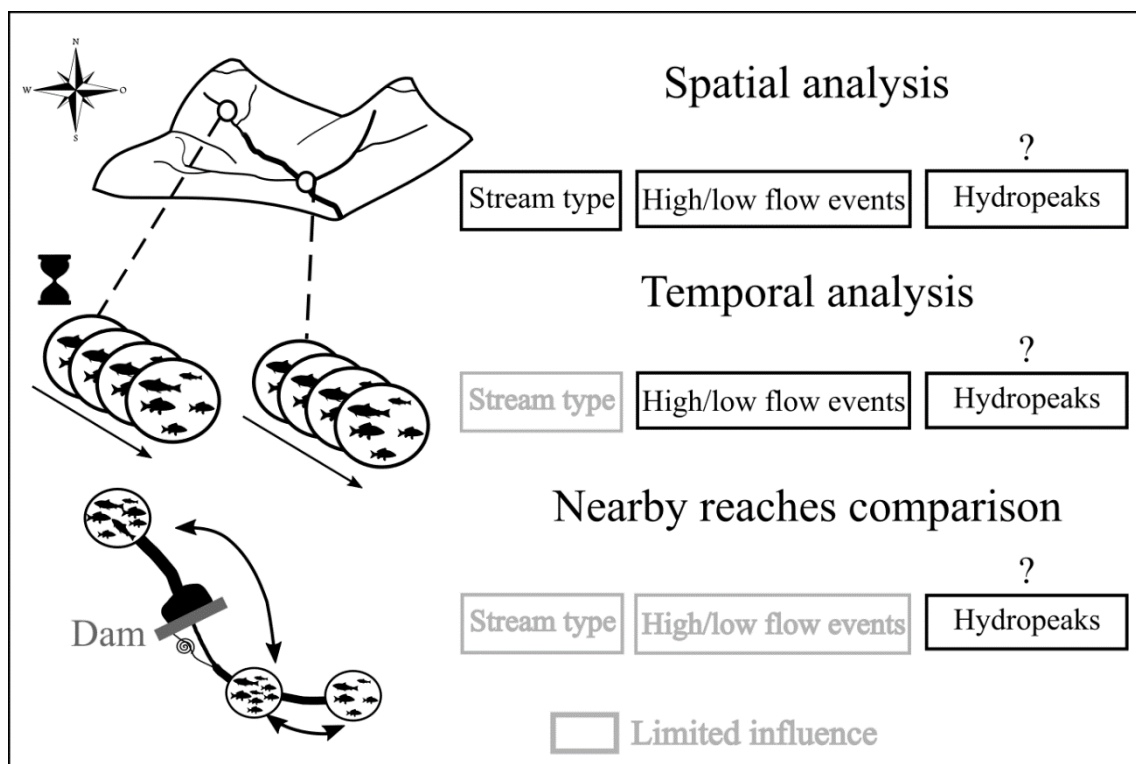


Figure II.1.1 Schematics of the three approaches used to study the relative influence of natural environmental drivers and hydropeaking events on fish assemblage structure. For each approach, factors assumed to have a major influence on the structure of fish assemblages are shown in black whereas others are in grey.

1.3. Materials and methods

Reach selection and characteristics

The dataset consisted of fish assemblage surveys ($n = 318$ reach x year combinations) conducted in 45 French stream reaches between 1990 and 2017, and corresponding hourly discharge time-series. Fish reaches were selected from two available databases ($n = 33$ from the national fish survey database www.naiades.eaufrance.fr; $n = 12$ surveyed by the national hydropower company “Electricité de France”, EDF). These reaches had inter-annual median daily discharges between 2.2 and 128 $\text{m}^3 \text{s}^{-1}$, slopes between 0.1 and 73.8 ‰ and widths at mean discharge between 7 and 89 m (Table I.2.3), according to the national extrapolation of environmental data available in Pella et al. (2012). Most selected reaches were situated downstream of hydropeaking power plants, except four reaches that were not influenced by hydropeaking. Two of them were situated upstream from hydropower plants, two others in bypassed sections not influenced by hydropeaking. These four reaches belonged to a subset of 15 reaches involved in the analysis of nearby reaches. These 15 reaches were themselves grouped to six groups of two or three nearby reaches, which were used for paired comparisons (Figure II.1.2).

Reach selection was strongly constrained by the availability of hourly discharge data measured close to the fish reaches (we imposed a distance < 25 km and the absence of major obstacle or tributary between the gauging and fish reach). We used the database of Pella et al. (2012), which includes estimates of reach mean annual flow over the French river network, to check the mean annual discharge of tributaries relative to the fish reach discharge; this relative discharge was on average 2%, with only 3/45 cases above 10% (kept in the analyses to avoid removing long fish time-series).

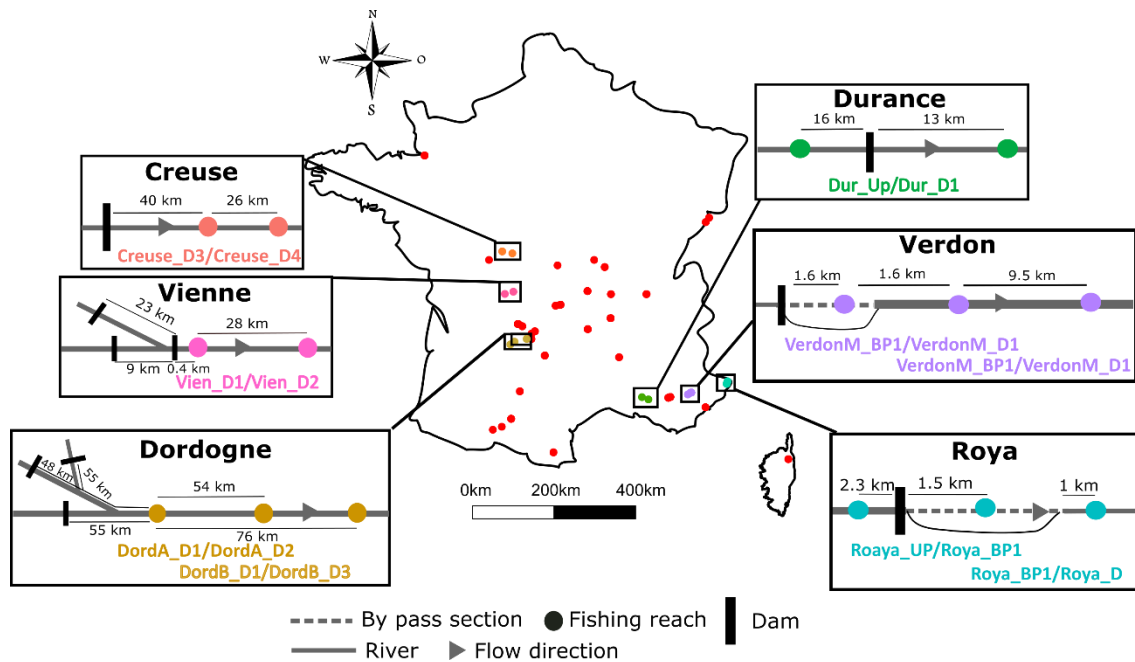


Figure II.1.2. Reach locations in continental France and schematics of nearby reaches (from six rivers) with different hydropeaking pressure. Reach codes are from Table II.1.3.

Fish data

Fish were sampled by electrofishing between 1990 and 2017 between July 1 and October 30 (average sampling date September 5; SD = 25 days), when young-of-the-year individuals are catchable and easily identifiable. Three sampling methods were used among surveys. For 10 reaches, generally small ones, the whole reach was most frequently prospected by wading (De Lury 2014). This method could involve several passages, but we retained only the first one for consistency among reaches. In 30 larger reaches, fish were mostly frequently sampled by wading or by boat using point abundance samples (Nelva et al. 1979), i.e. more than 75 electrofishing points (estimated sampling area of each point: 7 m²) distributed throughout the reach. For five reaches, fish were mostly frequently sampled in more than 30 larger habitat units of varying areas, distributed between geomorphic units (e.g, a riffle or a pool) in proportion of their availability within the reach (Vadas and Orth 1993; Lamouroux et al. 1999). The area of these habitat units depended on the size of distinct habitat elements (e.g, a group of boulders in the centre of the channel) and the inherent variability of areas sampled without enclosures (e.g, in the centre channel, the area sampled depended on current velocity).

When the sampling method changed at a reach over years, which occurred in seven reaches, we split the data as sampled in two different reaches to avoid bias in the temporal

analysis. Finally, fish individual length was reported for only 40% of the data, strongly reducing the statistical power of analyses of size class density variations. Therefore, analyses of size class variations are not reported here.

The sampled area was reported in all cases, allowing to estimate fish species densities per survey (number of individuals per 100 m²). These values were log(1+x)-transformed to approach normality in our analyses.

Environmental data

Defining seasons

We used two seasons for describing annual reach environmental conditions at the most important periods for fish life cycle. The “Spring” season lasted from 1th March to 31th May, encompassing most of the spawning period of the studied fish species (except brown trout). “Summer” was defined as the period from 1th June to 30th September (or to the sampling date if earlier), during which young-of-the-year fish are actively feeding.

Hourly discharge and temperature data

Hourly discharge data came from the national gauging network (n = 38 reaches, www.hydro.eaufrance.fr) or from EDF (n = 7). For the latter, discharge was generally estimated by adding a theoretical bypassed base flow, the turbinéd discharge and eventually an overflow discharge over the dam. These reconstitutions could create additional uncertainty on hourly discharge estimates. Air temperature data came from daily mean estimations based on the closest air temperature station (SAFRAN, Durand et al. 1993).

Translations of discharge data into hydraulic characteristics and habitat suitability

We translated hourly discharge data into more proximate habitat variables describing reach hydraulics (wetted width, water depth, flow velocity) and hydraulic habitat suitability (weighted usable areas) for fish guilds (groups of species with comparable habitat use).

Hydraulic translations were made using the hydraulic geometry of Morel et al. (2020). In brief, these models improve the classical hydraulic geometry relationships of Leopold and Maddock (1953). They are based on the analysis of hydraulic data collected at the scale of stream reaches in 1327 stream reaches of France and New Zealand. Their input variables

include climatic, hydrologic, topographic and land use descriptors, all available over the French hydrographic network (Pella et al. 2012). These models provide the best estimates of reach hydraulics at a given discharge rate in the absence of detailed field hydraulic measurements. Morel et al. (2020) used cross-validations to quantify how their models predicted hydraulic variations between reaches. For example, they showed that the models predicted 86% and 65% of the variance in observed width and depth among French reaches. However, these models were less accurate when predicting how the rate of change in width and depth with discharge varied among reaches. In detail, the models explained only 35% (width) and 13% (depth) of the exponent of hydraulic geometry for width and depth (Figure II.2.3. in Morel et al. 2020).

Hydraulic habitat translations were made for two fish guilds using the statistical hydraulic habitat models of Lamouroux and Souchon (2002). These statistical habitat models predict a “weighted usable area” in the reach, at a given discharge rate, as a function of the hydraulic geometry of the reach (described above) and an estimate of average particle size (from Snelder et al. 2011). The weighted usable area is the product of the reach wetted area and an habitat value for the guild that varies between 0 and 1, depending on the suitability of velocities and water depth in the reach for the fish guild. In other words, the weighted usable area increases with both habitat quantity (wetted area) and quality (habitat value). Here, we used weighted usable area for two fish guilds (Lamouroux and Souchon 2002), the “midstream” fish guild grouping species selecting deep and fast-flowing microhabitats, and the “bank” guild grouping species selecting shallow and slow-flowing microhabitats. The “bank” guild is expected to be more affected by hydropeaking than the “midstream” guild, because hydropeaking generates frequent dewatering and rapid flow velocity variations in shallow habitats.

Identifying significant flow events (increases and decreases)

To describe hourly changes in discharge, including both natural and artificial events, we classified each hourly flow variation as “increasing”, “decreasing”, or “stable”. Hours with variations below $0.1 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$ were classified as “stable”. We defined an increasing event (respectively decreasing event) as a concatenation of successive increases (decreases), potentially including periods of “stable” hours if shorter than two hours in total. We defined the peak flow as the highest discharge of the event, at the beginning of the event for decreases and at the end for increases. In the same way, base flow is the lowest discharge of the event. In all subsequent analyses, we considered only significant events having a discharge ratio (i.e. peak to base flow ratio) higher than 30%. We found this empirical threshold appropriate (visually)

for selecting major natural changes in flow (typically floods) as well as most hydropeaking events in all study reaches (Figure II.1.A1). With this threshold, the number of events also strongly differed between reaches subject or not to hydropeaking.

Seasonal environmental descriptions

For each sampling reach × year combination, we considered a set of environmental variables (Table II.1.1) potentially affecting annual fish densities and calculated for the spring and summer seasons preceding sampling. These variables describe air temperature (T), median hydraulic conditions (variable abbreviations starting by “Med” in Table II.1.1), high flow hydraulics (starting by “Hi”), low flow hydraulics and habitats (“Lo”), frequencies of flow events (“Fr”) and ramping rates (“Rr”). We also described temperature and discharge conditions during fish sampling (“S”). All environmental variables were normalized prior to analyses to give them equal weights.

Correcting ramping rates (attenuation between the discharge station and the fish reach)

The hydraulic ramping-rates attenuate with the distance from the water release (Nestler et al. 1989; Hauer et al. 2013; Sauterleute and Charmasson 2014). The attenuation is site-specific and complicated to characterize, depending for example on flow velocity, bed morphology and roughness. Here, we decided to correct ramping rates empirically (for 80% of the studied reaches), as a function of distance between the gauging station and the fish sampling reach (mean = 3.5 km, SD = 6.0 km, max = 24.8 km). For this purpose, we used seven pairs of gauging stations located in the same hydropeaking rivers, with no flow obstacles or tributaries between them (distance between 1 and 30 km, 1/7 pair being located in a river independent from our dataset). For each pair of stations, we identified the time lag (hours) on the discharge time-series between both stations by numerical optimization, and identified paired significant events. We calculated an average attenuation coefficient for each pair of stations, then regressed attenuation coefficients against distance among pairs (forcing the attenuation to be null at distance zero). An attenuation of 0.4% per km was found for up-ramping rates of flow velocity ($R^2=0.63$) and 0.5% per km for down-ramping rates of wetted width ($R^2=0.45$).

Table II.1.1. Description of the environmental variables considered.

Variable group	Abbreviation	Description	Unit
Topography	Sl	Mean reach slope	‰
Temperature	T	Air temperature	°C
Median hydraulic conditions	Med_D	Median water depth	m
	Med_V	Median hourly flow velocity	m s ⁻¹
	Med_W	Median hourly wetted surface	m
High flow velocity	Hi_V	Maximum hourly flow velocity	m s ⁻¹
	Hi_V_d	Average daily duration of hourly flow velocity >0.7 m s ⁻¹	hours day ⁻¹
Low flow velocity	Lo_V	Minimum flow velocity	m s ⁻¹
	Lo_V_d	Average daily duration of hourly flow-velocity <0.2 m s ⁻¹	hours day ⁻¹
Low flow weighted usable area	Lo_HabM	Weighted usable area for 100 m of river, for the ‘midstream’ guild, at low flow 5% quantile (discharge below which hourly discharge is for 5% of the time)	m ²
	Lo_HabB	Weighted usable area for 100 m of river, for the ‘bank’ guild, at low flow 5% quantile (discharge below which hourly discharge is for 5% of the time)	m ²
Occurrence of flow events	Fr_Dec	Average daily occurrence of decrease events	nb day ⁻¹
	Fr_FDec	Average daily occurrence of rapid decrease events with wetted-width down-ramping-rate >0.6 m h ⁻¹	nb day ⁻¹
	Fr_Inc	Average daily occurrence of increase events	nb day ⁻¹
	Fr_FInc	Average daily occurrence of rapid increase events with flow velocity up-ramping-rate >0.07 m s ⁻¹ h ⁻¹	nb day ⁻¹
Ramping rate	Rr_V	Quantile 90% of flow velocity up-ramping-rate	m s ⁻¹ h ⁻¹
	Rr_W	Quantile 90% of wetted width down-ramping-rate	m h ⁻¹
Fish sampling conditions	S_Q	Flow during fish sampling	m ³ s ⁻¹
	S_T	Air temperature during fish sampling	°C

Data analyses

Spatial and temporal analyses

To study the link between annual fish densities and seasonal environmental variables, we used Coinertia Analyses (CoA; Dolédec and Chessel 1994; Mérioux and Ponton 1999), which compute successive pairs of environmental and fish multivariate axes being as covariant as possible. A CoA is a simultaneous analysis of the fish and environmental datasets that is appropriate when the number of variables (biological and environmental) is relatively high compared to the number of surveys. Optimizing the covariance implies that the fish and environmental axes are correlated and simultaneously explain a high variance (i.e. they summarize variations in fish assemblages and environmental variables among reaches). Here, the environmental and fish datasets were analysed following a “principal component analysis” logic. The environmental variables were standardized, but not the biological variables that had similar units and were only log-transformed.

We performed two different CoAs of the environmental and fish datasets, a “between-reach” CoA and a “within-reach” CoA, to analyse separately spatial effects (between reaches) and temporal effects (within reaches). The between-reach CoA is our spatial analysis among reaches. It is computed on interannual averages of fish and environmental variables. The within-reach CoA is our temporal analysis of the annual variations within reaches. It is computed on differences between annual variables and their interannual average (by reach). In other words, it removes differences between reaches to analyse relative annual changes.

We paid a particular attention to the position of nearby reaches on the between-reach fish factorial map (spatial analysis) to appreciate how changes in hydropeaking pressure have influenced the spatial ordination of fish assemblages.

Relations between environmental variables and fish densities

We reported the correlation between reach coordinates on the two CoA axes (environmental and fish axes) to appreciate how environmental variables and fish densities were related. We also used another measure of the overall similarity using a multivariate extension of the Pearson correlation coefficient called the RV-coefficient (Robert and Escoufier 1976).

The RV-coefficient ($RV(X, Y) = \frac{COVV(X, Y)}{\sqrt{VAV(X)VAV(Y)}}$) is calculated as the total co-inertia (i.e. sum of

eigenvalues of a CoA) divided by the square root of the product of the squared total inertias (sum of the eigenvalues) from the separate analyses of each dataset. RV-coefficient ranges from 0 to 1, with a high RV-coefficient indicating a high degree of co-structure. Finally, a permutation test was conducted on the datasets to check the significance of the co-structure (RV test). All analyses were performed using the R software (R Development Core Team 2020) “*ade4*” package (Dray et al. 2007).

1.4. Results

The dataset concerned 207,386 fish individuals, and we considered the densities of 13 species (Table II.1.2, Figure II.1.A2) with relative survey-averaged density above 1% of the total survey-averaged density. Fish assemblages were typical of those found along longitudinal gradients in Europe (Figure II.1.3A), with 17/45 reaches with relatively high densities of *Salmo trutta* (>10%; hereafter, “trout” reaches) and the other, larger streams dominated by cyprinids (hereafter, “cyprinid” reaches).

Significant flow events were mostly hydropeaking events. For example, flow decreases per day in spring averaged 0.4 (min=0.01, max=1.95) in hydropeaking reaches vs. 0.02 (min=0.01, max=0.03) in others. The average wetted-width down-ramping rate across all reaches was $0.68 \pm 0.42 \text{ m h}^{-1}$ (mean \pm sd), the average water depth down-ramping-rate was $0.03 \pm 0.01 \text{ m h}^{-1}$ and the flow velocity up-ramping-rate was $0.09 \pm 0.04 \text{ m s}^{-1} \text{ h}^{-1}$ (see details in Table II.1.3). Therefore, environmental variables describing the occurrence of flow events and ramping rates (abbreviations starting by “Fr” and “Rr” in Table II.1.1) mostly described

hydropeaking intensity. By contrast, variables describing high flows, low flows and median conditions (“Hi”, “Lo” and “Med”) were strongly influenced by floods and droughts.

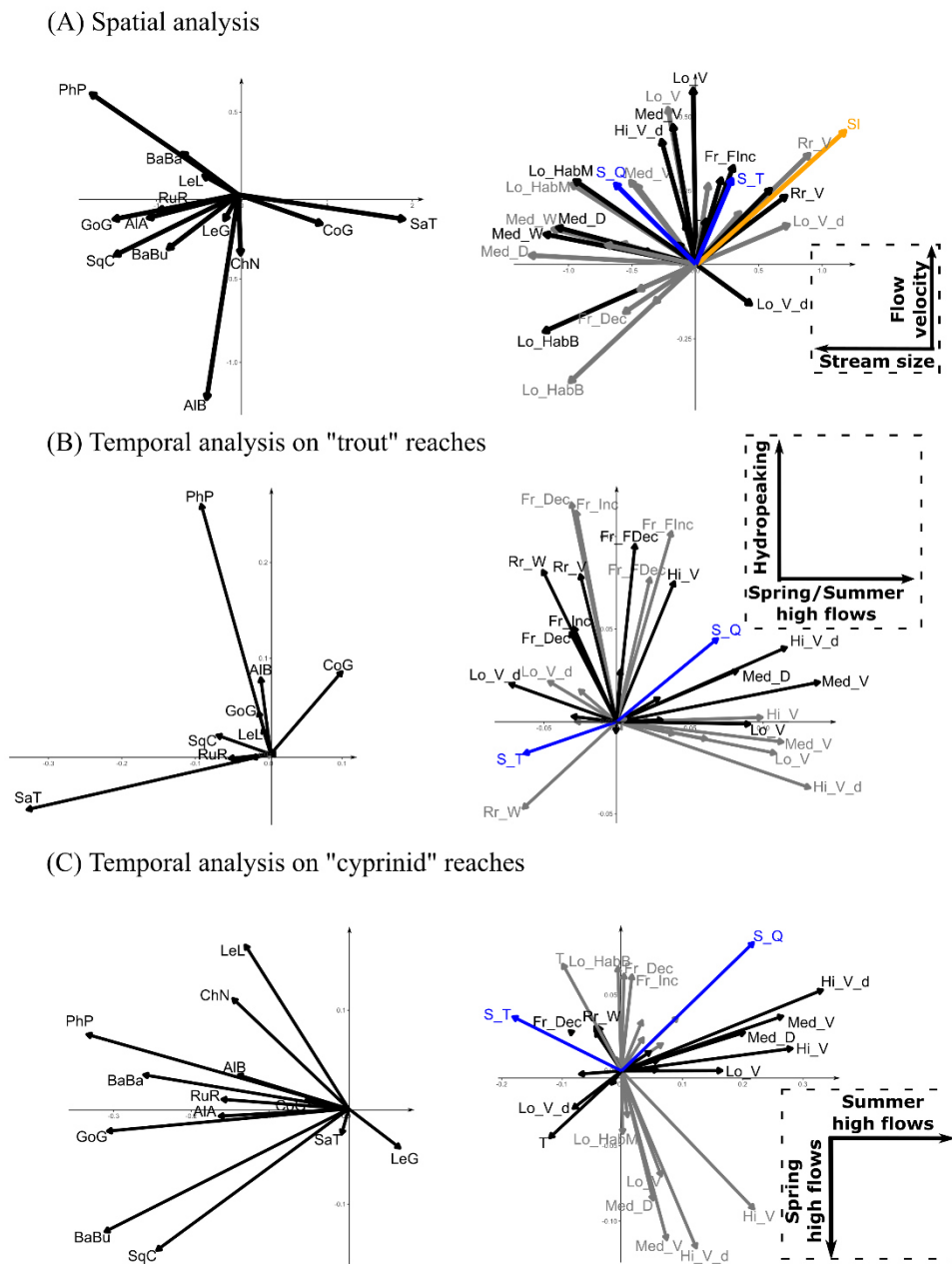


Figure II.1.3. Results of the CoA analyses on the fish and environmental datasets. (A): Between-reach spatial analysis (B): Within-reach temporal analysis on “trout reaches”. (C) Within-reach temporal analysis on “cyprinid reaches”. Left panels show the fish species scores on the first and second fish axes; right panels show the environmental variable scores on the first and second environmental axes. Environmental variables describing spring conditions are in grey; summer in black; sampling conditions in blue. Slope (in orange) is projected as supplementary variable. The dotted boxes on the right illustrate the interpretation of environmental axes. See Tables II.1.1 and II.1.2 for variable and species codes

Table II.1.2. List of the thirteen species studied.

Abbreviation	Scientific name	Common name
SaT	<i>Salmo trutta</i>	Brown trout
PhP	<i>Phoxinus phoxinus</i>	Minnow
CoG	<i>Cottus gobio</i>	Sculpin
LeL	<i>Leuciscus leuciscus</i>	Dace
BaBu	<i>Barbus barbus</i>	Barbel
ChN	<i>Chondrostoma nasus</i>	Nase
LeG	<i>Lepomis gibbosus</i>	Pumpkinseed
RuR	<i>Rutilus rutilus</i>	Roach
SqC	<i>Squalius cephalus</i>	Chub
GoG	<i>Gobio gobio</i>	Gudgeon
AlB	<i>Alburnoides bipunctatus</i>	Stream bleak
BaBa	<i>Barbatula barbatula</i>	Stone loach

Spatial analysis and positions of nearby reaches

The first and second axes of the between-reach CoA (Figure II.1.3A) explained 81% and 11% of the total inertia, respectively (see Table II.1.4 for the proportion of variance of the initial datasets taken into account by each CoA axes). Pearson correlation between the two datasets was 0.64 for the first axis and 0.49 for the second axis, and the two datasets were significantly related ($RV=0.26$, $P = 0.005$). The first axes of the fish and environmental factorial maps suggested that larger streams (i.e. high median depth and width, high weighted usable area, low slope) had lower densities of *Salmo trutta* and *Cottus gobio* and higher densities of other species such as *Squalius cephalus*, *Rutilus rutilus*, *Gobio gobio* and *Barbus barbus*. The second axis indicated that faster-flowing reaches had higher densities of *Phoxinus phoxinus* and *Barbatula barbatula* and lower densities of *Alburnoides bipunctatus*.

Accordingly, positions of reaches on the fish factorial map (Figure II.1.4A) indicated a traditional longitudinal gradient, with smaller “trout” reaches on the right and larger “cyprinids” reaches on the left. Positions of pairs of nearby reaches on the map (black arrows on Figure II.1.4A) suggested effects of hydropeaking intensity for cyprinid reaches more than for trout reaches. In particular, for four pairs of reaches on the left of the map, the reach with higher hydropeaking pressure was consistently situated towards the top or top-right of the map relative to its less impacted corresponding reach. This globally indicated, for paired reaches, higher relative abundance of *Phoxinus phoxinus* and/or *Salmon trutta* in the reaches with highest hydropeaking intensity. Figure II.1.4B highlights these differences for two species: higher

densities of *Phoxinus phoxinus* were observed in reaches with higher hydropeaking intensity whereas higher densities of *Squalius cephalus* were found in reaches with lower hydropeaking intensity.

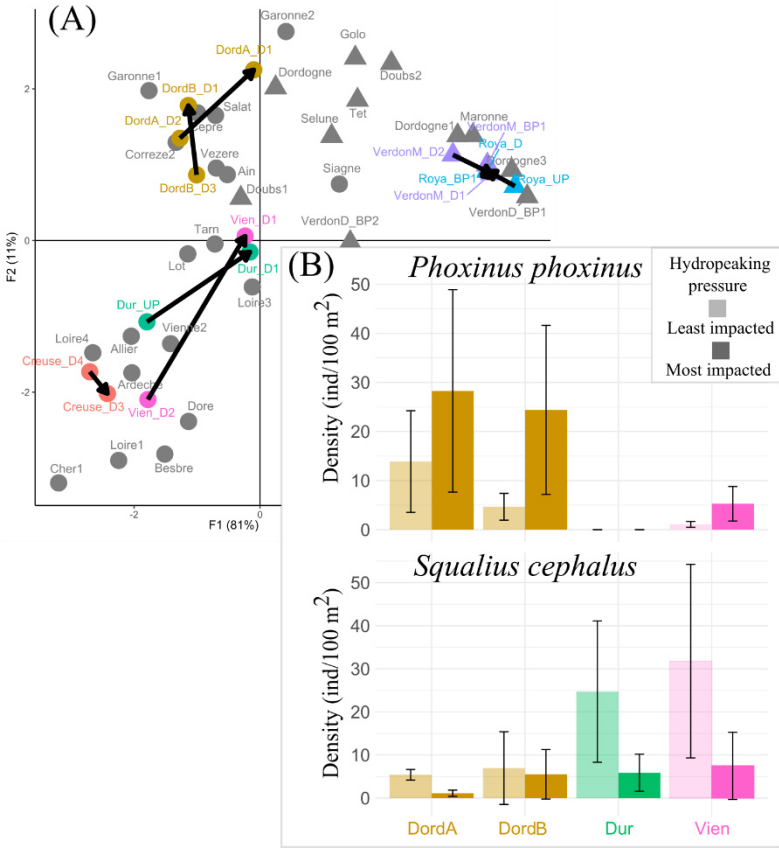


Figure II.1.4. Comparison of fish assemblages between nearby reaches. (A): Reach scores on the first and second axes of the fish dataset for the between-reach spatial analysis. Triangles correspond to “trout reaches” and circles to “cyprinid reaches”. Black arrows indicate the position of pairs of nearby reaches (same colour), with arrows going from the reach least influenced by hydropeaking to the most influenced. (B): Density of minnow *Php* and chub *Lec* in the four pairs of nearby reaches. Reach colour codes are from Figure II.1.2. Reach codes are from Table II.1.3.

Table II.1.3. Reach characteristics (see Table II.1.1 for variable codes). Reaches considered for the nearby reaches analysis are linked using brackets. Note that the two reaches indicated by a * correspond to a unique reach but with different dates.

Reach code	Geographical coordinates (X; Y) in Lambert 93	Median discharge Q50 $m^3 s^{-1}$	Slope ‰	Mean air temperature Spring; Summer °C	Rr_Vgrad $m s^{-1} h^{-1}$ Mean±sd	Fr_Dec Mean±sd	Fr_Inc Mean±sd
Ain	871774.242; 6526504.737	70.5	2.0	13.2; 21.0	0.05 ± 0.01	0.43 ± 0.12	0.37 ± 0.12
Allier	738589.163; 6446380.559	15.3	2.1	10.8; 17.9	0.06 ± 0.02	0.75 ± 0.32	0.70 ± 0.35
Ardeche	811952.726; 6384583.096	9.8	0.1	14.1; 22.2	0.09 ± 0.01	0.70 ± 0.25	0.77 ± 0.34
Besbre	752029.166; 6600455.770	4.1	1.1	12.6; 17.1	0.03 ± 0.01	0.20 ± 0.08	0.11 ± 0.05
Cepre	608335.903; 6424801.115	17.7	1.2	14.1; 18.6	0.08 ± 0.04	0.55 ± 0.40	0.55 ± 0.41
Cher1	669551.775; 6588271.080	7.0	0.4	13.1; 19.1	0.08 ± 0.03	0.69 ± 0.26	0.45 ± 0.16
Correze2	587688.181; 6453638.630	13.8	2.3	14.1; 19.2	0.06 ± 0.02	0.26 ± 0.11	0.15 ± 0.05
Creuse_D3	566106.558; 6615406.208	22.0	1.8	13.3; 19.6	0.04 ± 0.01	0.37 ± 0.08	0.32 ± 0.10
Creuse_D4	545127.844; 6622154.201	22.5	0.4	13.0; 19.5	0.03 ± 0.01	0.32 ± 0.09	0.25 ± 0.11
DordA_D1	600865.545; 6424853.320	96.1	0.8	13.8; 19.8	0.04 ± 0.01	0.08 ± 0.10	0.10 ± 0.08
DordA_D2*	570227.164; 6419870.682	115.6	4.1	13.9; 14.7	0.03 ± 0.01	0.08 ± 0.11	0.11 ± 0.11
DordB_D1*	570227.164; 6419870.682	96.1	0.8	13.9; 20.5	0.05 ± 0.02	0.38 ± 0.27	0.37 ± 0.25
DordB_D3	558010.860; 6413463.240	128.0	2.1	14.2; 20.6	0.04 ± 0.01	0.26 ± 0.18	0.23 ± 0.15
Dordogne	608936.299; 6436765.767	82.7	0.9	12.7; 18.3	0.05 ± 0.02	0.24 ± 0.25	0.25 ± 0.24
Dordogne1	664807.474; 6498563.755	3.2	8.2	10.8; 16.1	0.17 ± 0.1	0.62 ± 0.89	0.59 ± 0.87
Dordogne3	675890.967; 6500545.354	2.8	12.3	8.4; 15.8	0.26 ± 0.1	0.21 ± 0.12	0.24 ± 0.17
Dore	737411.593; 6531059.903	13.4	0.9	12.2; 18.5	0.03 ± 0.01	0.33 ± 0.23	0.29 ± 0.21
Doubs1	1005479.587; 6702034.457	32.5	1.3	9.9; 15.5	0.04 ± 0.01	0.44 ± 0.08	0.41 ± 0.08
Doubs2	998685.499; 6692083.909	25.9	2.8	8.7; 14.5	0.07 ± 0.01	0.63 ± 0.08	0.59 ± 0.10
Dur_D1	867476.940; 6299688.683	122.6	2.9	15.5; 24.5	0.12 ± 0.02	0.37 ± 0.12	0.34 ± 0.09
Dur_UP	889882.098; 6293508.414	122.6	2.3	14.7; 24.0	0.12 ± 0.13	0.03 ± 0.03	0.03 ± 0.02
Garonne1	557491.117; 6248020.216	91.8	3.0	13.6; 21.3	0.11 ± 0.03	0.57 ± 0.22	0.54 ± 0.16
Garonne2	513155.364; 6224770.194	47.6	3.5	12.3; 19.6	0.08 ± 0.02	0.51 ± 0.23	0.51 ± 0.22
Golo	1223972.662; 6177578.191	11.2	57.3	13.7; 21.4	0.09 ± 0.01	0.75 ± 0.39	0.71 ± 0.40
Loire1	790882.892; 6471148.745	24.8	3.2	11.0; 17.8	0.05 ± 0.01	0.57 ± 0.27	0.55 ± 0.29
Loire3	790895.984; 6524644.455	33.5	0.5	12.5; 18.3	0.11 ± 0.05	0.74 ± 0.12	0.79 ± 0.14
Loire4	775925.352; 6584819.553	48.1	2.1	12.1; 17.7	0.03 ± 0.02	0.38 ± 0.15	0.31 ± 0.11
Lot	638852.847; 6387661.801	68.0	4.9	12.8; 19.4	0.13 ± 0.03	0.99 ± 0.22	0.95 ± 0.21

Maronne	616560.143; 6441947.071	9.3	2.9	12.9; 18.7	0.09 ± 0.05	0.33 ± 0.37	0.33 ± 0.37
Roya_BP1	1066121.216; 6335287.829	6.4	36.2	11.1; 19.1	0.24 ± 0.13	0.28 ± 0.29	0.28 ± 0.28
Roya_D	1064803.026; 6332576.200	6.6	27.7	11.5; 20.2	0.14 ± 0.04	1.05 ± 0.32	0.94 ± 0.35
Roya_UP	1067468.239; 6340374.076	2.2	73.8	10.4; 19.0	0.08 ± 0.03	0.02 ± 0.02	0.03 ± 0.02
Salat	534701.500; 6230865.410	30.3	2.4	12.2; 18.2	0.06 ± 0.02	0.30 ± 0.12	0.32 ± 0.13
Selune	383599.079; 6841493.378	8.2	3.0	11.6; 17.1	0.06 ± 0.02	0.18 ± 0.08	0.16 ± 0.08
Siagne	1018695.535; 6280195.484	2.8	0.4	16.8; 23.0	0.39 ± 0.07	1.03 ± 0.38	1.14 ± 0.48
Tarn	579398.131; 6308816.030	83.6	1.3	14.9; 20.6	0.04 ± 0.01	0.51 ± 0.15	0.44 ± 0.13
Tet	657601.117; 6171763.877	7.1	10.3	14.0; 21.9	0.08 ± 0.02	0.22 ± 0.17	0.18 ± 0.09
VerdonD_BP1	934680.457; 6299317.267	16.9	1.0	14.0; 23.4	0.1 ± 0.17	0.01 ± 0.01	0.01 ± 0.01
VerdonD_BP2	929722.209; 6297495.920	17.3	5.7	14.5; 23.9	0.11 ± 0.19	0.01 ± 0.01	0.01 ± 0.01
VerdonM_BP1	983527.417; 6311283.309	9.5	8.1	10.2; 19.8	0.11 ± 0.25	0.01 ± 0.03	0.01 ± 0.03
VerdonM_D1	981513.856; 6310766.070	9.6	4.7	10.7; 19.4	0.14 ± 0.02	0.22 ± 0.06	0.24 ± 0.05
VerdonM_D2	976499.250; 6307373.744	9.9	6.2	11.2; 19.8	0.15 ± 0.02	0.22 ± 0.06	0.24 ± 0.05
Vezere	578479.213; 6458829.865	17.1	0.3	14.2; 18.9	0.07 ± 0.02	0.46 ± 0.16	0.42 ± 0.15
Vien_D1	570177.247; 6530340.952	35.2	1.9	12.3; 18.1	0.09 ± 0.03	0.48 ± 0.14	0.45 ± 0.10
Vien_D2	552401.5587; 6528649.95	46.5	1.6	12.3; 18.0	0.05 ± 0.01	0.29 ± 0.07	0.26 ± 0.07
Vienne2	518554.183; 6603719.964	63.3	2.3	12.8; 19.0	0.04 ± 0.01	0.26 ± 0.09	0.25 ± 0.08

Temporal analysis

We decided to apply the within-reach CoA separately on “trout” reaches (Figure II.1.3B) and on “cyprinid” reaches (Figure II.1.3C), because pooling these reaches made the axes hardly interpretable due to the different species involved.

The first and second CoA axes for “trout” reaches explained 44% and 27% of the total inertia, respectively (Table II.1.4). Pearson correlation between the two datasets was 0.54 for the first axis and 0.33 for the second axis and the two datasets were significantly related (RV=0.05, P = 0.04). The first axis of the fish and environmental factorial maps suggested that the major temporal effect was a decrease in density of *Salmo trutta* with high-flow events during spring and/or summer. The second axis, for which the correlation was low, suggested that the densities of *Phoxinus phoxinus* and secondarily *Cottus Gobio* were positively related to hydropeaking occurrence.

The first and second CoA axes for “cyprinid” reaches (Figure II.1.3C) explained 71% and 11% of the total inertia, respectively (see Table II.1.4 for details). Pearson correlation between the two datasets was 0.48 for the first axis and 0.44 for the second axis. The relationship between fish densities and the environment was significant (RV=0.14, P = 0.002). The first axis of the fish and environmental factorial maps suggested that the major temporal effect was a general decrease in the densities of most fish species with high-flow events during summer. The second axis suggested that spring high flows could increase the densities of *Leuciscus leuciscus* and *Chondrostoma nasus* relatively to the density of *Squalius cephalus*. Summer hydropeaks tended to have the opposite effect.

On both within-reach CoA analyses, high discharge and very cold temperature on sampling date tended to reduce observed densities of most species.

Table II.1.4. Summary statistics of the CoAs: RV coefficients; P-values of permutation tests; proportion of variance of each initial datasets taken into account by the two first axes; and Pearson correlation coefficients between the fish and environmental axes.

Analysis	Reaches involved	RV coeff.	P-value	Environment: variance explained	Fish density: variance explained	Pearson correlation $F1_{env} \times F1_{fish}$; $F2_{env} \times F2_{fish}$
Between-reach CoA (Spatial)	All	0.26	0.005	F1: 30% F2: 15%	F1: 47% F2: 16%	F1: 0.64 F2: 0.49
Within-reach CoA (Temporal)	“Trout” reaches	0.05	0.01	F1: 27% F2: 22%	F1: 42% F2: 20%	F1: 0.54 F2: 0.33
	“Cyprinid” reaches	0.14	0.002	F1: 29% F2: 18%	F1: 34% F2: 22%	F1: 0.48 F2: 0.44

1.5. Discussion

Secondary influence of hydropeaking compared to stream size and high-flow events

The spatial analysis (between-reach CoA) showed that the influence of hydropeaking on fish assemblage was secondary relative to the influence of stream size. In this analysis, the fish factorial map separated *Salmo trutta* and *Cottus gobio* preferably found in steep headwaters, *Phoxinus phoxinus* and *Barbatula barbatula* in intermediate-sized streams, and all other species in larger streams. Such an organization of fish assemblages along the upstream-downstream gradient has been largely described (e.g. Huet 1949, Vannote et al. 1980). However, we observed two exceptions to this upstream-downstream gradient on the second axis: the position of *Phoxinus phoxinus* and *Barbatula barbatula* (with high densities in faster-flowing reaches) opposed to *Alburnoides bipunctatus*. The computation of the second axis was certainly influenced by the spatial distribution of the studied reaches, some being within and others outside the heterogeneous geographic distribution of *Alburnoides bipunctatus*.

The temporal analysis (within-reach CoA) showed that the influence of hydropeaking on fish densities was secondary relative to the effects of high flows. In line with previous studies, we found that high-flow events in spring or summer reduced the densities of most species (Bischoff and Wolter 2001, Thieme et al. 2001, Cattaneo 2005, Bret et al. 2015). For

“cyprinid” reaches, the second axis of the environmental factorial map discriminated the effects of spring and summer high-flow events. Spring high-flows logically affected earlier spawners (i.e. March/April), such as *Leuciscus leuciscus* and *Chondrostoma nasus*, while summer high-flows affected species that spawn later (i.e. May/June), such as *Gobio gobio* and *Phoxinus phoxinus* (Lelek and Penaz 1963, Mills 1981, Lascaux et al. 2013).

Since most studies have shown that hydropeaking was linked to adverse consequences for fish (e.g. stranding, drifting and spawning ground scouring, Halleraker et al. 2003, Connor and Pflug 2004, Auer et al. 2017), frequent hydropeaks and high ramping rates were expected to be negatively related to the density of most species. However, our temporal and spatial analysis brought different findings. We propose three potential explanations for the secondary influence of hydropeaking observed here. First, within-reach, the variability of hydropeaking intensity between years was low, limiting our ability to show relationships between fish densities and hydropeaking descriptors. For example, the annual within-reach standard deviation for up-ramping rates of flow velocity was 44% of the interannual average. Second, the hydropeaking intensity in the reaches studied here is relatively low. For example, we found an average water-depth down-ramping-rate of 3.2 cm h⁻¹ for hydropeaking reaches (max = 10.6 cm h⁻¹) whereas Schmutz et al. (2015) showed an adverse effect of hydropeaking on fish assemblages for water level down-ramping rates above 15 cm h⁻¹. Halleraker et al. (2003) observed almost no stranding of juvenile salmon for water-depth down-ramping-rates below 18.6 cm h⁻¹. Although we cannot directly compare these values (our ramping rates are based on average depths, others on water levels), the down-ramping rates in our reaches were clearly lower. Third, since most French hydropower plants were built more than fifty years ago, the fish species that are currently present could have adapted to these highly variable environments. For example, studies have shown that many fish individuals move in response to temporal variations in habitat suitability (Pert and Erman 1994, Shirvell 1994, Bond and Jones 2015) and can adapt their behaviour against hydropeaking risks by using the less constraining habitats (Capra et al. 2017).

Focusing on young-of-the-year individuals could have revealed a stronger influence of hydropeaking compared to our analyses made without differentiating life stages. Indeed, young-of-the-year individuals have lower swimming capacity than adults and mostly use near-bank habitats (Moore and Stanley 1988), making them highly susceptible to drifting and stranding (Saltveit et al. 2001, Halleraker et al. 2003, Lechner et al. 2016). However, density-dependence

may offset the effects of hydropeaking in some populations (Ratikainen et al. 2008, Puffer et al. 2019). For example, using a population dynamic model for Atlantic salmon (*Salmo salar*) in a hydropeaking river in Norway, Sauterleute et al. (2016) showed that the stranding mortality of young-of-the-year individuals had weak effects on population dynamics.

Hydropeaking favours headwater species at the expense of medium-sized stream species, consistently in space and time

The comparison of nearby reaches showed that, for cyprinid reaches, stronger hydropeaking intensity was associated to higher densities of fish species typical of headwater streams (*Phoxinus phoxinus*, *Salmo trutta* and *Cottus gobio*) and lower densities of species typical of medium-sized streams (*Rutilus rutilus*, *Barbus barbus*, *Squalius cephalus*, *Chondrostoma nasus*). In contrast, for trout reaches, no clear trend was observed, indicating that headwater fish species were less influenced by hydropeaking than others. This result is consistent with the temporal analysis on trout reaches, where years with higher hydropeaking intensity had higher densities of fish species typical of headwater streams. Several previous studies have also shown that fish species typical of headwater streams may better withstand hydropeaking (Garcia De Jalon et al. 1988, Casado et al. 1989, Garcia De Jalon et al. 1994). Garcia De Jalon et al. (1994) found that, after the construction of a hydropeaking power plant on the Tera River (Spain), populations of almost all cyprinid species declined while the trout population persisted. However, on the Rio Duraton (Spain), Camargo and Garcia de Jalon (1990) found the opposite effect: cyprinid populations persisted or even increased whereas trout disappeared. These differences are difficult to interpret and likely depend on dam management, dam location along the river and/or the particular morphological characteristics of each hydropeaking reach.

Another way to study the influence of hydropeaking is to focus on the individual scale, for example by comparing the growth of individuals under different hydropeaking intensity. Such approaches suggest that Atlantic salmon (Puffer et al. 2017) may thrive in hydropeaking reaches, in contrast to the cyprinid humpback chub (*Gila cypha*) in medium-sized streams (Finch et al. 2015). A possible reason for the greater hydropeaking tolerance of headwater stream species may be their behavioural adaptation to naturally highly variable environments (Horwitz 1978). They may have developed ecological strategies to cope with frequent and rapid flow variations (Schlosser 1982, Oberdorff et al. 2001, Lytle and Poff 2004). For example,

rainbow trout (*Oncorhynchus mykiss*) can detect the rising limb of a flood, allowing a rapid search of hydraulic shelter (Gore et al. 1994). The freshwater sculpin (*Cottus gobio*) lives in coarse substrate interstices, limiting the risk of drifting during high flows (Keith et al. 2011). Minnow (*Phoxinus phoxinus*) spawns several times a year (Wootton and Mills 1979), reducing the mortality risk of a whole young-of-the-year cohort after a single intense hydropeaking event. Furthermore, due to the greater availability of rocks, tree roots and woody debris, headwater streams have a greater diversity of habitats and shelter than larger streams (Jackson and Sturm 2002, Benda et al. 2005, Gooderham et al. 2007).

Perspectives

We identified several biases that could have blurred the relationships between hydropeaking descriptors and fish densities. First, variations in electrofishing efficiency between surveys, related to environmental conditions during sampling, probably introduced noise in observed fish densities (Cauvy-Fraunié et al. 2020). Consistently, we found that higher air temperature or lower discharge rates during fish sampling resulted in higher densities. Second, variations in fish sampling methods between reaches could have influenced our spatial analysis. We checked that this influence was limited (results not shown) by repeating our analysis after introducing method-specific correction coefficients (up to a factor 5) on observed densities. This indicated that our spatial analysis was essentially driven by differences in species relative densities and little sensitive to the fish sampling method. Third, environmental descriptions could be improved. In particular, air temperature alone did not allow to evaluate the potential influence of water temperature variations induced by hydropeaking (known as thermopeaking, Zolezzi et al. 2011). In addition, although they are relatively accurate for describing hydraulic differences between reaches, the general hydraulic translations of Morel et al. (2020) cannot reflect the presence of shelter or particular substrate configurations. More importantly, hydraulic geometry models are uncertain for describing the rate of change in width and depth with discharge. Field measurements would have been desirable for improving our hydraulic descriptions. However, using more accurate descriptions would unlikely affect our conclusions, because we described many aspects of the frequency and ramping rates of hydropeaks, all of which had a secondary influence on density annual variations. Finally, all environmental characteristics of reaches (hydraulic geometry, substrate composition, shelter availability) could have changed over the study period.

In spite of the large dataset used here, increasing the range of hydropeaking intensity studied would help to identify thresholds over which significant adverse impacts are observed on fish assemblages. In particular, it is possible that higher hydropeaking intensity negatively affects headwater species (*Phoxinus phoxinus* and *Cottus Gobio*). Since each country has its own rules for managing hydropeaking, international comparisons will help to extend the range of hydropeaking intensity considered. The number of reaches considered could also be increased by using environmental DNA techniques that allow rapid, semi-quantitative assessments of fish community structure in a non-invasive way (Lodge et al. 2012; Taberlet et al. 2012; Pont et al. 2018).

In the future, there is a need to improve our understanding of the interactions between hydropeaking and other stresses for aquatic biota (e.g. changes in water temperature or quality; Zolezzi et al. 2011; Bruno et al. 2013; Vanzo et al. 2016) to determine whether their effects are additive, synergistic or antagonistic. This could be achieved with analyses similar to ours, but including complementary environmental descriptors (e.g. turbidity, water temperature) and more reaches with unique or multiple pressures (e.g. Acreman et al. 2014; Bondar-Kunze et al. 2016). Finally, understanding taxa behavioural response to hydropeaking could help identifying improved management measures (Metcher et al. 2017). For example, the development of models of habitat selection adapted to highly variable environments, taking into account the history of habitat conditions, could help to predict the amount of suitable habitat for different taxa under different management scenarios.

1.6. Conclusion

We found that the influence of hydropeaking was secondary compared to the well-known organization of fish assemblages along the longitudinal gradient of rivers, or the frequently observed negative influence of floods on recruitment. Our temporal analyses suggest that, within the range of hydropeaking intensity considered, small changes in hydropeaking management should have limited effects on fish assemblage structure. However, further analyses covering a wider range of hydropeaking intensity are needed to assess possible threshold effects. Consistently in space and time, we found that hydropeaking affected fish species typical of medium-sized streams more intensively than those of headwater streams. Although this result remains to be confirmed with a larger dataset, it suggests that flow should be managed cautiously in medium-sized streams. Because past studies focused more on

salmonid species (Moreira et al. 2019), more attention is deserved on assemblages of larger streams.

1.7. Acknowledgements

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1.9. Appendix

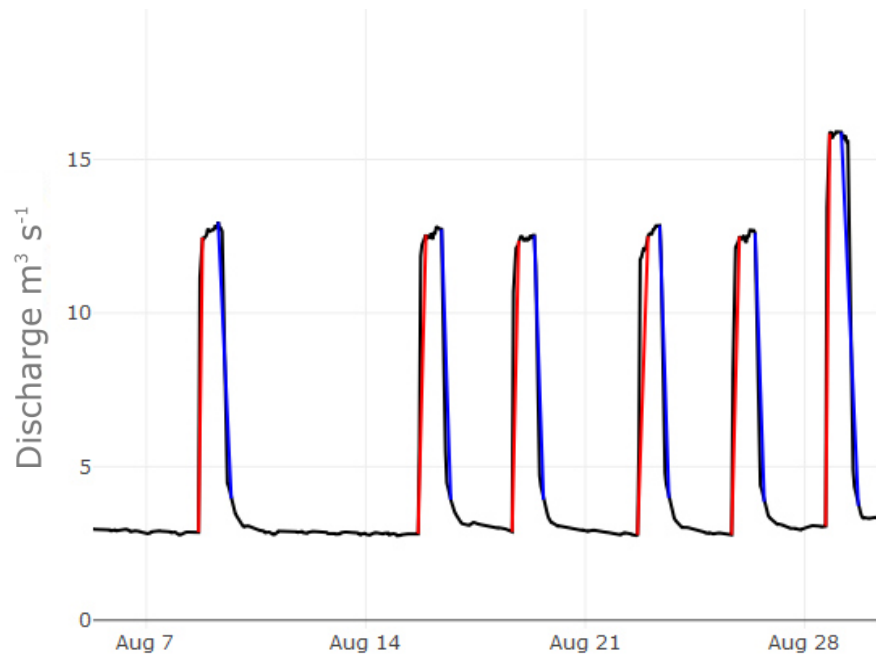


Figure II.1.A1. Example of a discharge time-series from the reach “Verdon_D1” and of identified increasing (in red) and decreasing events (in blue).

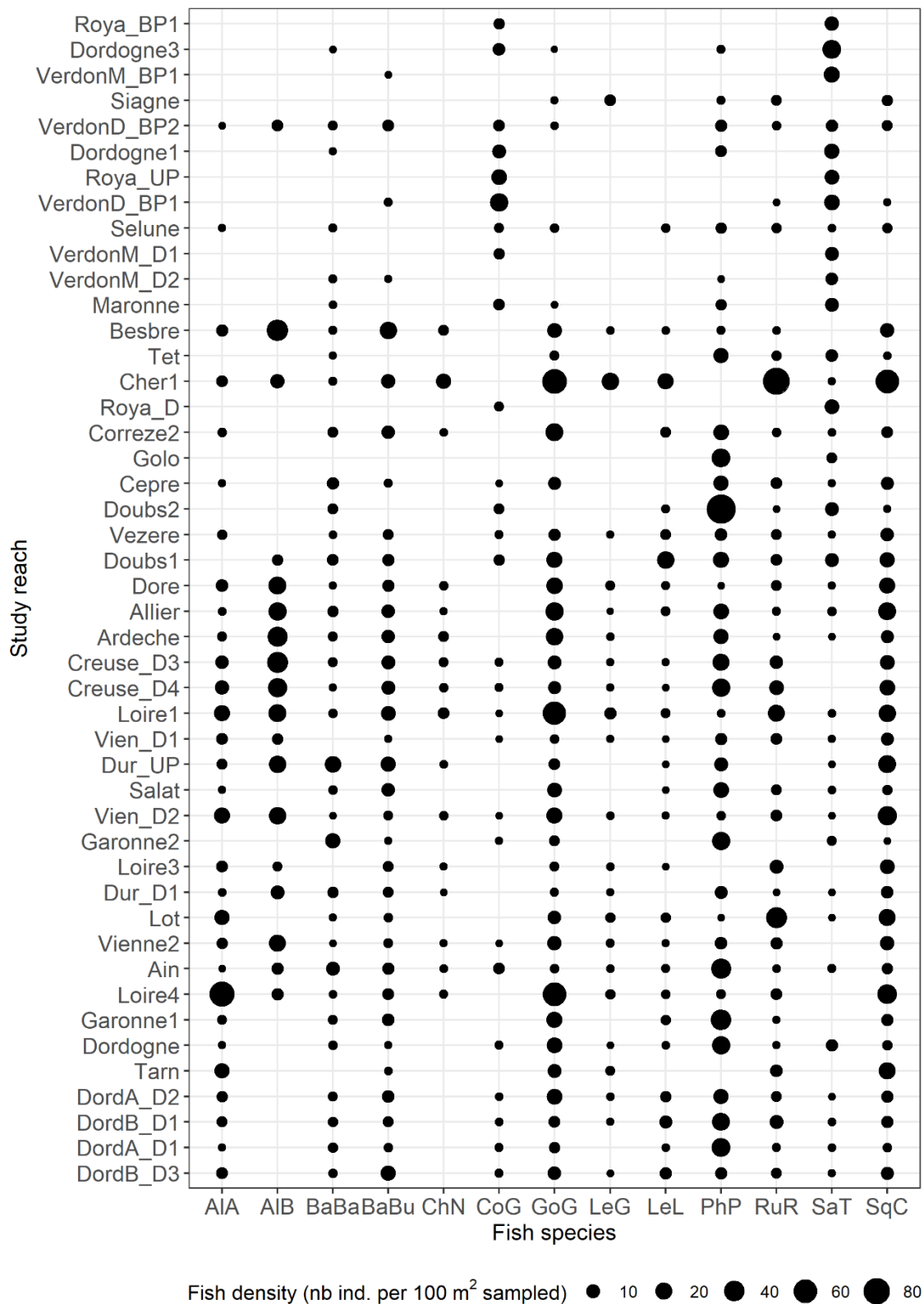


Figure II.1.A2. Interannual average of fish species density (number of individuals per 100 m² sampled) in each reach. Fish species and reaches are ordered according to their position on the first axis (F1) of the between-reach CoA performed on the fish dataset. See Tables II.1.1 and II.1.3 for species and reach codes.

2. JUDES ET AL. (B) :

Past hydraulics influence microhabitat selection by macroinvertebrates and fish in hydropeaking rivers.

Judes C, Capra H, Gouraud V, Pella H, Lamouroux, N.

2.1. Abstract

Hydropeaking hydropower plants are the major source of renewable energy meeting sub-daily peaks in electricity demand. They induce rapid artificial flow variations, highly variable velocities, drift and stranding risks for aquatic organisms. An improved mechanistic understanding of microhabitat selection by organisms is needed to better understand the effects of hydropeaking on communities. In hydropeaking reaches, microhabitat selection likely depends on both present and past hydraulics (flow velocity and water depth); this study aims to assess their relative impact. For this purpose, we used observations of fish abundance in 1,180 microhabitats (507 sampled by electrofishing, 673 by snorkeling) and of macroinvertebrate abundance in 36 microhabitats (both hyporheic and benthic) in a medium-sized river. We described past hydraulics of microhabitats over the 15 days preceding sampling, using a 2D hydrodynamic model, by identifying microhabitats dewatering (drying during $> 10\text{h}$) or with high-velocity conditions ($> 1.3 \text{ m s}^{-1}$ during $> 10\text{h}$). Macroinvertebrates habitat guilds responded significantly to past hydraulics, with abundances 3.5-15.3 times lower in dewatering habitats. Consequently, their preference for present hydraulics was different from that observed in rivers without hydropeaking. For more mobile fish, responses were weaker and different, with a “bank” guild selecting dewatering microhabitats and, secondarily, a “midstream” guild avoiding them. Their selection of present hydraulics was similar to that observed in rivers without hydropeaking. Overall, past hydraulics influenced microhabitat selection, with stronger effects on macroinvertebrates and stronger effects of dewatering than of high past velocities. However, high past velocities force fish to move and macroinvertebrates to hide.

Keywords: Habitat preferences, Flow variations, 2D hydrodynamic model, Behavior, Dewatering responses, Hydropower

2.2. Introduction

Hydropeaking hydropower plants are the major source of renewable energy that meets sub-daily peaks in electricity demand. By producing electricity on demand, they create frequent rapid flow variations known as hydropeaking. Hydropeaking influences the habitats of aquatic organisms, with strong spatial and temporal variations in point flow velocity, water depth and shear stress (hydraulic conditions). In particular, near-shore areas may be subject to dewatering during base flow (i.e., become temporarily dry when turbines are shut down), which may result in stranding of individuals using shallow and slow-flowing habitats (Saltveit et al. 2001; Halleraker et al. 2003). Midstream habitats may be subject to high flow velocity during peak flow (when turbines are on), which may cause forced drift of individuals with low swimming ability (Bruno et al. 2013).

Hydropeaking often results in a decrease in abundance, biomass and species diversity in both fish and macroinvertebrate communities (Schmutz et al. 2015; Kjaerstad et al. 2018; Vila-Martínez et al. 2019). However, these negative effects are not systematic and may depend on hydropeaking hydraulic characteristics. For example, Judes et al. (2021) showed, in rivers with moderate hydraulic variations, that hydropeaking could have weaker effects than floods on fish community dynamics and did not greatly modify the organization of fish communities along longitudinal gradients. To improve our mechanistic understanding of hydropeaking influences on biota, we need to better understand individual responses to changes in the spatial and temporal variations of point hydraulic conditions (i.e. microhabitat scale). The microhabitat scale (here corresponding to fixed patches of $\sim 7\text{m}^2$ for fish, 0.05 m^2 for benthic macroinvertebrates and 6 L of hyporheic water for hyporheic macroinvertebrates (Stubbington et al. 2016)) is particularly suited for identifying the key hydraulic drivers of biological response to hydropeaking. Several studies quantified key hydraulic conditions in microhabitats for fish and macroinvertebrates drifting and stranding processes (Saltveit et al. 2001; Halleraker et al. 2003; Auer et al. 2017). For example, Halleraker et al. (2003) showed that stranding of juvenile brown trout (*Salmo trutta*) occurs with dewatering vertical water level gradients higher than 0.10 cm h^{-1} . By contrast, little is known concerning how microhabitat selection of fish and macroinvertebrates is influenced by variations in point hydraulic conditions.

In rivers without hydropeaking and associated sub-daily variations, microhabitat selection by fish and macroinvertebrates is usually predicted from present hydraulic conditions and substrate size (Forcellini et al., in press.; Lamouroux et al., 1999; Plichard et al., 2020). In hydropeaking rivers, past hydraulic variability during the weeks preceding sampling is expected to influence microhabitat selection by aquatic organisms. Indeed, experiments on fish individual behavior (Green 1971; Roy et al. 2018) indicated that fish can memorize environmental conditions over durations up to two weeks. Individuals perceive temporal variations in hydraulic conditions (Patton et al. 2015) and may avoid habitats that are frequently dewatered or have major variations in flow velocity. For example, using telemetry in the Rhône River (France) to monitor 18 individual fish, Capra et al. (2017) suggested that fish memorize spatial and temporal environmental variations during the two weeks preceding sampling so as to use the “least constraining” microhabitats. Organisms may also have strong habitat fidelity even after their habitats become unsuitable (Kemp et al. 2003). Several studies showed that some fish species are reluctant to move across the river during sudden flow increases and consequently use habitats with higher flow velocity and/or deeper habitats (Pert et al. 1994; Shirvell 1994; Kemp et al. 2003). This behavior may be explained by the energy cost associated with displacement and/or a higher risk of predation. Less mobile taxa, which include many macroinvertebrates, may be unable to respond instantaneously to a rapid shift in habitat conditions (Blinn et al. 1995). Some macroinvertebrates taxa can be removed from hydropeaking reaches by passive or active drift during low or high flow (Bruno et al. 2013). However, in adapting to naturally variable microhabitat conditions, some taxa have developed morphological and behavioral adaptations to maximize colonization of available habitat and can withstand extreme habitat conditions (e.g., resistance to desiccation). For instance, *Asellus aquaticus* (crustaceans) may pass through a desiccation-resistant life stage, allowing them to occupy intermittent stream habitats (Tachet et al. 2002). Thus, in hydropeaking rivers, such taxa could actively select dewatering habitats. Other macroinvertebrate taxa may also colonize subsurface hyporheic habitats to escape from variable benthic hydraulic conditions (Dole-Olivier et al. 1997).

Studying the effects of past hydraulics on microhabitat selection by aquatic organisms from field data is challenging. A first challenge is to describe past hydraulic conditions in

microhabitats. Spatially explicit hydrodynamic models, such as two-dimensional (2D) models that map vertically averaged flow velocities at various discharge rates, are useful for this purpose. However, calibrating and testing 2D models is time-consuming, expensive, and requires an appropriate amount of quality field measurements. A second challenge is to sample organisms at several discharge rates in order to have a sufficient number of microhabitat samples with various combinations of past and present hydraulic conditions. Addressing this challenge requires extensive fieldwork.

In this study, we combined extensive biological sampling in microhabitats at various discharge rate with results of a calibrated 2D hydrodynamic model in a hydropeaking reach to weight the relative effects of past and present hydraulic conditions on microhabitat selection. Specifically, we recorded fish taxa abundance in 1,187 microhabitats and the abundance of benthic and hyporheic macroinvertebrate taxa in 36 microhabitats along a 6 km reach of a hydropeaking reach of a medium-sized French river (the Ain River). We studied the responses of taxa that had significant microhabitat selection documented in literature. We grouped them into a few habitat guilds with comparable habitat selection. The 2D hydrodynamic model was used to estimate past hydraulics at each microhabitat during the 15 days preceding sampling (Capra et al., 2017).

For fish, we expected “midstream” species, using fast-flowing and deep habitats, would avoid dewatering areas and sustain high flow velocity variations to reduce their displacement. By contrast, fish using shallow and slow-flowing habitats along the banks could be expected to be forced to use dewatering habitats.

For macroinvertebrates, given their reduced mobility, we expected that past hydraulic conditions would have a stronger influence on their microhabitat selection than for fish. They should be disfavored by past dewatering and high flow velocity periods. Consequently, we also expected macroinvertebrate selection for present hydraulics to be different in hydropeaking rivers than those without hydropeaking. Finally, we expected different responses in benthic and in hyporheic macroinvertebrate assemblages, with a weaker effect of dewatering and high flow velocities on hyporheic macroinvertebrates, the hyporheic zone acting as shelter.

2.3. Materials and methods

Study reach

The Ain River in eastern France flows from the Jura mountains to the Rhône River, with a catchment area of 3,630 km². The study reach is 6 km long and 110 m wide, with a mean discharge of 103 m³ s⁻¹, an altitude of 230 m and a Strahler order of 5. It includes a diversity of morphological units (runs, riffles and pools), secondary channels and tributaries. Substrate is dominated by cobbles and the reach contains a few woody debris but little macrophyte cover. The reach is located 20 km downstream from the Allement hydropower plant (46° 06' 44" N, 5° 25' 20" E), the last of a series of five hydropeaking hydropower plants along the river between Vouglans and the Rhône confluence. According to data measured by DREAL Rhône-Alpes (between 1960 and 2019) at Pont-d'Ain (7.5 km upstream of the study reach), mean daily discharge is generally between 13.5 m³ s⁻¹ (exceeded 95% of the time) and 278 m³ s⁻¹ (exceeded 5% of the time). The study reach is subject to frequent sub-daily discharge variations, with base flow generally between 14 m³ s⁻¹ and (occasionally) 150 m³ s⁻¹ and peak flow generally between 40 m³ s⁻¹ and 200 m³ s⁻¹ (Figure II.2.1.). Discharge is more stable during weekends and low-flow periods (June-September).

Reach hydraulics: the 2D model

A 2D unsteady hydrodynamic model (mapping flow velocities averaged over the vertical; Rubar 2D; Bazin et al. 2017) was built, based on a digital elevation model obtained from topographic and bathymetric LiDAR surveys carried out in 2015 and 2016. Model calibrations used water surface levels derived from the LiDAR surveys at 16 m³ s⁻¹ and from field surveys at 90 m³ s⁻¹. Calibrations were made so that the absolute difference between the water level simulated by the model and that measured in the field was less than 10 cm at any measuring point. We used the model to translate the hourly flow time-series given by the gauging station of Pont d'Ain, seven kilometers upstream of the study site (from <http://hydro.eaufrance.fr>), into maps of hourly hydraulic time-series (flow velocity, water level and water depth) over the 403,591 nodes of the 2 m-edge rectangular mesh of the model.

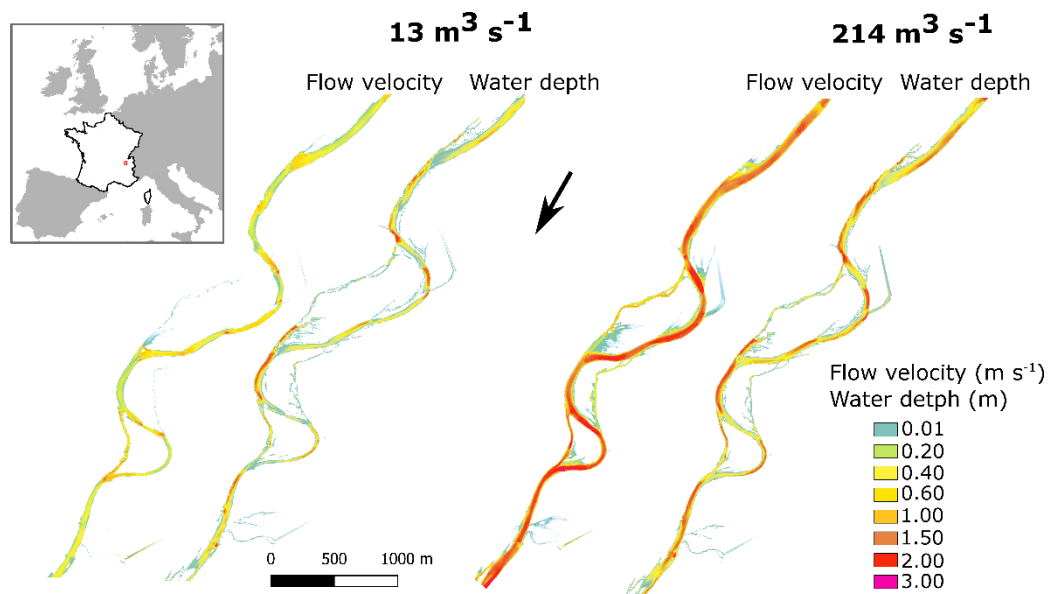


Figure II.2.1. Location of the Ain River study reach and maps of its flow velocity and water depth for the maximum and the minimum flow discharge encountered over the study period.

Sampling

Fish sampling

Fish species abundance was estimated by electrofishing in 507 microhabitats and by snorkeling in 673 microhabitats. With both protocols, the sampled surface area of microhabitats was approximately 7 m², fish being attracted (electrofishing) or observable (snorkeling) within a radius of about 1.5 m (although this distance can depend on fish size; Regis et al., 1981)

Electrofishing was conducted by a team of three or four operators from a motorboat in deep areas and by wading in shallow areas, approaching the microhabitat as discreetly as possible to minimize fish escape. An anode was immersed and held steady, and all fish around the anode were captured with a landing net, identified, measured and released. Microhabitat positions were recorded by GPS with a precision of 5 m. Electrofishing surveys covered different flow conditions (Figure II.2.2.) and microhabitat locations were chosen to cover diverse combinations of past and present hydraulic conditions. In practice, the 2D model was used to draw maps of fictive past hydraulic conditions corresponding to a typical hydropeaking week, to help finding these different combinations of past and present hydraulics in the field. Sampling at different flows also reduced the correlation between present and past hydraulic

conditions (e.g., the expected negative correlation between dewatering frequency and water depth).

Snorkeling observations targeted only large individuals of species that are difficult to sample by electrofishing (Plichard et al. 2017). Observations were made along six longitudinal transects, regularly spaced laterally across the reach, in the direction of flow over the entire study reach, during base flow only to ensure fish identification ($\sim 16 \text{ m}^3 \text{ s}^{-1}$). Two persons drifted along the transect in a downstream direction: (1) an experienced snorkeler detecting and identifying fish, followed by (2) an hydrospeeder recording the observations and GPS positions with a waterproof recorder. As reported by others (Chamberland et al. 2014), we did not frequently observed strong escape behavior while snorkeling and judged that most fish were observed by snorkelers. Underwater visibility, estimated as the distance at which snorkelers could see their bright swimming fins, was 5 m. Fish were observed and identified when in a 1.5 m radius around the snorkeler, and several fish individuals were associated to the same GPS position when observed simultaneously. Therefore, each GPS position in the dataset was considered as a microhabitat of $\sim 7 \text{ m}^2$, containing one or several fish. When drifting, snorkelers observed large fish (estimated length $> 25 \text{ cm}$) of eight species (*Barbus barbus*, *Squalius cephalus*, *Chondrostoma nasus*, *Thymallus thymallus*, *Perca fluviatilis*, *Esox lucius*, *Cyprinus carpio*, *Salmo trutta fario*) and smaller individuals of *Thymallus thymallus* only (estimated length $< 25 \text{ cm}$).

All snorkeling microhabitats were presence-only (microhabitats with fish presence), unlike the electrofishing and macroinvertebrate microhabitats. To enable common statistical processing of all data, we created fictive snorkeling microhabitats with fish absence (“pseudo-absence microhabitats”; Manly et al. 2002). In practice, for each taxon \times microhabitat combination, we randomly picked $n = 10$ pseudo-absence microhabitats among the nodes of the 2D model network. At this step, we considered only nodes with water depth $> 30 \text{ cm}$, as snorkeling was not conducted in shallower habitats. The choice of $n = 10$ pseudo-absence microhabitats was intended to provide a global prevalence comparable with that of the electrofishing data. We tested the sensitivity of results to this choice by repeating the analysis for $n=20$.

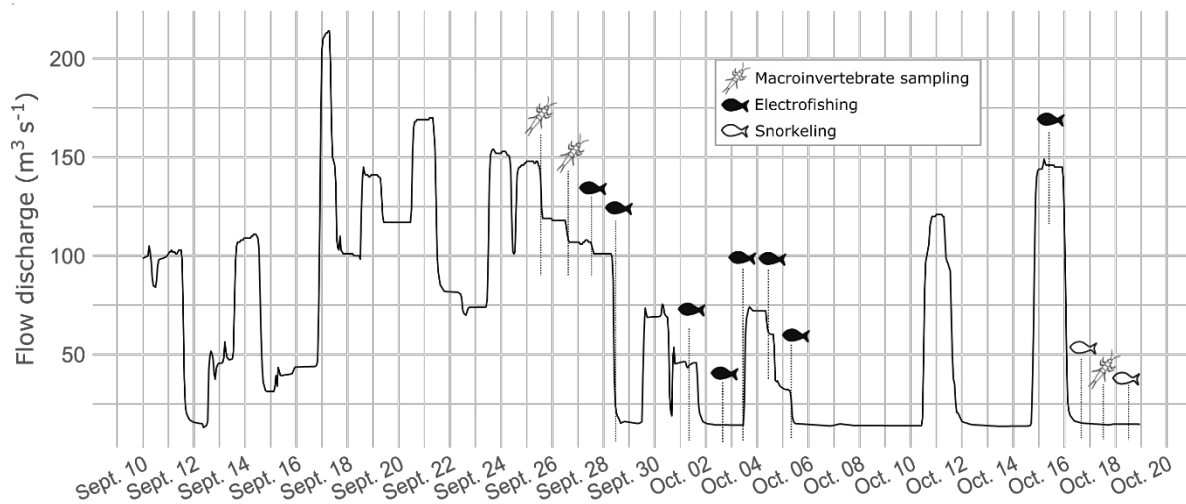


Figure II.2.2. Hourly discharge at Pont d'Ain (7.5 km upstream the study reach) during the 15 days preceding sampling and during sampling (2018). The vertical lines represent indicate sampling days at noon.

Macroinvertebrate sampling

We sampled benthic and hyporheic macroinvertebrates in 36 microhabitats, under different flow conditions (Figure II.2.2.). Similarly to the procedure used for fish, we used the 2D model to draw maps of fictive past hydraulic conditions corresponding to a typical hydropeaking week, to help finding different combinations of past and present hydraulics in the field. We chose microhabitats in six cross-sections with low and six with high velocity, distributed along the reach to have different present and past flow velocity. Within each cross-section, we selected three points with low ($0 \leq \text{depth} < 0.2$), medium ($0.2 \leq \text{depth} < 0.5$) and high water depth ($0.5 \leq \text{depth} < 0.8$) (and thus different dewatering frequencies).

We sampled benthic macroinvertebrates with a Hess sampler (surface area 0.05 m^2 , $250 \mu\text{m}$ mesh size) and recorded their positions by GPS. Then, within a radius of one meter around the Hess sampler, hyporheic macroinvertebrates were sampled with a Bou-Rouch pump (Bou et al. 1967; Dole-Olivier et al. 2014), which extracted 6L of water from 30 cm below the stream bed (using a planted steel pipe) to catch organisms living in the interstices of substrate particles. The water was filtered through a sieve with $63 \mu\text{m}$ mesh size. Macroinvertebrates were preserved in 96% ethanol and were sorted, counted and identified to the lowest practical taxonomic level using a microscope in the laboratory (list of references used for macroinvertebrate identification in Appendix, list II.2.A1).

Classification in species guilds

We grouped fish and macroinvertebrate individuals into a few habitat guilds with comparable habitat selection according to Plichard et al. (2020) and Forcellini et al. (in press), who synthesized a large part of the available information on fish and macroinvertebrate microhabitat selection in a wide range of mostly non-hydropeaking European rivers. This grouping by guilds was used to increase the statistical power of our analyses and the potential transferability of our results in rivers with other species composition.

Fish at electrofishing points were first grouped by size class, using the taxa definitions of Plichard et al. (2020). These taxa combined a specific code and one or several size classes (1: <8 cm; 2: 8–18 cm, 3:18–30 cm; 4: >30 cm; Table II.2.1.). For example, taxon Lel_cl123 corresponds to *Leuciscus Leuciscus* (Lel) fish with sizes < 30 cm. We defined two fish guilds for which we expected different influence of past hydraulics on microhabitat selection. The ‘bank’ guild grouped together taxa selecting shallow and slow-flowing habitats, thus incurring high dewatering risk. Conversely, the ‘midstream’ guild grouped together species selecting deep and fast-flowing habitats, typically found in the center channel, which should better sustain high flow velocity variations. Observed graylings (*Thymallus thymallus*) were also assigned to the midstream guild (Mallet et al. 2000). Plichard et al. (2020) summarized the microhabitat selection by fish taxa for microhabitat velocity V using the statistic AGV_V , which in short corresponds to the average microhabitat velocity that would be used by the taxa if velocities between 0 and 0.94 m s^{-1} were uniformly available in the river. Similarly, AVG_D summarizes selection for depth D over the depth range 0-3 m. Our midstream guild comprised the nine taxa with the highest value for the product AVG_V*AVG_D , and our bank guild the eight taxa with the lowest value. The number of taxa per guild was a compromise between guild abundance and magnitude of habitat selection.

For macroinvertebrates, we defined two guilds according to selection for bottom shear stress reported in Forcellini et al. (in press), where shear stress was measured using hemispheres (FST, Statzner & Müller, 1989) numbered from 0 to 19 (low to high shear stress). As done by Plichard et al. (2020) for fish, Forcellini et al. (in press) summarized microhabitat selection by macroinvertebrates, using AVG_V and AVG_FST , which is the equivalent of AVG_V but over the FST range 0-19. The ‘limnophilic’ guild grouped together taxa selecting low shear stress

(AVG_FST < 5), and thus expected to be negatively affected by high flow velocity variations. Conversely, the ‘rheophilic’ guild corresponded to taxa selecting high shear stress (AVG_FST > 8).

Present and past microhabitat hydraulics

In each electrofishing and macroinvertebrates sampling microhabitat, we measured the present water depth (D in m), and present flow velocity (V_{40} in m s^{-1} ; measured at 40% of water depth from the bottom with an electromagnetic 30 Hz current meter and averaged over 10 seconds, using a Marsh McBirney FLO MATE 2000).

We described past hydraulic conditions using the 2D hydraulic model simulations for flows observed during the 15 days preceding sampling. The duration of 15 days was consistent with previous experiments on fish individual learning (Green 1971; Roy et al. 2018) and previous field studies on hydropeaking (Capra et al., 2017). This 15 days duration also allowed to account for typical discharge variations observed in the Ain River (Figure II.2.2.). Nevertheless, we tested the sensitivity of results to our choice of a duration of 15 days, by repeating our analyses for durations of 5 and 10 days before sampling.

For estimating past hydraulics at a given microhabitat (electrofishing point or macroinvertebrate sample), we associated the sampled microhabitat to a node of the 2D model that (1) had comparable water depth, and (2) was as close as possible from the sampled microhabitat. We judged the primary use of a “depth similarity criteria” as essential for an optimum estimation of the dewatering frequency of the microhabitat. Indeed, for a given measurement discharge, water depth and past dewatering frequency are expected to be strongly correlated. In addition, even if the morphology of the river had changed locally between the 2D model calibration and the biological survey, we expected that velocity variations for a given water depth was well represented by the 2D model. In the Ain River, mesohabitats (e.g., riffles, run, pools) have surface areas of several hundred m^2 , and the 2D model is expected to well reflect hydraulic behavior of these mesohabitats, event it can be locally imprecise (Guay et al. 2000). In practice, we selected the closest 2D node that had a modeled depth differing from the measured depth at the microhabitat by less than 10 cm. For snorkeling observations, depth measurement was not available and we assigned snorkeling microhabitats to the closest 2D node.

The past hydraulic conditions during the 15 days preceding sampling were described with two variables coded as boolean categories:

(1) Duration of dewatering: we considered the microhabitat as “dewatering” if the dewatering time (depth = 0 cm) over the 15-days period before sampling was >10 hours, and as “non-dewatering” if ≤ 10 hours. We tested the sensitivity of results to our choice of a duration of 10 hours, by repeating our analyses for a duration of 1 hour.

(2) Duration of high flow velocity conditions ($>1.3 \text{ m s}^{-1}$): We considered that microhabitats had “high past velocities” if the total duration with velocity $>1.3 \text{ m s}^{-1}$ was >10 hours, and “low past-velocities” if ≤ 10 hours. We chose a threshold of 1.3 m.s^{-1} because this value is above the velocity used by most aquatic organisms (Plichard et al., 2020; Forcellini et al., in press), and is also frequently reached in many microhabitats of the Ain River. Here again, we tested the sensitivity of results to our choice of a threshold of 1.3 m.s^{-1} , by repeating our analyses for a threshold of 0.7 m.s^{-1} .

Microhabitat selection models by guild

For each dataset separately (electrofishing, snorkeling, benthic and hyporheic macroinvertebrates), we related guild abundance to past and present microhabitat characteristics (measured when available, modeled otherwise). Following Plichard et al. (2020) and Forcellini et al. (in press), we used GLMs with B-spline transformations of the present hydraulic variable (enabling non-linear responses) and assuming a negative binomial distribution of abundance (accounting for abundance overdispersion). We used splines with two degrees of freedom, with a single knot positioned at the median value (Plichard et al., 2020). To avoid overparameterization and due to limited statistical power, we had to consider models involving combinations of a single present hydraulic variable (PresHyd = V_{40} or D) and a single past hydraulic variable (PastHyd = Dew or HV). Consistently, we looked at the inter-correlations between present and past hydraulic variables to interpret the results.

For each PresHyd \times PastHyd combination, the abundance Y_i of a guild in microhabitat i was assumed to follow a negative binomial distribution of mean μ_i and dispersion parameter Θ :

$$Y_i \sim \text{NB}(\mu_i, \Theta)$$

Three GLMs of increasing complexity were compared to explain μ_i as a function of hydraulics:

M0 (no microhabitat selection): $\log(\mu_i) = \beta_0$

M1 (habitat selection with present hydraulic conditions only): $\log(\mu_i) = \beta_0 + f(\text{PresHyd}_i)$

M2 (habitat selection with present and past hydraulic conditions): $\log(\mu_i) = \beta_0 + f(\text{PresHyd}_i) + \beta_1 \text{PastHyd}_i$

where β_0 is the intercept, $f()$ is a spline transformation of the present hydraulic variable PresHyd_i , and β_1 the coefficient of the past hydraulics effect. In M0, microhabitat variables have no influence on abundance, in M1 present hydraulic conditions have an influence, and in M2 there is an additive effect of past hydraulics.

We fitted all models using the R software (R Development Core Team 2018) and the `glm.nb` function of the ‘MASS’ package (Venables et al. 2002), combined with spline functions of the ‘splines’ package. We used likelihood ratio tests comparing M0 vs. M1 to test the influence of present hydraulics on microhabitat selection, and tests comparing M1 vs. M2 to assess for an additive effect of past hydraulics. Following Plichard et al. (2020), we used non-parametric Spearman Rho rank correlation (Spearman 1904) to assess fits; this is an appropriate statistic for overdispersed data such as our abundance data, based on the correlation between the ranks of predicted and observed abundance.

Influence of hydropeaking on taxa selection for present hydraulics

For fish and macroinvertebrate taxa (benthic and hyporheic), we computed an average preferred velocity `AGV_V` and depth `AVG_D` as defined by Plichard et al. (2020), but corresponding to the fits of our M1 model by taxa. We then compared our values with those of Plichard (2020) for fish and Forcellini et al. (in press) for macroinvertebrates, to estimate how hydropeaking modifies the selection of present microhabitat hydraulics generally observed in rivers without hydropeaking. We used only electrofishing data for the fish comparison, because fish size was not available in snorkeling data, preventing comparison with the size classes of Plichard et al. (2020).

2.4. Results

Biological assemblages

We sampled 3,642 fish of 23 species by electrofishing. The bank guild contained 2,344 individuals and was composed mainly of *Phoxinus phoxinus* cl12 ($N=1,785$). The midstream guild contained 73 individuals, mainly *Barbus barbus* cl34 ($N=27$) (Table II.2.1.). We sampled 1,610 fish of 12 species by snorkeling (mainly *Thymallus thymallus*, $N=444$; *Barbus barbus*, $N=437$ and *Chondrostoma nasus*, $N=238$). In the snorkeling dataset, large *Barbus barbus*, large *Chondrostoma nasus* and all *Thymallus thymallus* belonged to the midstream guild, with many more individuals sampled than with electrofishing ($N=356$) (Table II.2.1.).

We sampled 48,275 macroinvertebrates: 38,196 in benthic samples and 10,079 in hyporheic samples. The full list of taxa of both datasets are available as Appendix (Table II.2.A1). The benthic dataset contained 149 taxa and the hyporheic dataset 97 taxa. For the benthic dataset, the limnophilic guild contained 687 individuals (principally composed of *Chironomini*, $N=612$) and the rheophilic guild contained 2988 individuals (principally composed of *Esolus*, $N=2,021$) (Table II.2.2.). For the hyporheic dataset, the limnophilic guild contained 170 individuals (principally composed of *Chironomini*, $N=140$) and the rheophilic guild contained 961 individuals (principally composed of *Esolus*, $N=754$) (Table II.2.A2.).

Table II.2.1. Fish guilds, species, taxa codes, with total abundance and occurrence in microhabitats.

Dataset	Guild	Family	Scientific name	Common name	Taxa code	Abundance	Occurrence
Electrofishing	Bank N=2344	Cyprinidae	<i>Phoxinus phoxinus</i>	Minnow	PhP_cl12	1785	134
		Cyprinidae	<i>Squalius cephalus</i>	Chub	SqC_cl1	217	47
		Cyprinidae	<i>Rutilus rutilus</i>	Roach	RuR_cl1	122	15
		Balitoridae	<i>Barbatula barbatula</i>	Stone loach	BaBa_cl12	116	57
		Cyprinidae	<i>Telestes soufia</i>	Blageon	TeS_cl1	57	17
		Cyprinidae	<i>Gobio gobio</i>	Gudgeon	GoG_cl1	30	16
		Percidae	<i>Perca fluviatilis</i>	Perch	PER_cl12	11	11
		Centrarchidae	<i>Lepomis gibbosus</i>	Pumpkinseed	LeG_cl123	6	5
	Midstream N=73	Cyprinidae	<i>Barbus barbus</i>	Barbel	BaBu_cl34	27	17
		Salmonidae	<i>Thymallus thymallus</i>	Grayling	ThT_cl2	15	10
		Cyprinidae	<i>Chondrostoma nasus</i>	Nase	ChN_cl34	12	7
		Cyprinidae	<i>Barbus barbus</i>	Barbel	BaBu_cl2	8	8
		Cyprinidae	<i>Alburnus alburnus</i>	Bleak	AIA_cl23	4	5
		Salmonidae	<i>Thymallus thymallus</i>	Grayling	ThT_cl4	3	2
Salmonidae		<i>Thymallus thymallus</i>	Grayling	ThT_cl3	2	3	
	Cyprinidae	<i>Rutilus rutilus</i>	Roach	RuR_cl34	2	2	
Snorkeling	Midstream N= 1119	Salmonidae	<i>Thymallus thymallus</i>	Grayling	ThT_cl234	444	347
		Cyprinidae	<i>Barbus barbus</i>	Barbel	BaBu_cl34	437	164
		Cyprinidae	<i>Chondrostoma nasus</i>	Common nase	ChN_cl34	238	43

Table II.2.2. Benthic macroinvertebrate guilds, family, genus, taxa codes, with total abundance and occurrence in microhabitats.

Guild	Family	Tribe	Genus	Taxa	Code taxa	Abundance	Occurrence
Limnophilic N=687	Chironomidae	Chironomini			CHIR	612	23
	Sphaeriidae		<i>Pisidium spp.</i>		PISI	70	15
	Tabanidae				TABA	3	3
	Baetidae (non Baetis)		<i>Procloeon spp.</i>	<i>Procloeon bifidum</i>	PBIF	2	1
Rheophilic N=2988	Elmidae		<i>Esolus spp.</i>		ESOL	2021	34
	Hydropsychidae		<i>Cheumatopsyche spp.</i>	<i>Cheumatopsyche lepida</i>	CLEP	393	14
	Psychomyiidae		<i>Psychomyia spp.</i>	<i>Psychomyia pusilla</i>	PPUS	214	14
	Elmidae		<i>Elmis spp.</i>		ELMI	192	17
	Baetidae		<i>Baetis spp.</i>	<i>Baetis fuscatus</i>	BFUS	102	14
	Hydropsychidae		<i>Hydropsyche spp.</i>	<i>Hydropsyche incognita</i>	HINC	48	10
	Psychodidae				PSYC	7	4
	Heptageniidae		<i>Heptagenia spp.</i>	<i>Heptagenia sulphurea</i>	HSUL	6	3
	Baetidae		<i>Baetis spp.</i>	<i>Baetis vardarensis</i>	BVAR	3	1
	Hydropsychidae		<i>Hydropsyche spp.</i>	<i>Hydropsyche exocellata</i>	HEXO	1	1
	Baetidae		<i>Baetis spp.</i>	<i>Baetis rhodani</i>	BRHO	1	1

Present and past hydraulic variables and their intercorrelation (Figure II.2.3)

Present depth and velocity typically ranged between 0-4 m and 0-2 m s⁻¹ in the fish datasets (Figure II.2.3A.). By contrast, depth was generally shallower than 0.8 m and velocity lower than 1 m s⁻¹ in the macroinvertebrate dataset, due to sampling limits. Water depth and flow velocity were poorly correlated (and with different directions) for the fish data (electrofishing: $r=0.13$, $P<0.05$; snorkeling: $r=-0.48$, $P<0.05$) (Figure II.2.3.A). The correlation was greater in the macroinvertebrate dataset ($r=0.57$; $P<0.05$).

When calculating past hydraulics using the 2D hydrodynamic model, 76% of the electrofishing microhabitats and 75% of the macroinvertebrate microhabitats were associated with a model node within a radius of 5.5 m around the sampled microhabitat. In the electrofishing dataset, 102/507 microhabitats were dewatering habitats and 255/507 had high past velocities (Figure II.2.3B.). The snorkeling dataset contained no dewatering microhabitats and 342/673 microhabitats with high past velocities. A little less than half of the

macroinvertebrate samples (32/72) were dewatering and a higher proportion (44/72) had past low velocities. For fish (electrofishing) and macroinvertebrates, all combinations of dewatering × high past velocity habitats were sampled (Figure II.2.3B.). Nevertheless, dewatering habitats were generally those with low past velocity for both fish and macroinvertebrates (Xhi2 test, $P < 0.05$).

Correlations between present and past hydraulics were limited ($r^2 < 0.30$ in all cases). The strongest correlation was between flow velocity and high past velocities (Figure II.2.3C.), especially for the electrofishing and the macroinvertebrate datasets. Dewatering habitats also often had lower flow velocities and depths (Figure II.2.3D.).

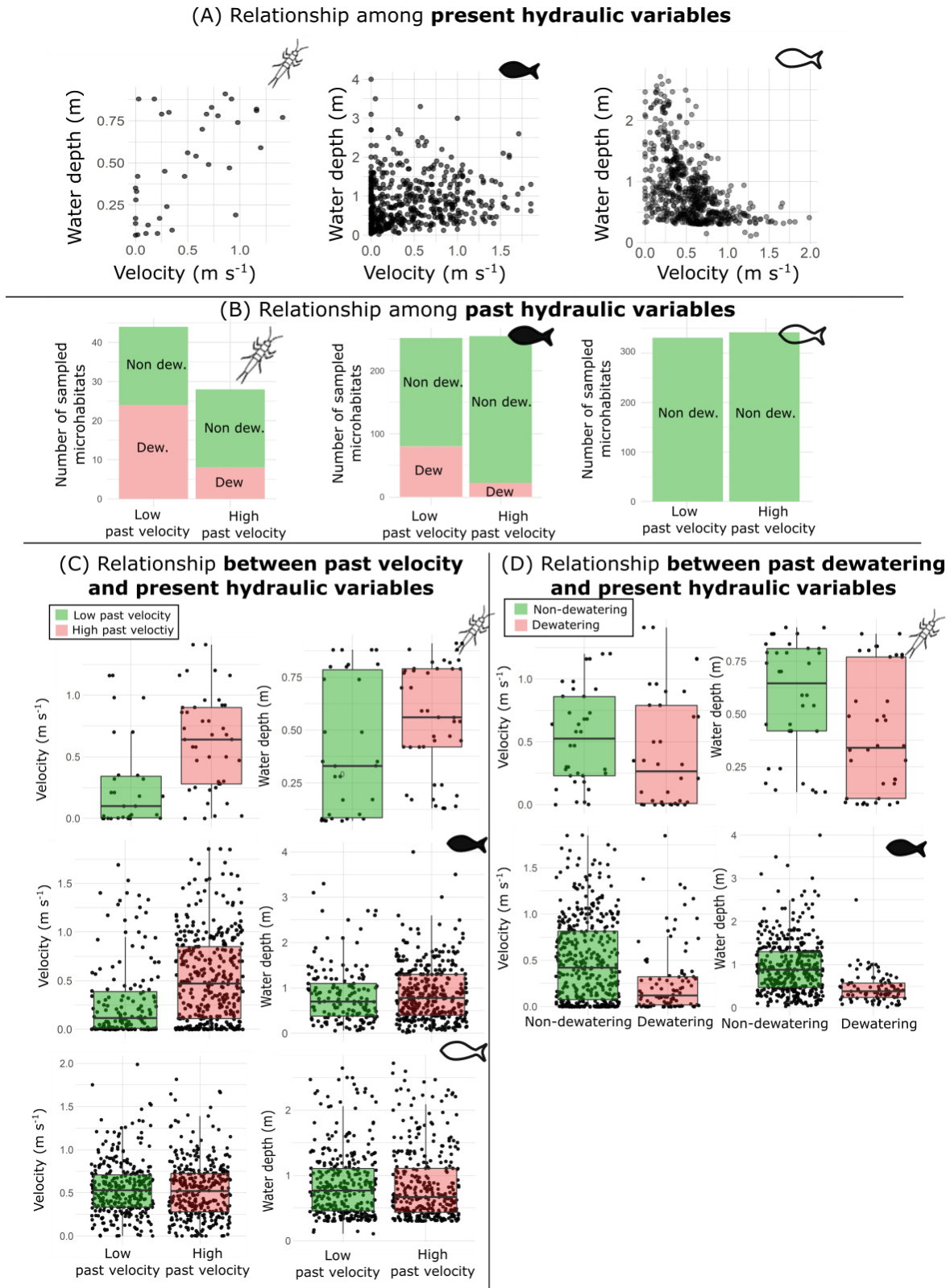





Figure II.2.3. Relationship (A) among present hydraulic variables, (B) among past hydraulic variables and (C,D) between present and past hydraulic variables for macroinvertebrates () , fish sampled by electrofishing () , and fish sampled by snorkeling () . Points represent microhabitats.

Microhabitat selection models by guilds

As expected from the fish guild definitions, the midstream guild used higher present velocities and depths than the bank guild, according to both electrofishing and snorkeling data. The bank guild significantly avoided fast-flowing and deep microhabitats (Table II.2.3., Figure II.2.4.). Differences in response to flow velocity between guilds, however, were less clear for macroinvertebrates than for fish (Figure II.2.4A.). Rheophilic macroinvertebrate guild (benthic and hyporheic) significantly avoided shallow microhabitats (Table II.2.3. and Figure II.2.4A.). Results for hyporheic macroinvertebrates are presented in Appendix (Table II.2.A3. and Figure II.2.A1).

Several significant additive effects of past hydraulics were observed (indicated by asterisks in Figure II.2.4.). Macroinvertebrates responded more significantly to past hydraulics, all macroinvertebrate guilds being 3.5-15.3 times less abundant in dewatering habitats (Figure II.2.4A.). Consistently, Spearman Rho values for macroinvertebrate M2 models involving dewatering (between 0.27 and 0.64, Table II.2.3. and Table II.2.A3.) were much higher than the corresponding values for M1 models (between 0.04 and 0.35, Table II.2.4. and Table II.2.A3.). Secondly, benthic rheophilic macroinvertebrates selected microhabitats with high past velocities but not hyporheic macroinvertebrates. For fish (electrofishing), responses were weaker and clearly different, with the bank guild selecting dewatering microhabitats (Figure II.2.4A.) and, less evidently, the midstream guild avoiding dewatering microhabitats. Midstream fish of the snorkeling dataset selected microhabitats with high past velocities.

The sensitivity tests concerning the choice of a 15 days duration for calculating past hydraulics and a 10 hours duration for defining dewatering microhabitats did not modify any of our results (significance tests in Table II.2.3, Figure II.2.4. and Table II.2.A3.).

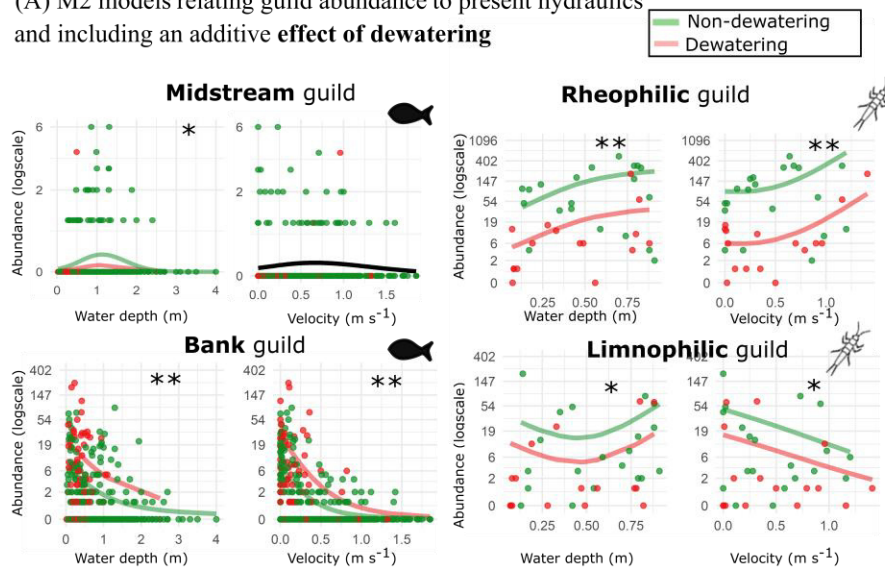
By contrast, a threshold of 0.7 m.s^{-1} instead of 1.3 m.s^{-1} for defining microhabitats with high past velocities and, a number of 20 instead of 10 pseudo-absence when building model on the snorkeling dataset modified some of our (secondary) results on the effects of high past velocities. With a lower 0.7 m.s^{-1} threshold, the bank fish guild significantly selected high past velocities (M2 models) and the midstream fish (electrofishing) guild avoided them (M2 model with velocity). In addition, the selection of high past velocities by midstream fish (snorkeling)

was no longer significant with a 0.7 m.s⁻¹ threshold to define past high velocity or a number of 20 instead of 10 pseudo-absence when building models.

Table II.2.5. Fitting statistics for models M0 (no microhabitat selection), M1 (effects of present hydraulics) and M2 (additional effect of past hydraulics), including AIC and Spearman Rho values. M2 models correspond to those shown in Figure II.2.4. Asterisks indicate significance of likelihood ratio tests comparing M1 vs. M0 or M2 vs. M1, with (*) for P<0.05 and (**) for P<0.01. In bold: abundance is significantly higher in past high velocity or dewatering habitat; Underlined: abundance is lower.

Model type	Hydraulic variables involved	Dataset									
		Electrofishing data				Snorkeling data		Benthic macroinvertebrate data			
		Bank guild		Midstream guild		Midstream guild		Limnophilic guild		Rheophilic guild	
		AIC	Spea. Rho	AIC	Spea. Rho	AIC	Spea. Rho	AIC	Spea. Rho	AIC	Spea. Rho
M0		1780		392		4108		256		273	
M1	Flow velocity	1670**	0.41	395	0.11	4847**	0.16	258	0.09	370**	0.13
M2	Flow velocity + Dewatering	1650**	0.44	<u>392*</u>	0.14			<u>256*</u>	0.27	<u>353**</u>	0.61
	Flow velocity+ Past velocity	1672	0.40	395	0.11	4843*	0.15	259	0.09	369*	0.31
M1	Water depth	1734**	0.43	385**	0.10	4933	0.04	259	0.04	370**	0.35
M2	Water depth+ Dewatering	1725**	0.43	386	0.13			<u>258*</u>	0.44	<u>358**</u>	0.53
	Water depth+ Past velocity	1734	0.44	384	0.12	4931*	0.03	259	0.15	366**	0.46

(A) M2 models relating guild abundance to present hydraulics and including an additive effect of dewatering



(B) M2 models relating guild abundance to present hydraulics and including an additive effect of past velocity

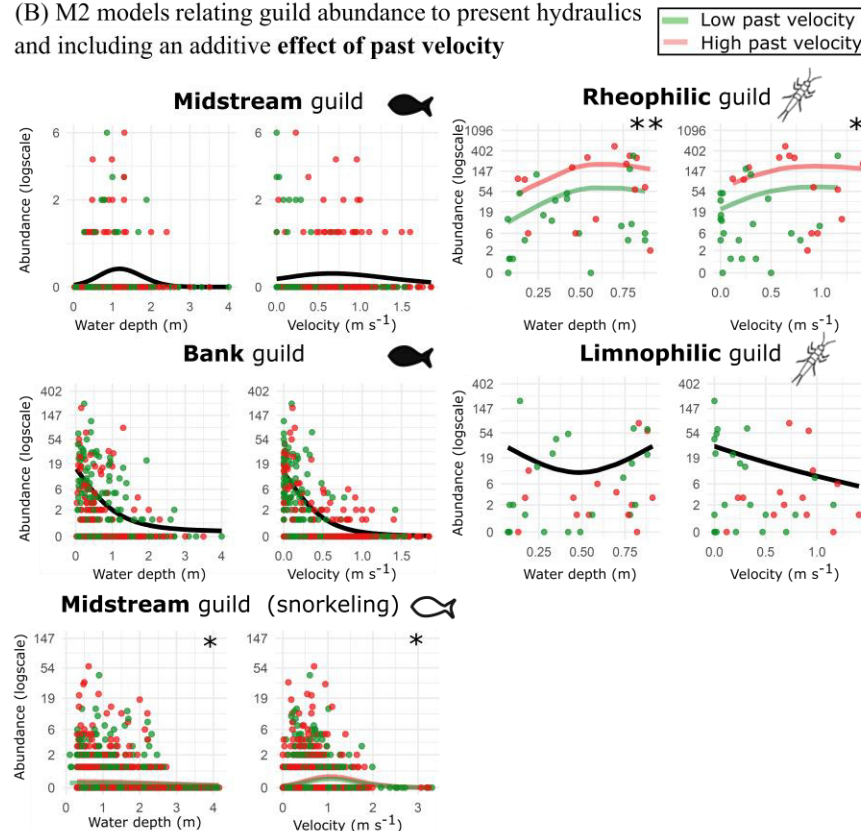


Figure II.2.4. Fits of M2 models relating guild abundance to present hydraulics and including an additive effect of dewatering (A) or past velocity (B). Red and green curves reflect the effect of past hydraulic variables, when significant. Graphs are shown for the electrofishing (🐟) snorkeling (🏊) and benthic macroinvertebrate (🐛) data sets. Stars show the significance of the past hydraulics effect () $P < 0.01$; (*) $P < 0.05$.**

Influence of hydropeaking on taxa selection for present hydraulics

Microhabitat selection for present hydraulics could be compared between the present study and the literature for nine fish taxa and ten macroinvertebrate taxa. Present velocity and water depth selection by fish taxa corresponded to those reported in the literature (Figure II.2.5A.) and had comparable Spearman Rho values (Figure II.2.5B.). By contrast, present velocity and water depth selection by macroinvertebrate taxa did not match values reported in the literature (Figure II.2.5C.) and had lower Spearman Rho values here (Figure II.2.5D.).

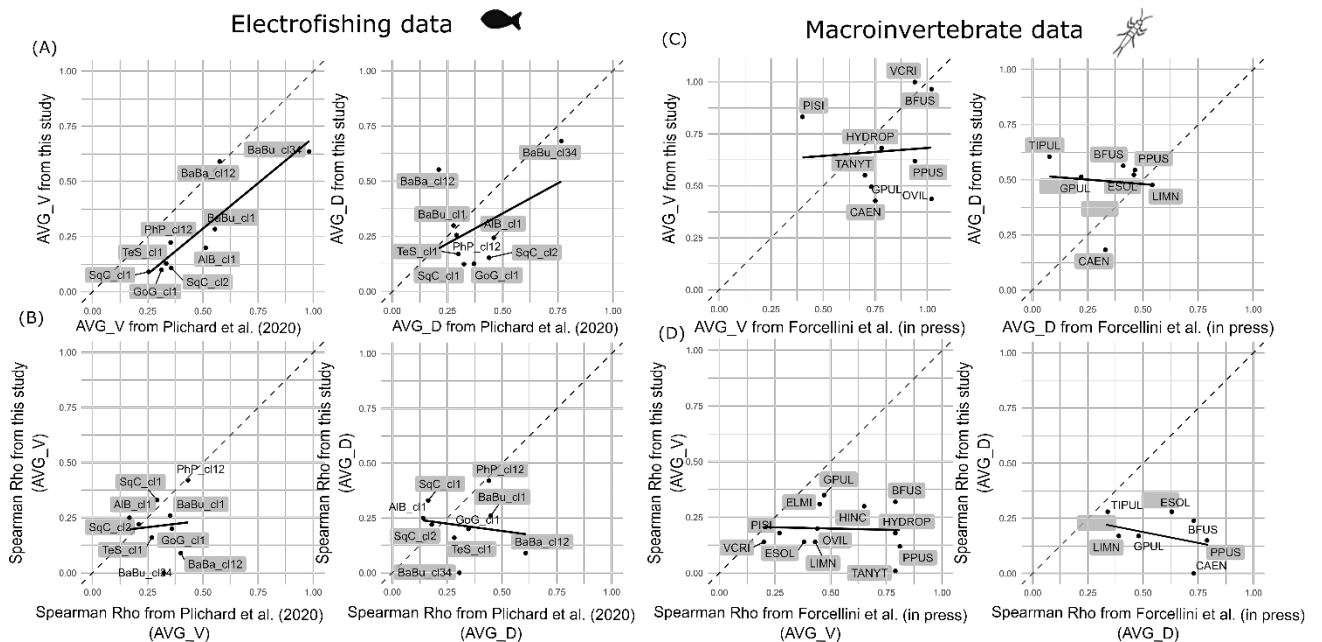


Figure II.2.5. Comparison of the average preferred velocity (AVG_V, corresponding to model M1) obtained in this study with data from Plichard et al. (2020) for fish and from Forcellini et al. (in press) for macroinvertebrates. Axis regressions (full lines) are shown as well as the $y = x$ lines (dotted lines). For Plichard et al. (2020), AVG_V: $y = -0.76x - 0.09$, $R^2 = 0.76$, $P < 0.01$; Spearman Rho: $-0.48x + 0.33$, $R^2 = 0.13$, $P = 0.34$. AVG_D: $y = 0.54x + 0.08$, $R^2 = 0.21$, $P = 0.22$; Spearman Rho: $-0.13x + 0.26$, $R^2 = 0.03$, $P = 0.66$. For Forcellini et al. (in press), AVG_V: $y = 0.08x + 0.59$, $R^2 = 0.02$, $p\text{-value} = 0.62$; Spearman Rho: $0.56x + 0.091$, $R^2 = 0.03$, $P = 0.63$, AVG_D: $y = -0.10x + 0.52$, $R^2 = 0.01$, $P = 0.80$; Spearman Rho: $-0.24x + 0.33$, $R^2 = 0.12$, $P = 0.39$. GPUL: *Gammarus pulex*; HYDROP: *Hydropsyche contubernalis*; TANYT: *Tanytarsini* (tribe); LIMN: *Limnomysis benedeni*; OVIL: *Orectochilus villosus*; VCRI: *Valvata cristata*; PISI: *Pisidium* (genus); TIPUL: *Tipula* (genus). See table II.2.1 and II.2.2 for other taxa names.

2.5. Discussion

By studying the combined influence of present and past hydraulics on microhabitat selection, we improved our mechanistic understanding of the impact of hydropeaking on fish and macroinvertebrate guilds. We found that both limnophilic and rheophilic macroinvertebrates were 3.5-15.3 times less abundant in dewatering microhabitats. This confirms findings such as those of Blinn et al. (1995), who reported a four-fold lower macroinvertebrate biomass in dewatering habitats of the Colorado River. Consistently with this result, we also showed that the average velocity and water depth preferences of some macroinvertebrate taxa differed from those previously established in mainly non-hydropeaking rivers (Figure II.2.5.). This suggests that macroinvertebrates are not able to maintain habitat preferences when flow changes too rapidly or frequently: they likely stay at the same location, undergoing different hydraulic conditions according to flow conditions.

We found no major difference in response to dewatering or to past high velocities between benthic and hyporheic macroinvertebrates. Thus, in the Ain River the hyporheic areas does not seem to offer shelter under hydropeaking conditions. We sampled hyporheic macroinvertebrates at a depth of 30 cm depth in the Ain River it is certainly not deep enough to reach the permanently water-saturated area.

In contrast to macroinvertebrates, fish followed their preferred habitat preferences observed in other rivers and were less influenced by past hydraulics. Nevertheless, fish from the “bank” guild probably stayed along the bank and moved to dewatering microhabitats when flow increased, in order to remain within their strict range of preferred hydraulic conditions. This result contrasts with many studies concerning salmonid juveniles, also living near the banks, and indicating that only a fraction of individuals relocate when flow changes (Shirvell 1994; Kemp et al. 2003; Korman et al. 2009). High velocities in the Ain River and the different species considered here (mostly cyprinids) may explain these differences. In the Ain River, fish from the bank guild are probably exposed to a high risk of stranding, particularly because cobble bars have very low slopes (Tuhtan et al. 2012). It would be interesting to quantify the influence of horizontal down-ramping rate (water surface retreat rate) on fish stranding near these cobble bars. The fish “midstream” guild also followed their preferred range of habitat, and tended to

avoid dewatering and stressful microhabitats (Reebs 1996; Capra et al. 2017). Although it concerned other species (large barbel, catfish and chub), the telemetry experiment by Capra et al. (2017) also reported that fish could avoid dewatering microhabitats. However, due to the small number (N=73) of fish involved in this present result, this result deserves generalization.

Observed microhabitat selection by fish and macroinvertebrates was not negatively affected by high past velocities, suggesting a weaker influence of high past velocities compared to dewatering. In addition, the statistical significance of the weak responses to high past velocities depended on the threshold chosen for defining high past velocities, indicating unstable results. However, considering that hydropeaking has occurred since the 1930s in the Ain River, environmental filtering may have selected only species that can cope with rapid and frequent variations in hydraulic conditions. Furthermore, our results suggest that high velocities force fish to move (sticking to their general hydraulic preference) and macroinvertebrates to find flow-shelter or attach to the substrate (e.g. with silk draglines, tarsal claws, or a muscular foot; Holomuzki et al. 2000). Moving (fish) or staying in sub-optimal habitat conditions (macroinvertebrates) may create energetic costs that influence community structure on the long term and explain reach-scale effects of hydropeaking (Judes et al., 2021). More detailed observations of behavior at high flows (e.g. by snorkeling or with cameras), experimental/physiologic experiments in flumes, or additional comparisons between reaches subjected to different degrees of hydropeaking (Schmutz et al., 2015; Judes et al., 2021) will be useful to confirm this interpretation.

We identify four major limits and ways of improvement in our study. First, we pooled microhabitat samples under low and high flow conditions due to a limited statistical power. However, habitat availability strongly changes according to flow conditions. For example, in the Ain, 77% of the wetted surface is less than 1 m deep at $14 \text{ m}^3 \text{ s}^{-1}$ versus 33% at $214 \text{ m}^3 \text{ s}^{-1}$. Such differences in habitat availability could influence species microhabitat selection (Schooley 1994; Arthur et al. 1996). Further sampling could target a more detailed analysis of the effects of habitat availability. Similarly, improved analyses should also consider the effects of woody debris, macrophyte cover, tributary proximity and/or thermal refugia. Secondly, discharge before and during our sampling period combined hydropeaks and artificial releases of intermediate flows (around $100 \text{ m}^3 \text{ s}^{-1}$, Figure II.2.2.) to compensate for low discharge in the Rhône River. The duration of intermediate flow may influence observed fish and

macroinvertebrates microhabitat selection. Future sampling will need to be implemented during different hydropeaking regimes, especially for macroinvertebrates sampling, which was conducted at only three flow conditions here. Thirdly, because our results were little sensitive to a number of our methodological choices (duration considered for past hydraulics, threshold used for defining dewatering habitats and high past velocities), additional experiments/data would be useful to specify the key quantitative drivers of biological responses. Finally, although the 2D hydrodynamic model allowed us to estimate past hydraulics at each microhabitat, its accuracy and the methods used for associating field observations with model nodes would deserve further investigation (see Guay et al., 2000).

In conclusion, our microhabitat-scale study shows a stronger effect of dewatering than high past velocities on macroinvertebrates, and secondarily fish. Although it failed to identify critical past velocity thresholds for hydropeaking management, it suggests that fish are forced to move and macroinvertebrate to hide due to these high past velocities. Comparing our results with data collected in other rivers and at a larger variety of flows, combined with experimental studies, should help further identifying the key hydropeaking characteristics to consider in mitigation policies.

2.6. Acknowledgments

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2.8. Appendix

List II.2.A1. List of references used for macroinvertebrate identification.

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Table II.2.A1. Abundance per taxa in the benthic and hyporheic area.

Taxonomic group	Taxa	Abundance on the benthic area	Abundance on the hyporheic area
BASOMMATOPHORA	<i>Gyraulus spp.</i>	1	0
BIVALVIA	<i>Pisidium spp.</i>	70	28
	Sphaeriidae	1	0
BRYOZOA	BRYOZOA	1	0
CLADOCERA	Cladocera	769	188
COLEOPTERA	<i>Esolus spp.</i>	2021	754
	Dryopidae	687	46
	<i>Elmis spp.</i>	192	19
	<i>Oulimnius spp.</i>	192	32
	<i>Limnius spp.</i>	168	32
	<i>Dryops spp.</i>	167	82
	<i>Riolus spp.</i>	158	6
	<i>Stenelmis canaliculata</i>	44	66
	<i>Bidessus minutissimus</i>	24	18
	Hydroporinae	18	8
	<i>Bidessus spp.</i>	12	27
	Elmidae	12	131
	<i>Haliphus spp.</i>	10	1
	Hydrophilinae	9	0
	<i>Orectochilus villosus</i>	8	1
	<i>Brychius elevatus</i>	3	0
	Haliplidae	2	0
	<i>Laccobius spp.</i>	2	0
	<i>Stenelmis spp.</i>	2	0
	<i>Peltodytes rotundatus</i>	1	0
<i>Platambus maculatus</i>	1	0	
<i>Pomatinus substriatus</i>	0	1	
COLLEMBOLA	Collembola	16	6
CRUSTACES Malacostraca	<i>Gammarus pulex</i>	979	136
	Asellidae	411	113
	Amphipoda	403	126
	<i>Gammarus spp.</i>	306	73
	<i>Asellus aquaticus</i>	203	94
	Niphargidae	159	399
	<i>Crangonyx pseudogracilis</i>	96	80
	Gammaridae	63	14
CRUSTACEA Others	Cyclopoida	1309	1494
	Calanoida	41	0
	Harpacticoida	1	3
DIPTERA	Tanytarsini	3632	150
	Orthocladinae	3093	90

Chironomidae	1500	158
Tanypodinae	1067	668
<i>Chironomini</i>	612	140
Hemerodromiinae	239	8
<i>Antocha vitripennis</i>	221	1
Ceratopogoninae	117	44
<i>Simulium spp.</i>	57	1
Tipulidae	45	2
Rhagionidae	8	0
Psychodidae	7	1
Hexatomini	4	1
Atherix spp.	3	0
Atrichops	3	1
Simuliidae	3	0
Tabanidae	3	0
Clinocerinae	2	0
Dasyheleinae	2	0
Epididae	1	0
Forcipomyinae	1	0
<i>Hexatoma spp.</i>	1	0
Limoniini	0	1
Diamesinae	4	0
Dolichopodidae	1	0
<hr/>		
EPHEMEROPTERA		
<i>Caenis spp.</i>	574	135
<i>Rhithrogena spp.</i>	264	14
<i>Potamanthus luteus</i>	176	46
<i>Baetis spp.</i>	175	3
Heptageniidae	173	14
<i>Baetis fuscatus</i>	102	1
<i>Habroleptoides confusa</i>	72	16
Baetidae	65	1
<i>Heptagenia spp.</i>	17	2
<i>Cloeon spp.</i>	6	0
<i>Heptagenia sulphurea</i>	6	0
<i>Ecdyonurus spp.</i>	5	0
<i>Ecdyonurus aurantiacus</i>	5	0
<i>Ephemera spp.</i>	4	5
<i>Baetis vardarensis</i>	3	0
<i>Procloeon spp.</i>	2	0
<i>Procloeon bifidum</i>	2	2
<i>Alainites muticus</i>	1	0
<i>Baetis rhodani</i>	1	0
<i>Cloeon dipterum</i>	1	0
<i>Choroterpes picteti</i>	1	7
<i>Ephemera danica</i>	1	1
<i>Serratella ignita</i>	1	0
<i>Caenis luctuosa</i>	0	1

	Leptophlebiidae	0	2
GASTEROPODA	Planorbidae	6	0
	<i>Valvata cristata</i>	5	10
	<i>Valvata spp.</i>	4	146
	<i>Bathyomphalus contortus</i>	2	0
	<i>Bithynia spp.</i>	2	0
	<i>Planorbarius corneus</i>	1	0
	<i>Potamopyrgus antipodarum</i>	1	0
	<i>Planorbarius spp.</i>	0	2
HETEROPTERA	<i>Micronecta spp.</i>	857	87
	Corixinae	2	0
HIRUDINEA	<i>Erpobdella spp.</i>	19	1
	<i>Erpobdella octoculata</i>	8	1
	Glossiphoniidae	2	1
	<i>Helobdella spp.</i>	0	1
HYDROZOA	Hydrozoa	64	15
NEMATHELMINTHA	Nemathelmintha	127	279
NEMATODA	Nematoda	13	9
NEMERTEA	<i>Prostoma spp.</i>	92	22
ODONATA	<i>Onychogomphus spp.</i>	21	3
	<i>Orthetrum spp.</i>	2	0
	Sympetrinae	2	0
	<i>Calopteryx spp.</i>	1	0
	Coenagrionidae	1	0
	<i>Crocothemis erythraea</i>	1	0
	Gomphidae	1	1
	<i>Onychogomphus forcipatus</i>	1	0
OLIGOCHAETA	Oligochaeta	5061	1033
OSTRACODA	Ostracoda	4523	983
PLECOPTERA	<i>Leuctra fusca</i>	18	1
	<i>Leuctra spp.</i>	14	6
	<i>Siphonoperla spp.</i>	7	8
	Leuctridae	0	1
PLUMATELLIDA	<i>Cristatella mucedo</i>	4	1
TRICHOPTERA	<i>Hydroptila spp.</i>	1486	31
	<i>Athripsodes spp.</i>	827	195
	<i>Setodes argentipunctellus</i>	732	206
	<i>Cheumatopsyche lepida</i>	393	183
	<i>Hydropsyche spp.</i>	386	36
	Hydroptilidae	346	11
	<i>Psychomyia pusilla</i>	214	0
	Leptoceridae	76	2
	<i>Hydroptila vectis</i>	54	1
	<i>Hydroptila angulata</i>	49	2
	<i>Hydropsyche incognita</i>	48	3
	<i>Oecetis spp.</i>	13	1

	Psychomyidae	13	0
	<i>Rhyacophila spp.</i>	13	0
	Hydropsychidae	12	7
	<i>Tinodes spp.</i>	9	0
	<i>Athripsodes cinereus</i>	7	0
	<i>Mystacides spp.</i>	7	0
	Polycentropodidae	4	1
	TRICHOPTERA	4	1
	<i>Mystacides azurea</i>	3	0
	<i>Tinodes waeneri</i>	2	0
	<i>Ceraclea spp.</i>	1	0
	<i>Ecnomus spp.</i>	1	0
	<i>Hydropsyche exocellata</i>	1	0
	<i>Lepidostoma spp.</i>	1	0
	<i>Lepidostoma hirtum</i>	1	0
	Lepidostomatidae	1	0
TRICLADIDA	<i>Polycelis spp.</i>	77	34
	Tricladida	54	34
	<i>Polycelis nigra tenuis</i>	23	15
	<i>Planaria torva</i>	0	2
TROMBIDIFORMES	Hydracarina	1403	1165
TURBELLARIA	<i>Dugesia spp.</i>	208	32
	<i>Dendrocoelum lacteum</i>	25	12
	Planariidae	1	0

Table II.2.A2. Benthic macroinvertebrate guilds, family, genus, taxa codes, with total abundance and occurrence in microhabitats.

Guild	Family	Tribe	Genus	Taxa	Code taxa	Abundance	Occurrence
Limnophilic N=170	Chironomidae	Chironomini			CHIR	140	17
	Sphaeriidae		<i>Pisidium spp.</i>		PISI	28	10
	Baetidae (non Baetis)		<i>Proclouon spp.</i>	<i>Proclouon bifidum</i>	PBIF	2	2
Rheophilic N=961	Elmidae		<i>Esolus spp.</i>		ESOL	754	31
	Hydropsychidae		<i>Cheumatopsyche spp.</i>	<i>Cheumatopsyche lepida</i>	CLEP	183	6
	Elmidae		<i>Elmis spp.</i>		ELMI	19	8
	Hydropsychidae		<i>Hydropsyche spp.</i>	<i>Hydropsyche incognita</i>	HINC	3	2
	Psychodidae				PSYC	1	1
	Baetidae		<i>Baetis spp.</i>	<i>Baetis fuscatus</i>	BFUS	1	1

Hyporheic macroinvertebrates

(A) M2 models relating guild abundance to present hydraulics and including an additive **effect of dewatering**

(B) M2 models relating guild abundance to present hydraulics and including an additive **effect of past velocity**

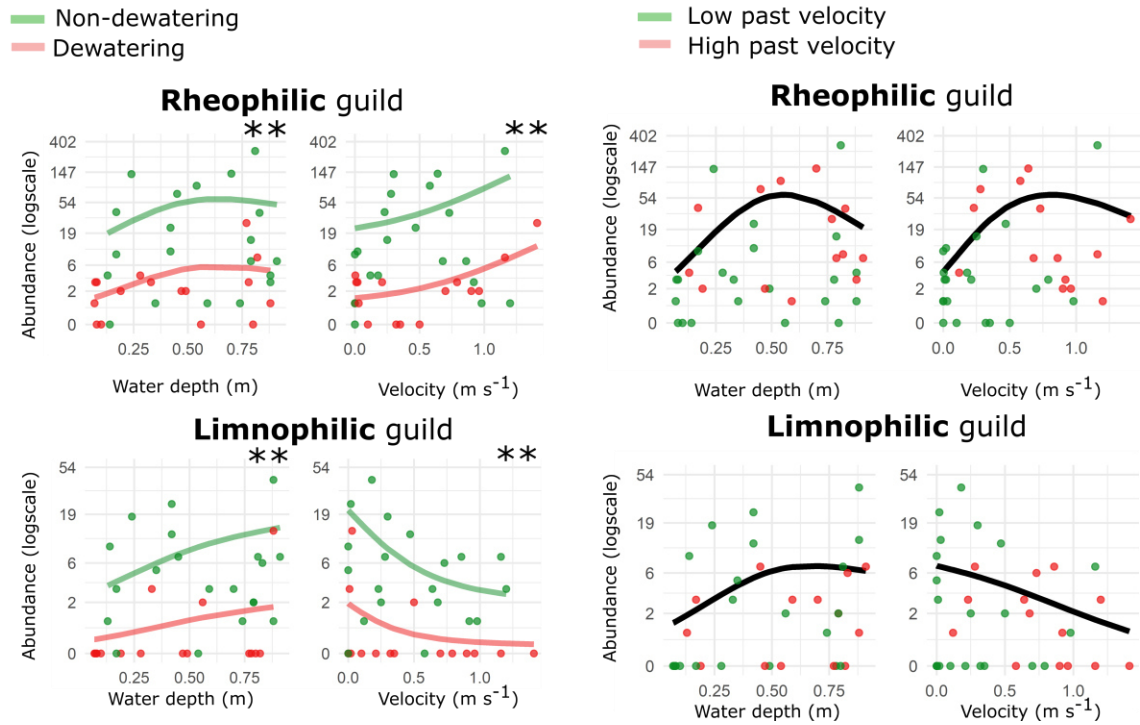


Figure II.2.A1. Fits of M2 models relating guild abundance for hyporheic macroinvertebrates to present hydraulics and including an additive effect of dewatering (A) or past velocity (B) for the hyporheic macroinvertebrates data. Red and green curves reflect the effect of the past hydraulic variables, when significant. Stars show the significance of the past hydraulics effect () P<0.01; (*) P<0.05.**

Table II.2.A3. Fitting statistics for models M0 (no microhabitat selection), M1 (effects of present hydraulics) and M2 (additional effect of past hydraulics), including AIC and Spearman Rho values. M2 models correspond to those shown in Figure 4. Asterisks indicate significance of likelihood ratio tests comparing M1 vs. M0 or M2 vs. M1, with (*) for P<0.05 and (**) for P<0.01. In bold: abundance is significantly higher in past high velocity or dewatering habitat; Underlined: abundance is lower.

Model type	Hydraulic variables involved	Hyporheic macroinvertebrate data			
		Limnophilic guild		Rheophilic guild	
		AIC	Spea. Rho	AIC	Spea. Rho
M0		179		281	
M1	Flow velocity	180	0.13	277**	0.18
M2	Flow velocity + Dewatering	<u>168**</u>	0.62	<u>261**</u>	0.52
	Flow velocity+ Past velocity	181	0.11	281	0.15
M1	Water depth	181	0.14	280	0.19
M2	Water depth+ Dewatering	<u>172**</u>	0.64	<u>267**</u>	0.49
	Water depth+ Past velocity	180	0.30	282	0.18

3. BATZ ET AL. (SOUMIS) :

Habitat dynamics in hydropeaking rivers: the impact of flow frequency and duration on patch-scale habitat dynamics.

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3.1. Abstract

Alterations in the riverine flow regime lead to biodiversity loss and ecosystem degradation worldwide. However, our mechanistic understanding of how frequently recurring hydropeaks, as caused by intermittent hydropower production, affect ecological processes is limited. Here, we link hydropeaking research and disturbance ecology by reviewing the impacts of altered flow frequency and duration on aquatic habitats across different spatial scales. We characterize habitats by their temporal persistency and apply novel metrics to quantify flow regime alterations. We conclude that (i) a time series approach is needed to fully capture ecological effects due to the multi-event nature of hydropeaking, (ii) additional metrics are required to quantify the temporal shifts of habitats on the spatio-temporal scale that is relevant for the organisms under consideration (i.e. patch scale) and that (iii) strategies aiming at enhancing the ecological resilience of regulated rivers require managers to actively account for habitat heterogeneity, patchiness and their dynamics.

Keywords : Flow alteration; heterogeneity; shifting habitat mosaic; organism perception; landscape metrics

3.2. Introduction

The flow regime is a fundamental control modulating and maintaining fluvial hydromorphological and biological processes through space and time (e.g. Kennedy et al. 2016, Palmer and Ruhi 2019, Poff et al. 1997, Polvi et al. 2020). Flow regime components (see definitions in Box 1) such as magnitude, frequency, relative duration, timing and rate of change (Poff et al. 1997) affect the abiotic and biotic structure and functioning of fluvial ecosystems. Habitat properties as well as their diversity, arrangement and dynamics are largely driven by the interaction of the flow regime with river reach morphology (e.g. Frissell et al. 1986, Stanford et al. 2005, Tockner et al. 2000). Accordingly, habitats can be regarded as having a spatial and a temporal dimension, with temporal dynamics mainly being driven by flow variations and spatial heterogeneity resulting from the geomorphic diversity of a river reach (e.g. fluvial landform arrangement). Organisms have evolved and adapted their life history to the local habitat dynamics over millennia (e.g. Miller et al. 2020, Poff et al. 1997) and developed strategies to deal with natural disturbances and seasonal changes in spatio-temporal habitat arrangement and availability (e.g. Hitchman et al. 2018, Winemiller et al. 2010).

Over the past century flow regimes have been increasingly affected by direct human water exploitation such as hydropower production (e.g. Kennedy et al. 2016, Lange et al. 2019, Poff and Schmidt 2016, Schmitt et al. 2018). Nilsson et al. (2005) calculated that dams regulate the flow regime of 83% of the 292 world's largest rivers (31% strong regulation; 52% moderate). In addition, a predicted increase in global hydropower capacity of 73% over the next few decades is expected to decrease the number of free-flowing large rivers from 120 to 25 (Zarfl et al. 2015). Given the rapid development of volatile renewable energy sources (wind and solar), on-demand or intermittent hydropower production (as opposed to continuous run-of-river production) is expected to increase to assure power system stability (e.g. Kougiyas et al. 2019).

When water stored in a reservoir is returned to the river for on-demand hydropower production, a hydropeaking reach is formed that is characterized by rapid and frequent sub-daily flow fluctuations (e.g. Bruder et al. 2016). Peak flows can easily be ten times higher than the daily minimum flow (e.g. Premstaller et al. 2017, Tonolla et al. 2017) and peak frequency two orders of magnitude larger than in natural systems (Archer and Newson 2002, Greimel et al. 2016). Depending on river reach morphology, changes in flow and water levels due to hydropeaking alter habitat dynamics by creating artificial dewatering zones or inducing rapid

changes of local habitat conditions (Holzapfel et al. 2017, Parasiewicz 2008, Person 2013, Schneider et al. 2017, Vanzo et al. 2016). Most native organisms are not capable of adapting to such pronounced dynamics (Palmer and Ruhi 2019), and impacts have been shown to affect the structure, abundance and diversity of aquatic invertebrates (Kennedy et al. 2016), fish (Wegscheider et al. 2020) and riparian vegetation (Bejarano et al. 2020b), as well as the overall food web structure (Holzapfel et al. 2017). In addition, hydropeaking can impact sediment distribution and mobility (Vericat et al. 2020), water turbidity (Hauer et al. 2019), water temperature (Vanzo et al. 2016), water gas saturation (Pulg et al. 2016) and river soundscape (Lumsdon et al. 2018).

Understanding the spatio-temporal link between flow-induced alterations on habitat dynamics and the structuring and functioning of ecological communities is fundamental to developing sustainable and effective management strategies for the conservation and restoration of fluvial systems worldwide (Frissell et al. 1986, Newson and Newson 2000, Palmer and Ruhi 2019, Stanford et al. 2005). Several approaches have therefore been proposed to assess sub-daily flow alterations (for a recent review, see Bejarano et al. 2020a) and modelling has been used to derive reach habitat distribution at base and peak flow (i.e. flow magnitude) in order to assess impacts of hydropeaking on habitat availability (e.g. Holzapfel et al. 2017, Person 2013, Schneider et al. 2017). These approaches have found their way into application and are progressively used to develop mitigation measures as required by several legal frameworks worldwide (for a recent review, see Moreira et al. 2019).

Hydropeaking, however, not only changes flow magnitude but also significantly affects flow frequency and relative duration (see example in Figure II.3.1). In natural systems, a correlation between flow frequency and magnitude can be observed (Biggs et al. 2005). Following flow regulation, flood magnitude can, however, become almost decoupled from frequency as examples for the Maggia River in Switzerland (Perona et al. 2009), the Ume River in Sweden (Widén et al. 2021) and the Coalburn catchment in the UK (Archer and Newson 2002) show. In addition, repeated sub-daily hydropeaking can increase flow frequency and decrease relative duration (Archer and Newson 2002, Clausen and Biggs 1997).

Evidence from disturbance ecology shows that flow frequency and relative duration significantly matter for the abiotic and biotic integrity of fluvial ecosystems (Chanut et al. 2019, Halleraker 2001, Robinson 2012), especially when the alterations propagate to the habitats at reach (Freeman et al. 2001, Parasiewicz 2008) and patch scale (Beisel et al. 2000, Bowen et al.

1998, Miller et al. 2020, Palmer et al. 2000, Winemiller et al. 2010). Consequently, approaches comparing reach-scale habitat availability at base and peak flow neglect (i) the importance of the temporal dynamics within a single event, i.e. between the two flow extremes; (ii) the hierarchical temporal complexity inherent in hydropeaking regimes, with single events being nested within a time series (or trajectory) of multiple events (*sensu* Ryo et al. 2019); and (iii) the scale-dependency of effects on, for instance, habitats ranging from reach- to patch-scale.

In this article, we review how alterations in temporal flow regime components (i.e. frequency and relative duration) propagate down to the habitat dynamics on different spatial scales (i.e. reach- to patch scale) and suggest new avenues for such quantification for research and application, with special emphasis on the patch-scale. We focus on hydropeaking since this has a major anthropogenic impact on the two temporal components of the flow regime (Harby and Noack 2013). However, the concepts discussed here can easily be transferred or adapted to other types of flow regime alterations (e.g. residual flow), their management (e.g. e-flows) as well as to other kind of regimes (e.g. temperature, sediment transport, ice).

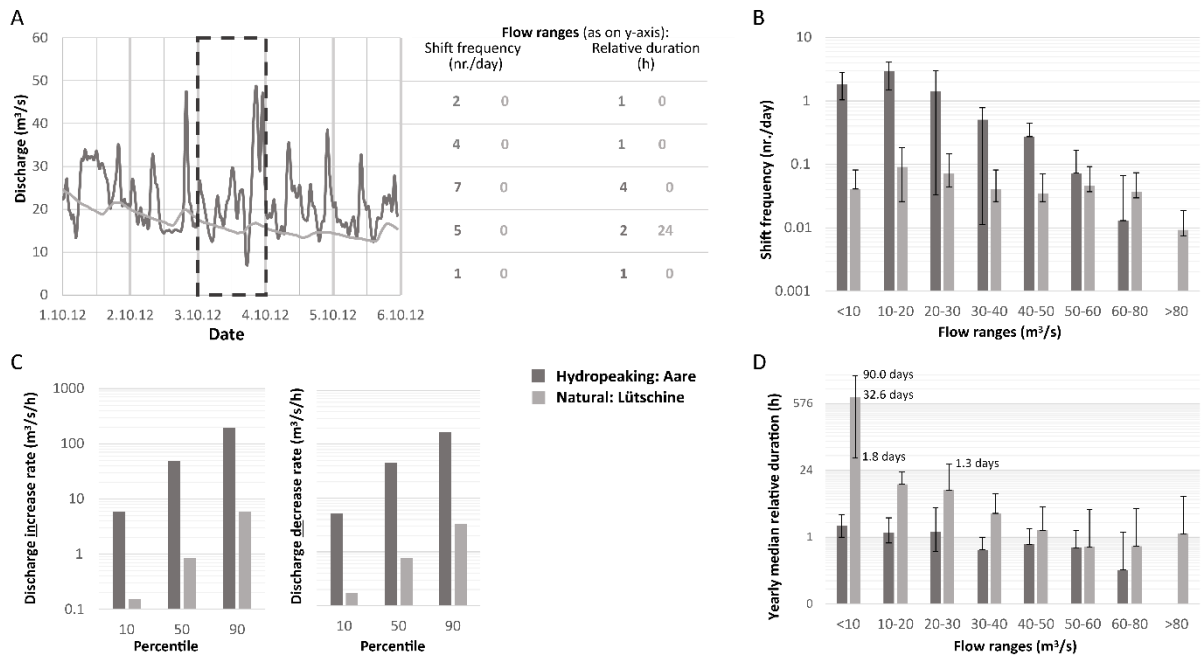


Figure II.3.1. Comparison of two neighboring mountain rivers in Switzerland, with the Aare being affected by hydropeaking (station 2019; FOEN 2020), whereas hydrological alterations for the Lüttschine can be neglected (station 2109; FOEN 2020). Both catchments are comparable in glacier surface, altitudinal gradient and climatic/weather conditions (see Tonolla et al. 2017). For a more direct comparison, flows of the Lüttschine have been multiplied by a factor of 1.46, corresponding to the size ratio between the two catchments. A shows the hydrographs for Aare and Lüttschine for a few exemplary days in October 2012 and the regime components (table) calculated for a 24h window (dashed line) for five flow ranges, each equaling $10\text{m}^3/\text{s}$ (see y-axis). Frequency represents the number of time flow switches into a given flow range. Relative duration reflects the average duration of the flow in a specific flow range (see also definitions in Box 1). B, C and D compare three regime components (frequency, rate of change, relative duration) averaged over five successive winters (Dec.-Feb. for the years 2012-2017). The whiskers indicate the maximum and minimum, respectively, during the period analyzed. Note the logarithmic scale of the y-axis. Hydropeaking frequency is up to two orders of magnitude higher than flow frequency in the natural regime (B). Relative duration (D) is negatively related to frequency, with low flows showing high relative durations under natural regime as compared to hydropeaking. Note also the high interannual variation for the relative duration for flow class $<10\text{ m}^3/\text{s}$, ranging from stable flows over 90 consecutive days (= the entire winter) for the natural regime to 1,8 days in the hydropeaking regime. Moreover, the rate of change appears to be two orders of magnitude higher under hydropeaking than for the natural regime.

3.3. Habitat shifts at the reach scale

Near-natural river reaches are characterized by a high diversity of hydraulic and geomorphic conditions forming a diverse mosaic of habitats within the reach (Newson and Newson 2000, Stanford et al. 2005; see definition in Box 1). Morphological structures such as boulders or instream wood can locally buffer and/or intensify hydraulic conditions (e.g. Yarnell et al. 2006). A diverse environment offers a high diversity of niches for different organism groups, species and life stages (Tews et al. 2004) and has been shown to affect demographic processes such as birth, death, immigration or emigration (Lowe et al. 2006) due to spatio-temporal variation in ambient characteristics, resource availability or biotic interactions (e.g. competition, predation; Hitchman et al. 2018).

The habitat mosaic in rivers shifts (Stanford et al. 2005) meaning that the spatial distribution of habitats is changing over time. Traditionally, the shifting habitat mosaic concept has been used to represent absolute shifts in the spatial positions of habitat following flood-induced geomorphic changes caused by erosion and deposition processes. For instance, sediment movement frequency proved to be a major determinant in benthic community development (ASCE 1992). The flood-induced shifting habitat mosaic also contributes to resilience and diversity within a river ecosystem. For instance, the provision of diverse refugia for differential use by various species and functional groups is a major factor for survival and recolonization following disturbance (Lake 2000, Winemiller et al. 2010).

However, shifts can also represent temporary fluctuations as they occur during smaller non-morphogenic floods (or “flow pulses” *sensu*, Tockner et al. 2000), when the hydraulic conditions fluctuate back and forth without major geomorphic adjustments. These temporary shifts are habitat specific, with different habitat types responding differently to change (Palmer et al. 2000, Weber et al. 2013, Winemiller et al. 2010) as a function of their lateral and vertical connectivity (Chanut et al. 2019, Tockner et al. 2000). Lancaster and Hildrew (1993), for instance, identified patches exhibiting low shear stress and current velocity independently of flow variation, while other habitat patches with the same initial hydraulic conditions experienced increased shear stress with increasing flow. Consequently, a river reach can be seen as a continuously shifting mosaic of habitats that follows fluctuations in flow, be they floods or flow pulses. Hydropeaking has influenced the shifting habitat mosaic by significantly accelerating shift frequency and reducing the relative duration between the shifts (Archer and Newson 2002, Clausen and Biggs 1997).

Each shift in the habitat mosaic caused by flow fluctuation is associated with a shift in habitat availability at the reach scale (see definitions in Box 1). Since each species or life stage requires a particular set of habitat conditions for e.g. resting, feeding or reproduction, the availability of suitable habitats directly affects individual fitness (e.g. reproductive success; Hitchman et al. 2018). For instance, the temporal availability of suitable habitats at reach scale was correlated with fish species abundance at a given life stage (e.g. juvenile or adult; Stalnaker et al. 1996). Flow managers therefore often use the relationships between habitat availability and flow to maximize reach scale habitat availability for a given target fish species (Boavida et al. 2015, Capra et al. 1995, Parasiewicz 2008). Freeman et al. (2001) showed, however, that the temporal persistency in habitat availability for a reach of the hydropeaking-impacted Tallapoosa River (US) was more important for ensuring an abundance of juvenile fish (all species) than the median habitat availability. Similarly, Hedger et al. (2018) showed via modelling that stranding-induced mortality (i.e. rapidly dewatered habitats) of juvenile Atlantic salmon during a single hydropeaking event can be buffered by natural populations dynamics, a process that is ineffective in the case of frequent hydropeaking (i.e. frequent mosaic shifts). Similarly, the persistency of spawning grounds and shallow habitats for the early life stages of fish at the reach scale have been shown to have a positive effect on the population size (Bowen et al. 1998). For invertebrates, the first hydropeaking event after a longer period without hydropeaking (i.e. period with high persistency) caused pronounced drift rates whereas the impacts of subsequent daily hydropeaking events were lower (Bruno et al. 2016, Irvine 1985).

To summarize, the high frequency and low relative duration of hydropeaking events affects the number of shifts and the related persistency of available habitats at the reach scale, particularly by creating potential habitat bottlenecks (i.e. limited temporal availability of key habitats; Bowen et al. 1998). Long lasting habitat bottlenecks can affect population size (Stalnaker et al. 1996). It is therefore expected that a small number of large daily flow shifts and associated habitat shifts at the reach scale are less detrimental to the fish community than a large number of smaller shifts (Senay et al. 2017). However, the cumulative indirect effects on survival and reproduction and their propagation to the population level are difficult to capture (Judes et al. 2021).

Box 1: Glossary

Flow regime components are driven by river size and catchment characteristics such as climate, geology, topography and land cover (Poff et al. 1997):

Magnitude: represents a simple measure (e.g. min, max, difference) of flow for a given time interval (Poff et al. 1997).

Rate of change or flashiness: defines how quickly flow changes over time (Poff et al. 1997).

Frequency: can be expressed as the flood return period (Poff et al. 1997). For flow regulation like hydropeaking, a definition based on the number of times flow changes into a given flow magnitude class (e.g. Archer and Newson 2002) seems more appropriate.

Relative duration: is defined relative to a particular flow event (e.g. “a floodplain may be inundated for a specific number of days by a ten-year flood” Poff et al. 1997) and is opposed to the more commonly used cumulative duration which aggregates flows over a defined time interval (e.g. “the number of days in a year when flow exceeds some value” Poff et al. 1997).

Timing or predictability: refers to the regularity with which flows of a given magnitude occur on different time scales (Poff et al. 1997).

Habitat: corresponds to particular ambient conditions typically defined and aggregated on various spatial scales by means of dominant physico-chemical environmental characteristics (e.g. Newson and Newson 2000). Each species and life cycle stage requires a certain array of habitats to satisfy needs such as nutrition, reproduction, resting or refuge (e.g. Hitchman et al. 2018).

Habit mosaic: comprises a spatial arrangement of habitat types and is commonly defined at the reach scale (Stanford et al. 2005). The diversity of habitats found within a mosaic is river-type specific – different river types and watersheds lead to different habitat mosaics (Brennan et al. 2019) depending on the various drivers operating on different scales (Polvi et al. 2020).

Reach: defines a river section that is delimited by breaks in channel slope, valley floor width and side-slopes, riparian vegetation and bank material (Frissell et al. 1986).

Patch: is defined as any geographically fixed area (Pickett and Rogers 1997); we consider patch sizes ranging between 0-100m², with the appropriate scale depending on the species

and age class studied and their respective mobility (Pringle et al. 1988, Winemiller et al. 2010).

Shift: a shift occurs when environmental characteristics change at different scale in space and/or time (Stanford et al. 2005). Different types of shifts can be distinguished:

Shift in habitat availability at the reach scale: changes of total or relative habitat area within a reach.

Spatial shifts of habitats: spatial movement of particular habitat types in time.

Habitat shifts within patches: changes in habitat type within a patch in time.

Persistency: as opposed to shifts, persistency defines stable habitat characteristics in space and time on different scales:

Persistency of habitat availability at the reach scale: refers to the temporal persistency of a sufficient quantity of a habitat type within a reach (see Bovee 1982, Bowen et al. 1998). The higher the persistency at the reach scale, the lower the number of shifts in habitat availability.

Patch persistency: refers to the temporal persistency of a habitat type within a patch. The higher the patch persistency, the lower the number of habitat shifts within the patch.

3.4. Habitat shifts at the patch scale

Flow variation not only causes shifts in habitat availability at the reach scale, but also influences the spatial arrangement of single habitats at the patch scale. As organisms perceive and respond to the habitat conditions immediately surrounding them, habitat dynamics at the patch scale can have a strong filtering effect on ecological processes (Hitchman et al. 2018, Pringle et al. 1988). In a river with a natural flow regime, habitats and related patches are typically defined based on dominant ambient conditions (e.g. dominant current velocity) since conditions stay fairly constant over a day, week or season, with floods often regarded as a punctual disturbance (e.g. Lake 2000, Tockner et al. 2000). In contrast, the flow in hydropeaking rivers varies so frequently and rapidly (Figure II.3.1) that the assumption of a patch matching typical or dominant ambient conditions (e.g. Newson and Newson 2000) does not hold anymore, therefore a decoupling of the geographically defined patch from physically defined dominant habitat properties must be presumed. It follows that shifts in hydropeaking rivers can be looked at either from the perspective of a single patch (habitat shifts within patches) or from the perspective of a given habitat type (spatial shifts of habitats; see also definitions in Box 1). Figure II.3.2 conceptualizes both types of shifts. The decision as to which

perspective to take depends on the species studied and the traits of the related life cycle stage (Turner et al. 2015, Winemiller et al. 2010).

Habitat shifts within patches represent the conditions that an organism in its respective life cycle stage would perceive if persisting in a patch (see also example in Box 2). This perspective is therefore strictly connected to patch persistency (see definitions in Box 1). Egg laying organisms such as macroinvertebrates and fish require specific conditions at reproduction sites for successful hatching and survival in the early life stages. For instance, to minimize the risk of egg-detachment from the substrate, bottom current velocity of patches used for fish spawning should not exceed 0.7 m/s (Bartoň et al. 2021). Similarly Kennedy et al. (2016) and Miller et al. (2020) showed that egg viability of macroinvertebrates is reduced by 80-98% if patches are dewatered for more than one consecutive hour (shown for *Baetis*, *Brachycentrus occidentalis*, *Hydropsyche occidentalis* and Chironomidae). The authors therefore conclude that the egg life stage represents a bottleneck in the life cycle that requires particular attention in hydropeaking mitigation. Moreover, the feeding efficiency of sessile filter-feeding macroinvertebrates (e.g. Simuliidae and Hydropsychidae) can be reduced by changes in flow conditions since filtering is optimized for a particular range of current velocities (Brooks and Haeusler 2016). For Chinook salmon larvae (*Oncorhynchus tshawytscha*), it has been shown that dewatering of patches should not last for more than 1 hour to avoid mortal stranding (Becker et al. 1982). Drift of salmonid larvae can be prevented when current velocities do not exceed 0.10-0.25 m/s (Heggenes and Traaen 1988). The frequency of inundation of a patch also influences plant response. Particularly the duration of peaking appears to impact the germination of sensitive plant species (Bejarano et al. 2020b).

A focus on the spatial shifts of habitats allows the perspective of a mobile organism that can follow its preferences for particular ambient conditions to be taken (see also example in Box 2). Some species and life stages have a limited range of mobility (i.e. most invertebrates and juvenile fish), but are able to follow habitat shifts when individual moving capacity equals or exceeds the rate of change in habitat conditions. If this requirement is not fulfilled, suitable habitats, although available at the reach scale, are not accessible. Kjærstad et al. (2018) found in the River Bævra (Norway) that it took 48 days for Chironomids and the mayfly *Baetis rhodani* to recolonize the dewatered zone after hydropeaking. Similarly, Gore (1985) calculated a recolonization lag of at least 75 days for every 200m from the upstream invertebrate drift source after disturbance in the Tongue River (US). Blinn et al. (1995) found that in the Colorado

River (US) the macroinvertebrate biomass in the permanently submerged area was four times larger than in the dewatering zone. Winemiller et al. (2010) state that in a resilient system the dispersal rate of species between patches should be significantly higher than the rate of patch disturbance, giving some indications of how to identify potential thresholds of anthropogenic disturbance. The authors stress, however, the importance of disturbance on the scale of the single patch as this allows competitively inferior species to colonize patches that would otherwise be dominated by more competitive species (i.e. intermediate disturbance concept).

The spatio-temporal habitat dynamics at patch scale may also affect highly mobile organisms such as adult fish, for which habitat availability is usually calculated at the reach scale. When facing changing habitat conditions, highly mobile organisms can choose to stay in a given patch or to seek preferred habitat conditions, immediately or at some point in time, when for instance a critical threshold is exceeded. The choice of moving or staying is associated with costs, such as the risk of predation, loss of energy, the abandonment of feeding territory or physical damage requiring some macroinvertebrate species to repair or rebuild their cases (Korman and Campana 2009). There are differences in the willingness to move, with some fish individuals being reluctant to change position when flow varies (e.g. Kemp et al. 2003, Korman and Campana 2009). Staying in a non-ideal patch may cause energy losses due to withstanding the current or due to a decrease in energy intake resulting from reduced feeding efficiency (Lagarrigue et al. 2002). The energetic costs of moving may as well be difficult to cover for some organisms during certain seasons as, for instance, fish metabolism slows down during winter and swimming capacity is considerably reduced to save energy (Cunjak et al. 1998). For fish, the decision to move therefore depends on the (1) frequency of habitat shift, (2) how much habitat conditions deviate from the optimal conditions, (3) the proximity to alternative habitats and (4) the relative duration of the unsuitable habitat condition (Capra et al. 2017). This lead Capra et al. (2017) to the assumption that fish may opt for a “least constraining” habitat selection by preferentially using patches with the lowest temporal habitat variation. This certainly explains why Geist et al. (2008) found that sturgeons (*Acipenser transmontanus*) occupy habitats where current velocities remain relatively constant independent of the flow. In hydropeaking reaches, such habitats are most probably found between the dewatering zone and the midstream where current velocities are generally too high. The spatio-temporal habitat dynamics also affect intra- and interspecific relationships (Puffer et al. 2017) and may propagate to the entire food web. For instance, patches with high habitat shifts may show low

macroinvertebrate availability, therefore affecting the food availability for fish using these patches (Holzapfel et al. 2017).

Summarizing, the patch scale allows the mechanisms behind the shifting habitat mosaic to be captured by assessing how the interactions between patches affect the behavior of organisms and their life cycle strategies (Hitchman et al. 2018).

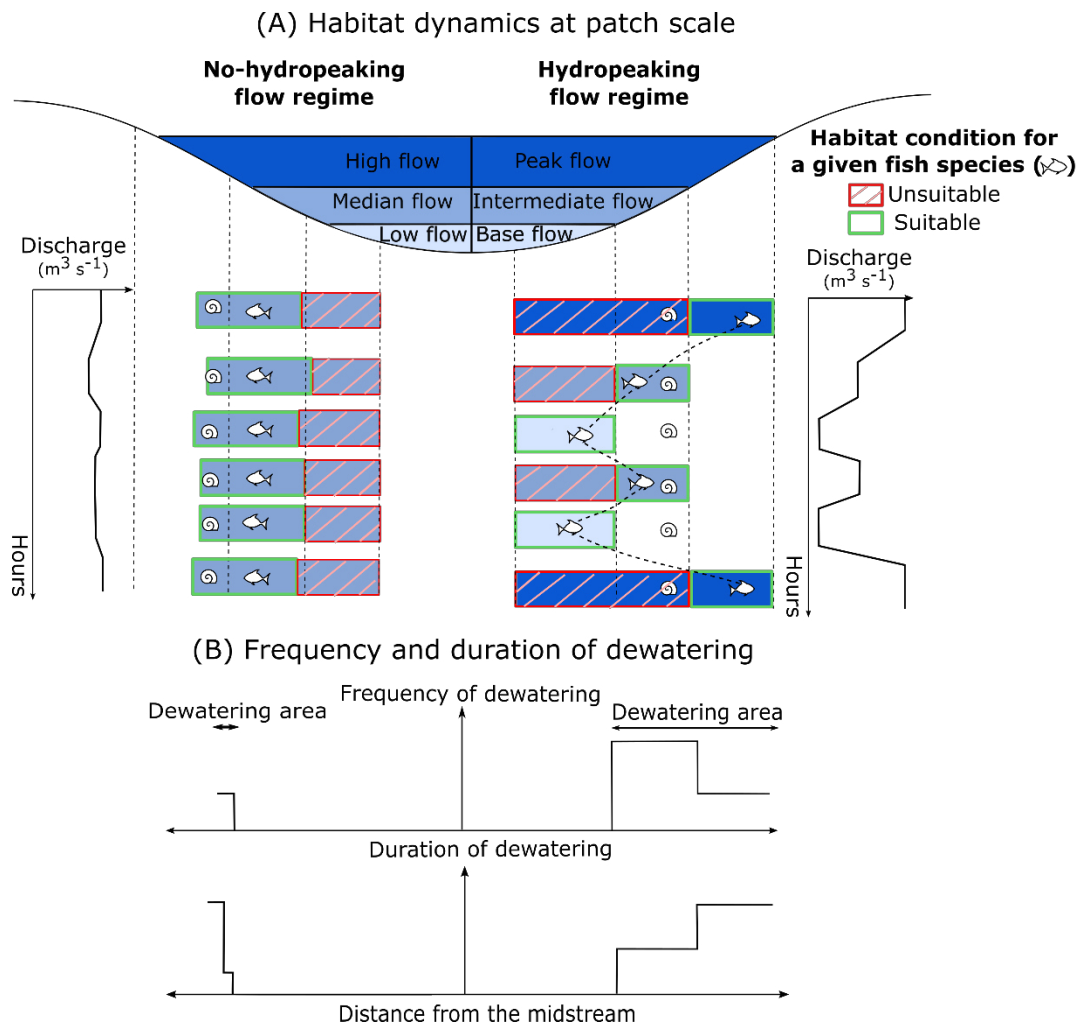


Figure II.3.2. (A) shows the habitat dynamics at the patch scale considering a typical day or week for a river section with a natural versus hydropeaking flow regime and (B) the related frequency and relative duration of dewatering. Invertebrates (⊙) have a low range of mobility. Under hydropeaking, invertebrates are affected by habitat shifts within patches, leading to e.g. dewatering and desiccation. The high frequency and low relative duration of dewatering strongly influences the spatial presence of low-mobile organisms. Fish (↔) are able to follow changing habitat conditions. Under hydropeaking, frequent spatial shifts of habitats force fish to change their position (i.e. the patch). Potential stranding may, among other impacts be controlled by the rate of change of dewatering at the patch scale, which is defined as spatial shifts of habitats over time.

Box 2: Example of habitat dynamics at the patch scale

The example presented here is based on a channelized reach of the Aare River in Switzerland (for details on the study site, see Tonolla et al. 2017 and Person 2013). The methodology consists of an adaptation of the analysis by Capra et al. (1995) to the patch-scale using hydraulic modelling to develop relationships between habitat metrics and flow characteristics. These metric-flow relationships are then applied to a flow time-series (same as in Figure II.3.1), which results in a time-series for each individual metric applied. The metric-specific time-series are used to assess how hydropeaking-induced alteration in flow frequency and relative duration affect habitat dynamics at the patch scale.

Metrics for habitat shifts within patches (see Box 1 for definition)

- Spatio-temporal habitat dominance is equal to the sum of the sizes of each habitat type in the patch over time. The metric expresses the average absolute size or average relative proportion of each habitat type in the patch (in our example reference size at base flow $Q=5\text{m}^3/\text{s}$) and represents the habitat conditions an organism would perceive most frequently.
- Shift index is inspired by the flashiness index of Baker et al. (2004) and represents the sum of size-changes for each habitat type divided by the patch size at base flow (in our example $Q=5\text{m}^3/\text{s}$) and by the length of the study period. The metric captures how often an organism perceives changes in habitat conditions.

Metrics for spatial shifts of habitats (see Box 1 for definition)

- Habitat expansion-contraction represents the size of a given habitat type at the patch scale for a given flow over time. The metric is expressed in terms of absolute surface and reflects the available space an organism has in a particular habitat at time t .
- Habitat displacement quantifies the distance between the centroid of the habitat of a given type at base flow and the centroid of the most proximate habitat of the same type at a given flow. The metric represents the distance an organism would have to travel when following particular habitat conditions.

Figure II.3.3 shows the modelling results, marking the positions of two exemplary patches (nr. 10 and 20) and the displacement of the associated habitat conditions (habitat type 1 and 2, respectively) when increasing the flow from base to peak-flow.

Figure II.3.4 illustrates the habitat shifts within patches for a few exemplary days in October 2012. Results for six consecutive winters (2012-2017) are then summarized in Table II.3.1. Both patches 10 and 20 show a wide range of spatio-temporal habitat dominance under hydropeaking flow while a clear dominance for habitat type 1 and 2, respectively, can be observed for the natural regime. The shift index under hydropeaking scores highest for patch 10 and reaches intermediate values for patch 20, while under natural flow both patches achieve comparatively low values.

Figure II.3.5 illustrates the spatial shifts of habitats for the same period in October as shown in Figure II.3.4. Summarizing the results from six consecutive winters in Table II.3.2, the difference between the two regimes is striking; for instance, the habitat is displaced with a rate of change of two orders of magnitude higher as compared to the natural regime.

Similar patterns can be observed for the expansion-contraction of habitat type 1 in patch 10. The example highlights the importance of considering the patch scale in hydropeaking analysis and assessment. Natural patch dynamics may, however, change in season. During snow/glacier melt or thunderstorms, the natural regime might show higher dynamics.

Although strong evidence exists (see text), the ecological implications of altered patch scale dynamics on e.g. ecological thresholds, tipping points and resilience when compared to natural regime dynamics have not yet been well defined and further investigations are critical for the development of more effective mitigation measures (see conclusions).

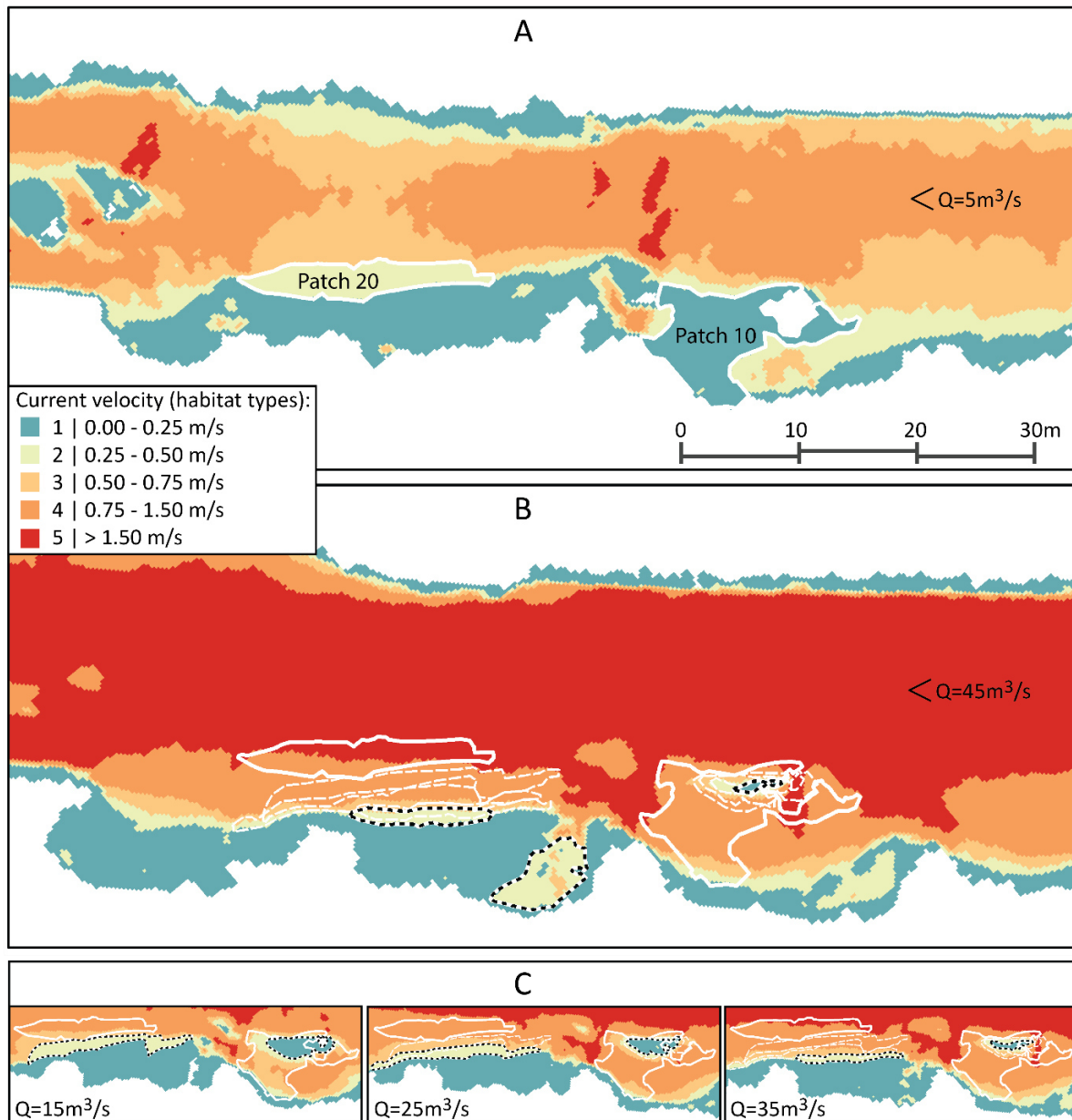


Figure II.3.3. Results from a 2D model and classification in five simple habitat types (current velocity classes) for a channelized, hydropeaking-affected reach with artificial groynes in the Aare River close to Innertkirchen in Switzerland. A: Habitat distribution at low flow ($5\text{ m}^3/\text{s}$), with two reference patches marked with the white line. Patch 10 is dominated by habitat type 1 and patch 20 is dominated by habitat type 2. B: Habitat distribution at peak flow ($45\text{ m}^3/\text{s}$), with the most proximate positions of habitat types 1 (for patch 10) and 2 (for patch 20) marked with a black and white dotted line and their trajectory from the original patches (white line) at base flow with a fine dotted white line. C: Shows the intermediate steps between A and B. Note that with increasing flow habitat type 1 contracts within patch 10, while habitat type 2 is displaced from patch 20 towards the margins.

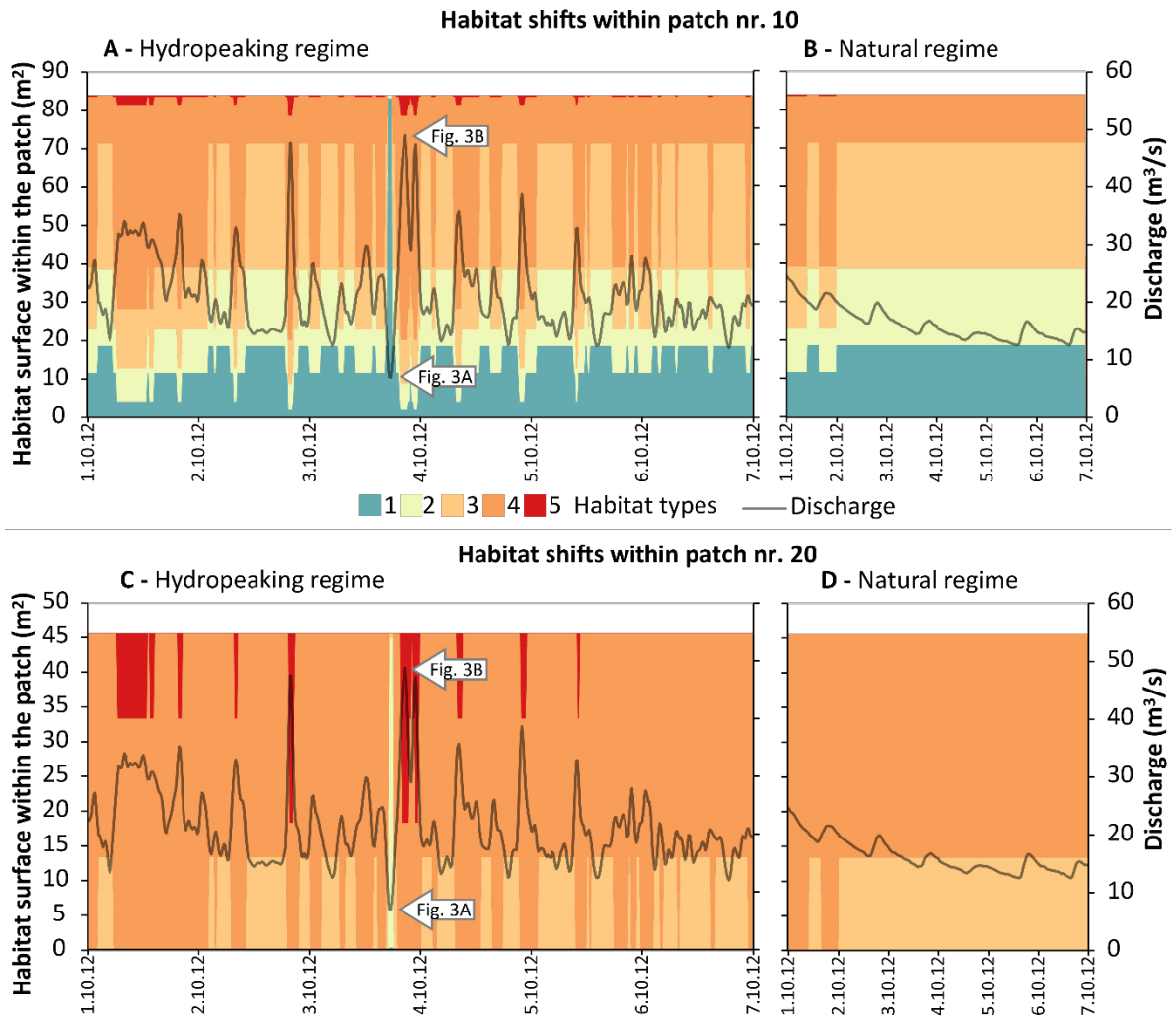


Figure II.3.4. Comparisons of habitat shifts within patches between hydropeaking and natural regime during a few exemplary days in autumn 2012 for patch 10 (A-B) and patch 20 (C-D). The coloring of the habitat types corresponds to the one described in Figure II.3.3. The grey line shows the flow over the defined period. The arrows indicate the timing of the situation as shown in Figure II.3.3. Although the proportions (i.e. magnitudes) of the different habitat types over the entire week are comparable between the two regimes, shifts under hydropeaking are much more frequent.

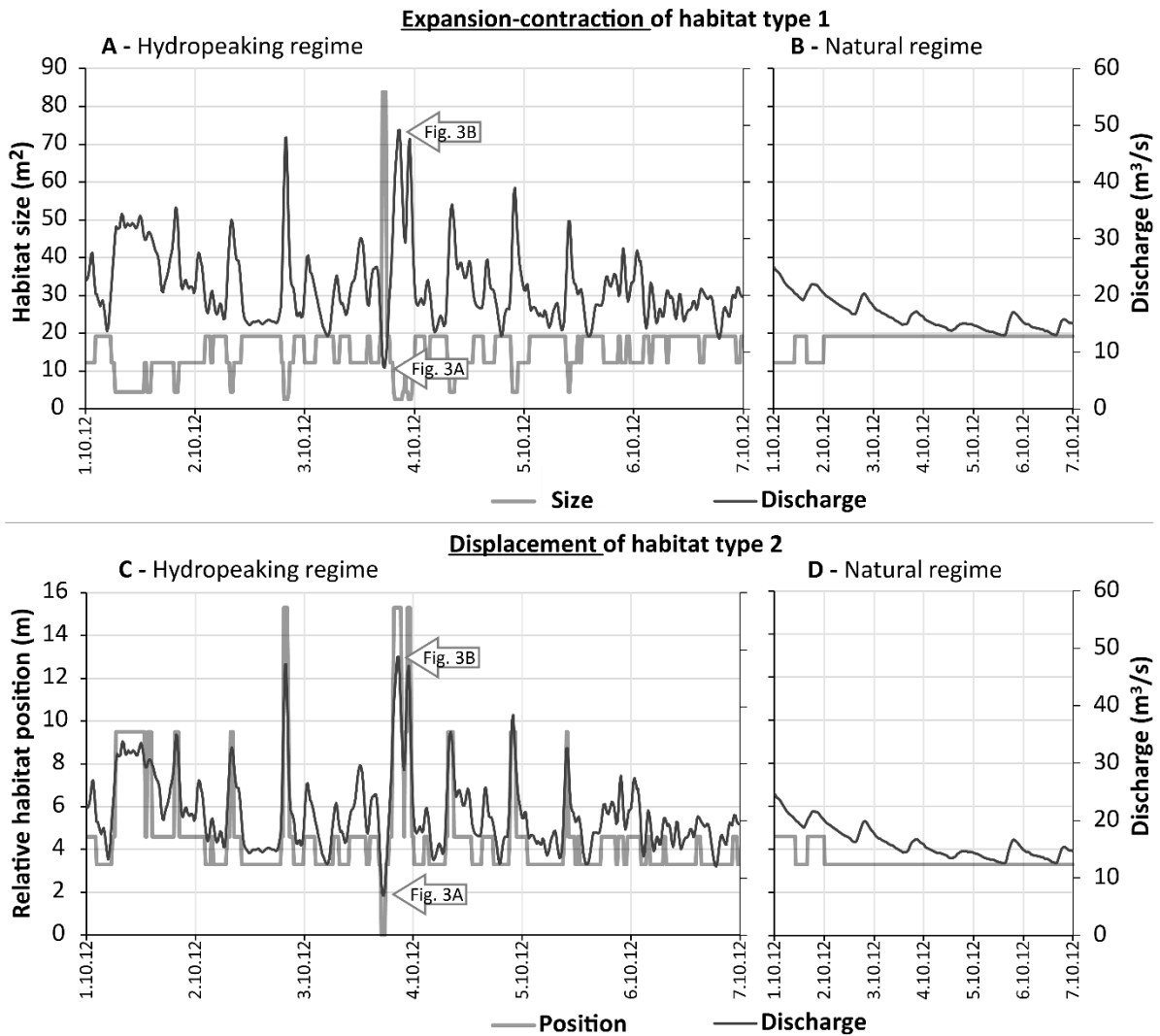


Figure II.3. 5. Comparisons of spatial shifts of habitats between hydropeaking and natural regime during a few exemplary days in autumn 2012. A-B habitat expansion-contraction of habitat type 1 (patch 10 in Figure II.3.3A). C-D displacement of the habitat type 2 relative to the position at Q5 (patch 20 in Figure II.3.3A). The grey line shows the flow over the defined period. The arrows indicate the timing of the situation as shown in Figure II.3.3. Note how much both metrics fluctuate under hydropeaking as compared to the natural regime.

Table II.3.1. Summary statistics for the habitat shifts within patches for hydropeaking and natural regime over the entire winter season (Dec.-Feb.) for six consecutive years (2012-2017; see also Figure II.3.1 and Figure II.3.4). The number indicates the average, with shading intensity reflecting increasing dominance or shift indices, respectively. In brackets, the minimum and maximum for the period are plotted to give an indication of interannual variation.

Habitat type	Habitat shifts for patch nr. 10				Habitat shifts for patch nr. 20			
	Dominance (%)		Shift index (%/h)		Dominance (%)		Shift index (%/h)	
	Hydrop.	Natural	Hydrop.	Natural	Hydrop.	Natural	Hydrop.	Natural
1	53.1% (+27.6/-22.4)	89.4% (+9.7/-16.7)	14.6% (+6.3/-4.0)	0.4% (+0.2/-0.3)	0.3% (+0.3/-0.2)	0.7% (+0.1/-0.2)	0.0% (+0.0/-0.0)	0.0% (+0.0/-0.0)
2	12.4% (+5.4/-6.1)	3.4% (+3.9/-2.5)	4.6% (+1.5/-1.7)	0.1% (+0.1/-0.1)	41.5% (+33.1/-27.4)	85.8% (+12.0/-20.2)	1.1% (+0.8/-0.6)	0.0% (+0.1/-0.0)
3	19.6% (+9.0/-10.4)	4.3% (+6.7/-4.3)	8.0% (+2.5/-3.1)	0.2% (+0.2/-0.2)	13.3% (+4.9/-5.5)	4.1% (+3.9/-2.7)	0.5% (+0.3/-0.2)	0.0% (+0.0/-0.0)
4	14.6% (+8.0/-10.8)	2.8% (+5.9/-2.8)	6.3% (+3.6/-4.4)	0.1% (+0.2/-0.1)	42.7% (+22.6/-25.7)	9.0% (+15.0/-9.0)	1.2% (+0.5/-0.4)	0.0% (+0.1/-0.0)
5	0.3% (+0.2/-0.3)	0.1% (+0.2/-0.0)	0.2% (+0.1/-0.2)	0.0% (+0.0/-0.0)	2.2% (+2.0/-2.1)	0.4% (+1.5/-0.4)	0.2% (+0.3/-0.2)	0.0% (+0.0/-0.0)

Table II.3.2. Summary statistics for the comparisons of spatial shifts of habitats between hydropeaking and natural regime for the entire winter season (Dec.-Feb.) for six consecutive years (2012-2017; see also Figure II.3.1 and Figure II.3.3). The number indicates the average, whereas the minimum and maximum for the period are given in brackets as an indication of interannual variation.

	Expansion-contraction of habitat type 1		Displacement of habitat type 2	
	Hydropeaking	Natural	Hydropeaking	Natural
Rate of change	294.8 m ² /day (+127.7/-81.2)	8.4 m ² /day (+5.7/-7.5)	15.5 m/day (+7.0/-4.8)	0.4 m/day (+0.2/-0.4)
Frequency	8.1 nr./day (+2.3/-4.6)	0.2 nr./day (+0.3/-0.2)	4.7 nr./day (+2.2/-1.6)	0.1 nr./day (+0.1/-0.1)
Relative duration	1.0 h (+0.3/-0.2)	6.1 days (+29.9/-6)	1.5 h (+0.9/-0.5)	15.7 days (+74.3/-15.4)

3.5. Challenges for patch-scale metrics

Most studies use the magnitude of a single hydropeaking event to quantify ecological impacts (e.g. Boavida et al. 2015, García et al. 2011, Holzapfel et al. 2017, Person 2013, Premstaller et al. 2017, Schneider et al. 2017, Tonolla et al. 2017). As ecological impacts of hydropeaking are also to be expected from repeated hydropeaking (see Figure II.3.1), it is fundamental to expand the assessment to multiple peaking events (Harby and Noack 2013, Ryo et al. 2019, Wolkovich et al. 2014). Time series analysis, as suggested for the evaluation of habitat availability at the reach scale (see Bovee 1982, Capra et al. 1995, Freeman et al. 2001, Parasiewicz 2008, Spurgeon et al. 2019, Boavida et al. 2015), provides a powerful tool to evaluate alteration in frequency and relative duration at the patch scale (see example in Box 2). As indicated above, it is the patch scale that best represents the habitat conditions that are perceived and exploited by the organism, but its importance is widely ignored in science and application (Pringle et al. 1988).

As proposed in our example in Box 2, habitat types can be predefined and their spatially explicit arrangement (i.e. the habitat mosaic) modelled for different flow stages. The habitat distribution for different flow stages can then be used to assess the dynamics of single patches under different flow scenarios (i.e. time series of altered versus natural flow), such as the relative duration and the frequency of habitat shifts within patches (e.g. dewatering) or the drift risk for invertebrates and fish associated with high current velocities (e.g. > 1 m/s). A time series approach also allows the patch-specific rates of change to be evaluated and hence to account for the species and their life stage specific moving capacity.

Methods are needed that integrate results retrieved from single patches into ecologically meaningful metrics at higher scales given that practical management often operates at the reach scale (Winemiller et al. 2010). Generally, metrics should be able to quantify the expected effects resulting from different management interventions and ideally be transparent, easy to calculate and simple to understand by scientists and non-scientists (Bruder et al. 2016, Pickett and Rogers 1997, Turner et al. 2015). Specifically, the chosen metrics should (i) capture the effects of altered flow regime components on ecological structures and functions of interest (e.g. particular species, life stages), (ii) consider the quality and accuracy of the available data (e.g. spatio-temporal resolution), (iii) account for the comparability of results (e.g. between different reach morphologies, catchments), (iv) avoid correlations between metrics and (v) maximize variance and range (Pringle et al. 1988, Turner et al. 2015). Moreover, summary statistics for

patch dynamics at the reach scale should not only consider the average of a metric, but also its variance (e.g. coefficient of variation, percentiles, range) given that variance is the emergent property of patch dynamics (Palmer et al. 1997, Pringle et al. 1988, Winemiller et al. 2010).

Over the past two decades landscape ecologists have explored how to quantify landscape patterns on different scales and how to relate these patterns to ecological processes (Pickett and Rogers 1997, Turner et al. 2015). This has led to a myriad of landscape metrics that can broadly be classified in addressing patch shape, size, configuration, juxtaposition, diversity and heterogeneity, density, connectivity, duration and formation (Pickett and Rogers 1997, Pringle et al. 1988, Turner et al. 2015). In aquatic ecology, landscape metrics have mostly been used for the assessment of habitat patch heterogeneity (Cooper et al. 1997, Winemiller et al. 2010). Cooper et al. (1997), for instance, experimentally proved that algae patch size and arrangement (fractal dimension) affect the density of invertebrate grazers. Beisel et al. (2000) showed that patch heterogeneity in terms of composition (number and proportion of patches) and configuration (spatial arrangement, shape, and contrasts between neighboring patches) affect invertebrate community structure in the Mortagne River, France. Similarly, Palmer et al. (2000) revealed that predictive power in the regression model for Chironomid and Copepod abundance could be significantly increased if the spatial distribution of patches (mean and standard deviation of patch size, modal patch size, perimeter-area ratio, patch shape, arrangement) was added. A field study by Hitchman et al. (2018) on the Upper Neosho River, US, indicated a relationship between fish species richness and patch type, size, number, diversity and abundance. Some further examples exist (e.g. Brown 2003, Newton et al. 2008, Yarnell et al. 2006), but the integration of landscape metrics into practical river management is still rare (e.g. Jacobson et al. 2009, Remo et al. 2013, Rohde et al. 2005).

3.6. Conclusions

In this article, we showed how hydropeaking induced alterations in the temporal flow regime components (i.e. frequency and relative duration) translate to impacts on the habitat dynamics at different spatial scales (i.e. reach to patch scale; see also Figure II.3.6). Four major conclusions can be drawn:

1. Neglected hydrological alterations: Most studies and methodological approaches have focused on the magnitude of single events, i.e. on individual hydropeaking events. Accordingly, important aspects of regime alteration emerging from frequent peaking

events, such as fundamental changes in flow frequency and relative duration, have been widely neglected in both science and practical management.

2. Mismatch in habitat scales: Most studies assessing the effects of hydropeaking assess habitat availability at the reach scale and rarely address alterations in habitat dynamics (i.e. shifts). We argue that it is the temporal dynamics at the patch scale that matters, this being the scale best representing the perception of an organism living in and moving between aquatic habitats and patches.
3. Underestimation of habitat dynamics: Habitat dynamics at the patch scale considering multiple hydropeaking events (i.e. time series) cannot be described by average habitat characteristics only. Particularly, frequent peaking causes habitat shifts within patches (= shifts of habitat type in a geographically fixed location) and spatial shifts of habitats (= spatial movement of particular ambient condition).
4. Metrics are needed: the extent to which habitat shifts within patches and/or spatial shifts of habitats need to be evaluated for impact assessment depends on the required persistency and degree of mobility of a species and its life stage. Preliminary metrics, as presented in Box 2 for both types of shifts, show differences exceeding an order of magnitude between unregulated and hydropeaking rivers. However, additional sensitive metrics need to be defined that are able to capture altered patch dynamics.

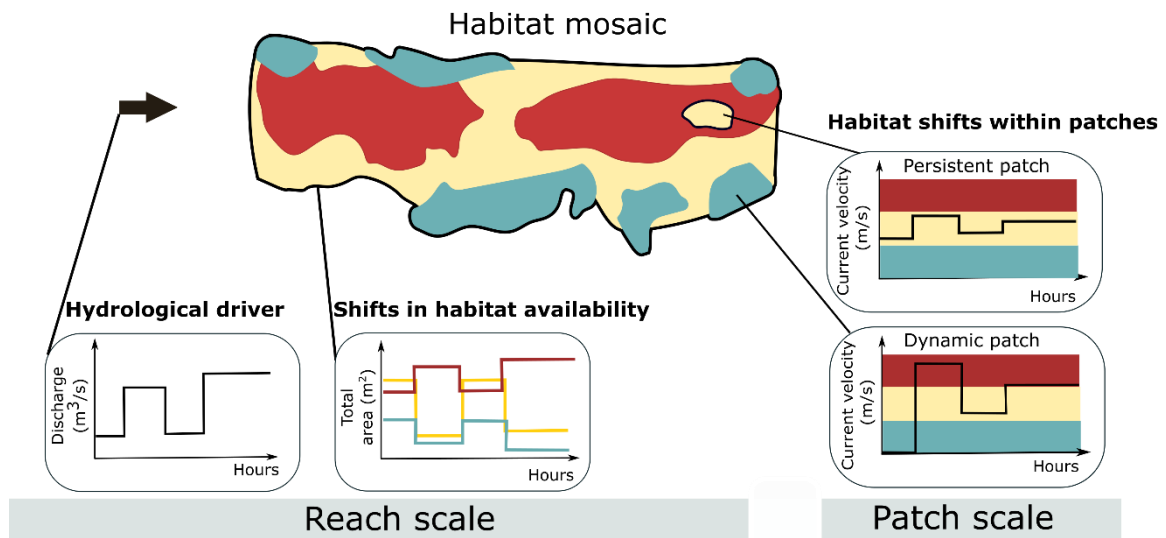


Figure II.3.6. Conceptual model summarizing the effect of altered flow regime components on the habitats at reach and patch scale.

3.7. Perspectives

The major conclusions listed above suggest several needs for action for both research and practice, which we have structured around four strongly interrelated points (see also Table II.3.3 for detailed questions):

- Assess ecological effects:** In the example (Box 2), we show that shifts at the patch scale in hydropeaking rivers can exceed those in unregulated rivers by an order of magnitude. The literature reviewed suggests that altered habitat dynamics may propagate down to the biotic level by affecting the survival of more sessile species and life stages (e.g. invertebrate eggs; Miller et al. 2020) as well as the energy budget of mobile species and life stages (e.g. adult fish; Capra et al. 2017). However, studies are needed to test how organisms react to altered dynamics (i.e. increase in shifts) at the patch scale due to anthropogenic changes in flow frequency and relative duration (i.e. multi event). Particularly empirical approaches, be they experimental or observational, are needed to understand the causal relationships of short, medium and long-term ecological responses to such alterations (see also Winemiller et al. 2010). This implies the identification of ecologically critical responses to habitat dynamics at the patch scale (e.g. persistency) and the definition of how these responses translate to the reach scale and beyond.

- Account for spatio-temporal variation: When looking at time series, the quantification of variance becomes essential (Palmer et al. 1997). Different species and life stages require different degrees of patch persistency, with requirements varying over days, weeks to seasons (i.e. low number of habitat shifts within patches during a sensitive period). On the other hand, natural disturbance at the scale of a single patch is essential to rejuvenate habitat characteristics (e.g. avoid clogging; Hauer et al. 2019) and/or to allow competitively inferior species to (re-)colonize patches otherwise dominated by more competitive species (i.e. intermediate disturbance concept; Winemiller et al. 2010). It follows that different patches (as a function of river morphology) show different habitat dynamics (e.g. persistency; Lancaster and Hildrew 1993) that may vary in time as a function of the flow regime. Approaches are needed that allow such variability to be captured and shifts for natural and hydrologically altered river systems to be compared.
- Develop management options: The patch scale allows a process-oriented approach that represents what organisms perceive when living and interacting with their environment (Pringle et al. 1988). Managers taking such a patch perspective therefore have the advantage of i) making the management goals explicit by allowing a spatio-temporal evaluation, ii) finding trade-offs for habitat requirements at the patch scale for different target species (e.g. persistency) and iii) planning of spatio-temporally explicit management schemes affecting the dynamics and structure of the habitat mosaic (Hitchman et al. 2018, Pickett and Rogers 1997, Pringle et al. 1988). Moreover, a patch scale approach will facilitate a quantitative comparison within and between river systems (Pringle et al. 1988). Although landscape ecologists have, for instance, extensive experience quantifying the shapes, sizes, configurations, diversity, density and connectivity of patches, a set of ecologically meaningful assessment metrics that can be used by river managers is missing. Research and collaborative learning (Weber et al. 2017) between research and practice is needed to develop management approaches that account for the patch scale.
- Explore transferability: We focused our article on the effects of hydropeaking since this an anthropogenic impact with significant influence on the temporal flow regime components (i.e. frequency and relative duration). However, we consider our findings to be transferable to other types of flow regime alterations. For instance, rivers affected

by residual flow may experience the opposite hydrological extremes if compared to hydropeaking (very stable *versus* very dynamic daily flows). The concepts presented here could therefore be used by managers to design more effective mitigation measures (e.g. E-flows). In addition, other regimes (e.g. temperature, sediment transport, ice) may influence habitat quality, and research is needed to assess to which extent the concepts presented here can be applied.

We are convinced that addressing the questions presented here will help promote a more comprehensive view of hydropeaking effects and lead to a management approach targeting on the resilience of impacted river systems.

Table II.3.3. Open questions for future research and practice to better account for the effects of temporal flow regime components (i.e. frequency and relative duration) on ecological processes on different spatial scales (i.e. reach to patch scale) in hydropeaking rivers.

Assess ecological effects:

- How much do spatial shifts of habitats affect the fitness of mobile species? How do habitat shifts within patches affect the fitness of sessile species?
- Do organisms adjust their behavior or physiology to compensate for altered habitat dynamics?
- Which factors trigger the movement of organisms during pulse and ramp disturbances (e.g. refuge seeking)?
- How do altered habitat dynamics affect biological interactions (e.g. intra- or interspecific competition)?
- How do arrangement and connectivity between patches affect the composition and diversity of aquatic communities?
- What functional characteristics (traits) of organisms should be considered for assessing the ecological effects of alterations in flow frequency and relative duration resulting from hydropeaking?

Account for spatio-temporal variation:

- How heterogeneous is patch persistency within a reach (i.e. patches that are naturally not persistent versus patches that are persistent)?

- Which spatio-temporal factors drive patch persistency (e.g. season, morphology, regime)? How much disturbance (with and without sediment transport) is necessary to ensure patch species abundance and diversity?

Develop management options:

- Which metrics from landscape ecology best capture the patch scale habitat dynamics for river systems? How can these metrics be used for practical river management?
- How can habitat dynamics at the patch scale be summarized and made available for reach-scale management?
- What are the minimum requirements (e.g. resolution, precision, frequency) for hydrological and morphological data in hydropeaking rivers to run time series analyses at the patch-scale?
- What measurements should be taken and what metrics be quantified for monitoring and evaluation of hydropeaking mitigation?
- From a management perspective, is it possible to increase the persistent habitat availability through small-scale morphological measures?

Explore transferability:

- Are the dynamics observed in residual flow reaches the exact inverse of those for hydropeaking rivers?
- To what extent can the concepts presented here be applied or adapted to turbidity, temperature and sound peaking caused by hydropeaking?
- Can we use the concepts presented here to assess the ecological impacts of morphogenic flows (i.e. flows causing sediment movement and turnover)?
- How are the temporal components of the hydrological regime (i.e. flow frequency, relative duration) affected by land-use alteration in the catchment or by changes resulting from climate warming?

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