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Effets des fluctuations de débit sur la réponse au stress des poissons : étude intégrative de la physiologie et du comportement chez le grand brochet (*Esox lucius* L.)

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Résumé

Le débit joue un rôle de première importance dans la modulation des caractéristiques physico-chimiques des rivières. Les poissons, à travers leur habitat, dépendent directement de cet ensemble de caractéristiques riveraines. De nombreuses études ont démontré qu'une altération du débit naturel des rivières, telle que par des installations hydro-électriques, a un effet négatif à l'échelle des populations et communautés de poissons. Par contre, les mécanismes qui sous-tendent ces relations sont toujours méconnus.

Les processus physiologiques des poissons déterminent la façon dont ils sélectionnent leur habitat. La réponse au stress a été proposée comme étant un mécanisme qui les guide à travers les changements qui surviennent dans leur environnement. Le comportement, le cortisol plasmatique, le glucose et le lactate sanguin sont des indicateurs de la réponse au stress chez les poissons.

Dans un premier temps, le mouvement de grands brochets *Esox lucius* L. a été observé dans deux rivières: l'une est régulée par éclusées, l'autre est non régulée et donc libre de barrage. Les résultats démontrent que le taux de mouvement chez des poissons qui habitent la rivière régulée est plus élevé que celui des poissons qui habitent dans la rivière non régulée. De plus, la direction de relation entre la distance parcourue par les poissons et le débit diffère entre rivières, et ce pour une même espèce.

Dans un deuxième temps, l'effet d'une élévation de vitesse d'eau sur le cortisol, glucose et lactate de brochets qui proviennent de deux rivières qui présentent des types de gestion de débit contrastés est évalué. Ce chapitre conclut que les poissons de la rivière régulée 1) relâchent moins de glucose dans leur sang, et 2) ont des mécanismes qui permettent une accumulation moindre de lactate dans leur sang, que les poissons de la rivière non régulée lorsqu'ils sont soumis à une augmentation de vitesse d'eau.

Dans un troisième temps, une approche analytique a été développée permettant de quantifier l'effet du débit sur la façon dont les brochets sélectionnent les conditions physiques de leur habitat, telle que la vitesse de l'eau. Les résultats des chapitres précédents suggèrent que les poissons de la rivière régulée sont soumis à des vitesses d'eau plus grandes que les poissons de la rivière non régulée. Ce nouvel outil permet de valider cette hypothèse.

En dernier lieu, les taux de base et maximaux de cortisol plasmatique, ainsi que de glucose et lactate sanguin ont été mesurés chez des brochets qui vivent dans les deux types de rivière. Ces indicateurs témoignent de la qualité de l'habitat dans lequel les poissons vivent. Nos résultats suggèrent que les poissons qui vivent dans la rivière régulée peuvent moduler leurs niveaux de base et maximaux en cortisol plasmatique dans le but d'éviter le stress chronique.

Cette thèse évalue les effets des changements de débit sur les poissons par des approches innovantes, situées à la frontière entre les domaines physiologiques et écologiques. Elle contribue à approfondir nos connaissances en ce qui a trait aux mécanismes par lesquels les poissons se distribuent à travers les différents habitats de rivière.

Mots clés: réponse au stress, rivière, poissons, sélection de l'habitat, cortisol, glucose, lactate, physiologie, *Esox lucius* L., mouvement.

Abstract

Flow is an important determinant of physicochemical characteristics of rivers. Fish communities in rivers are strongly dependant of their habitat, which is directly dictated by this set of characteristics. The loss of the natural flow regime, through regulation by hydroelectric facilities, for example, has the potential to directly affect the fish communities. Numerous studies have shown that the loss of natural flow regimes negatively impact fish populations and communities, but not much is known about the mechanisms that underlie such a relationship.

Physiological processes determine the way that fish select their habitat. The stress response has been proposed as a mechanism that guides fish throughout the environmental changes happening in their habitat. Indicators of the fish stress response comprise behaviour, plasma cortisol, and blood glucose and lactate.

First, northern pike *Esox lucius* L. movements were assessed in two rivers with contrasting flow regimes: a hydropeaking regulated river and an unregulated free-flowing river. Using manual tracking by radio-telemetry, we found that pike moved at a higher rate in the regulated river than in the unregulated river. Results also show that the direction of the relationship between movement of pike and flow can vary between rivers.

Second, the effect of a water velocity increase on plasma cortisol, blood glucose and blood lactate levels in wild pike originating from the two rivers with contrasting flow regimes were assessed. Our results show that blood glucose and lactate concentrations are significantly diminished for fish originating from the regulated river, in comparison to fish originating from the unregulated river, following an increase in water velocity.

Third, a novel analytical framework was developed that allow one to quantify the effect of the flow on fish selection of the physical conditions of their habitat (e.g. water velocity). Results obtained in the previous chapters suggest that pike living in the regulated river might be subjected to higher water velocities than fish living in the unregulated river. This novel tool will allow us to validate this hypothesis.

Lastly, basal and maximum acute stress-induced concentrations in plasma cortisol, and blood glucose and lactate were quantified in pike living in both the regulated and the unregulated rivers. These physiological parameters can give an indication of the fish habitat quality. Our results suggest that fish from the regulated river are able to modulate their plasma cortisol to dampen their HPI-axis responsiveness and avoid chronic stress.

This thesis assesses the effects of flow fluctuations on fish using novel approaches, situated at the intersection between the fields of physiology and ecology. It significantly contributes to broaden our knowledge of the mechanisms underlying fish habitat selection in rivers.

Key words: stress response, river, fish, habitat selection, cortisol, glucose, lactate, physiology, *Esox lucius* L., movement.

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Liste des abréviations

ACTH: hormone adrénocorticotrope/ *adrenocorticotropic hormone*

AIC: Akaike's Information Criterion

ANOVA: analysis of variance

ANN: artificial neural network

AUC: area-under-the-curve

bl: body length

CA: catécholamines/ *catecholamines*

ca: circa

cat: catalogue number

CRH: corticotropin releasing hormone

CVR: coefficient of variation of the residuals

D: distance

D_{std}: *standardized distance*

ELISA: enzyme-linked immuno-sorbent assay

ENFA: ecological niche factor analysis

F: F-statistic

FQRNT: Fonds Québécois de la Recherche sur la Nature et les Technologies

GAMM: generalized additive mixed modelling

GLMM: generalized linear mixed model

HCR: hormones corticotropes

HHI: hypothalamique-hypophysaire-interrénal

HPI: hypothalamic–pituitary–interrenal

HSC: hypothalamique-sympathique-chromaffines/ *hypothalamic-sympathetic-chromaffin cells*

HSI: habitat suitability index

ID: identity

Int.: intercept

LM: linear model

$MDPH_C$: *corrected version of the Minimal Distance travelled Per Hour*

MLR: multiple linear regressions

MWW: Mann-Whitney-Wilcoxon

NSERC: Natural Sciences and Engineering Research Council of Canada

NCCHE: National Centre for Computational Hydroscience and Engineering

NHM: numerical habitat modelling

$Pr\ (>|z|)$: *probability associated to z*

RSF: resource selection functions

SE: standard error

SS: sums of squares

ST: swimming tunnels

TL: total length

TMC: Tukey's multiple comparisons

ΔT: *travel time*

ΔT_{std}: *standardized travel time*

R^2_{adj}: *adjusted R-squared*

R^2_m: *marginal R-squared*

R^2_c: *conditional R-squared*

W: calculated Mann-Whitney U

z: Wald statistic

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Chapitre 1 Introduction

1.1. Le débit façonne les environnements aquatiques

1.1.1. Les régimes de débits naturels

Le débit joue un rôle déterminant dans les processus physico-chimiques qui façonnent les écosystèmes riverains (Bunn et Arthington 2002). D'un côté, le débit module les caractéristiques physiques des rivières, telles que la largeur du cours d'eau, l'arrangement des types d'habitat (c'est-à-dire la succession des rapides, des seuils et des bassins) ou encore la distribution des plantes aquatiques. De l'autre, la température de l'eau, la concentration en éléments nutritifs ou la quantité de matière organique dissoute constituent des caractéristiques chimiques des rivières qui sont également influencées par le débit. Puisque les communautés (c'est-à-dire richesse et abondance des espèces) de poissons dépendent directement de la structure de leur habitat (Poff et Allan 1995, Poff et al. 1997, Pusey et al. 2000), elles sont donc directement influencées par le régime de débit.

La dépendance des communautés de poissons d'eau douce aux conditions physiques de leur habitat est une preuve tangible de l'importance des régimes de débit naturels dans la conservation de la biodiversité des milieux aquatiques riverains. Un régime de débit naturel correspond à l'étendue de la variation du débit d'un système à différentes échelles de temps (horaire, hebdomadaire, mensuelle, saisonnière, annuelle, etc.) au cours de son histoire récente (Poff et al. 1997). Les communautés de poissons indigènes, c'est-à-dire l'assemblage d'espèces natives d'un cours d'eau, ont évolué en fonction du régime de débit et des conditions environnementales de leur habitat. Ainsi, des événements périodiques tels que les crues printanières ou l'étiage (la période de l'année où le niveau de la rivière atteint son niveau le plus bas) donnent un avantage certain aux espèces indigènes, c'est-à-dire aux espèces qui sont adaptées à ces particularités du régime de débit. Ceci peut prévenir l'établissement d'espèces envahissantes ou introduites et conserve, par le fait même, l'intégrité des communautés de poissons de rivière. Cet exemple cible plus particulièrement la synchronisation des cycles de vie des poissons avec les conditions de débit qui prévalent dans les habitats de leur rivière respective, mais de nombreux autres facteurs peuvent expliquer que le débit soit un élément important dans la conservation des populations de poissons. Pour n'en nommer que quelques-uns, nous pouvons penser à l'importance de la température, une condition environnementale étroitement liée au débit, dans le déclenchement de la migration des espèces pour le frai, ou bien à la quantité et la richesse d'espèces de plantes aquatiques, qui dépendent du débit pour l'apport de nutriments ou pour l'ancrage au substrat, qui constituent un refuge contre les prédateurs pour certaines espèces ou certains stades du cycle de vie des poissons.

1.1.2. Les modifications du régime de débits naturels des rivières

Le débit des rivières peut être modifié de façon naturelle ou anthropique. Les inondations ainsi que les sécheresses sont des événements exceptionnels et naturels qui causent des variations extrêmes dans les conditions hydriques d'un cours d'eau. La construction de barrages est une pratique très répandue mondialement et il va de soi que ces édifications sont susceptibles d'altérer de façon plus ou moins draconienne le régime de débit des rivières, selon la hauteur et la fonction du barrage (Johnson et al. 2008). Au courant des dernières décennies (années 1950-maintenant), le nombre de barrages qui régulent les rivières s'est multiplié, de telle sorte que la majorité des grandes rivières boréales du Canada sont maintenant régulées par de grands barrages (713 barrages > 5 m au Canada; Brandt et al. 2013).

En particulier, la gestion des débits par éclusées, appelée aussi régime d'éclusées hydroélectriques ou *hydropeaking* en anglais, implique des fluctuations rapides et drastiques des débits, c'est-à-dire un changement de plusieurs ordres de grandeur à l'intérieur de seulement quelques minutes ou heures (Cushman 1985). Ce type de régime permet de produire une grande quantité d'hydroélectricité lors des périodes de fortes demandes (Morrison et Smokorowski 2000).

1.1.3. Les effets des modifications du régime de débit sur les poissons

De nombreuses études ont identifié l'altération du régime de débit naturel comme une menace majeure pour l'intégrité des communautés de poissons de rivière (e.g. Bonner et Wilde 2000, Carlisle et al. 2011, Dieterman et Galat 2004, Quist et al. 2004). Ces études démontrent une concertation des efforts vers l'identification des effets de l'altération du débit sur des métriques des populations et communautés de poissons, tels que l'abondance et la richesse. Cette approche se concentre donc sur des métriques de poissons sur de grandes échelles spatiales et organisationnelles (c'est-à-dire espèces, populations, communautés). Ceci apporte une connaissance quantitative de la façon dont l'altération du débit affecte les abondances et la richesse de poissons en rivière, mais non mécanistique. Le lien entre l'altération des conditions environnementales des habitats des poissons, plus particulièrement ici les modifications du débit, et les communautés de poissons doit passer par l'étude de ces phénomènes à des échelles plus petites, telles que l'individu, l'organe et le cellulaire (Cooke et al. 2013a). Ces niveaux d'organisation sont souvent regroupés sous le terme «physiologie». Les études qui tentent d'expliquer les mécanismes physiologiques qui sous-tendent les effets des modifications de débit sont encore rares, et de nombreuses opportunités de recherche se situent à l'intersection entre la physiologie et l'écologie des populations ou communautés (Horodysky et al. 2015). À cette intersection, on retrouve notamment les réponses comportementales, qui sont le lien entre les changements qui agissent au niveau cellulaire ainsi que la sélection des poissons pour leur habitat. Une approche conjointe entre la physiologie et les réponses comportementales qui lui sont associées, communément appelée réponse au stress, sera privilégiée dans cette thèse afin d'évaluer les effets des changements de débit sur les poissons.

1.2. Le concept de stress

1.2.1. Le stress des animaux

Les bases du concept de stress ont été établies par H. Selye (1950, 1973), à des fins de recherches en physiologie humaine et études biomédicales. Le stress a été originellement défini par Selye comme étant une réponse non spécifique du corps à n'importe quel stimulus potentiellement nocif pour l'organisme. Par la suite, le concept de stress a été raffiné en y intégrant les notions d'homéostasie, préalablement décrite par Cannon (1932). L'homéostasie est définie comme l'équilibre physiologique interne dynamique d'un organisme. Toute déviation de cet équilibre, lui-même établi par des valeurs contrôles, doit être restaurée via l'allostasie, le processus de maintien de la stabilité interne. Par exemple, l'allostasie intervient lorsque des stimuli environnementaux ou des changements dans les valeurs contrôles de la physiologie d'un individu surviennent (Sterling et Eyer 1988). L'homéostasie est maintenue à travers l'équilibre de différents systèmes tels que le pH, la température du corps ou le niveau glycémique.

Plus récemment, les travaux de McEwen et Wingfield (2003) ont permis d'appliquer le concept de l'homéostasie, jusque là utilisé majoritairement dans des études biomédicales, à la biologie des populations en nature. Ainsi, de nouveaux termes tels que la charge allostatique, c'est-à-dire la quantité d'énergie à appliquer pour ramener la stabilité interne à des valeurs de contrôle et ainsi faire face aux stresseurs, ont été définis. Ces charges allostatiques peuvent être causées, entre autres, par une augmentation de la température ou du pH de l'eau, ou par des changements physiologiques internes reliés à la reproduction. Des adaptations physiologiques ou comportementales peuvent diminuer la quantité d'énergie à dépenser et ainsi diminuer la charge allostatique; c'est ce que l'on appelle la capacité adaptative de la réponse au stress. De plus, les stimuli environnementaux et internes menant à la charge allostatique sont additifs, ce qui signifie qu'un animal doit «travailler» encore plus fort pour ramener l'homéostasie lorsque les stimuli sont multiples. Lorsque les adaptations ne permettent pas de diminuer suffisamment la charge allostatique et que celle-ci devient trop grande pour une période prolongée, l'organisme entre dans la phase de surcharge allostatique (McEwen et Wingfield 2003). La surcharge allostatique amène soit une défaillance au niveau énergétique (déficit en énergie pour retrouver l'homéostasie), ou soit une dysfonction physiologique due à une action prolongée des mécanismes allostatiques (McEwen et Wingfield 2003). La défaillance ou dysfonction de l'organisme due au stress prolongé est parfois nommée: «le caractère mal-adaptatif de la réponse au stress» (de Kloet et al. 2005, Korte et al. 2005). Il peut être causé par des conditions prolongées de mauvaises conditions météorologiques, de changements dans les habitats, de parasitisme, ou de conflit social (Romero et al. 2009). Ainsi, le concept de stress est passé de la définition originale de Selye, un concept plutôt flou, à une définition plus précise qui englobe 3 concepts généraux: 1) les stimuli (environnementaux ou interne à l'organisme) qui sont un danger pour l'homéostasie, appelés stresseurs 2) la réponse rapide et urgente au stresseur appelée réponse au stress (lorsqu'une charge allostatique survient) et 3) une stimulation accrue et prolongée de la réponse au stress appelée stress chronique (défaillance de l'organisme, surcharge allostatique). C'est ce dernier, le stress chronique, qui est nuisible à la santé des individus et peut ainsi amener des maladies et pathologies reliées au stress (Breuner et al. 2008).

1.2.2. Le stress chez les poissons

Les recherches sur le stress spécifiquement appliquées aux poissons ont été premièrement révisées par Mazeaud et al. (1977). Par la suite, Schreck (1982), Barton et Iwama (1991), Wendelaar Bonga (1997) et Barton (2002) ont tous revu les principes du stress chez les poissons. La réponse au stress chez les poissons téléostéens est similaire à celle des vertébrés terrestres, à quelques différences près (Wendelaar-Bonga 1997). Les stresseurs peuvent être de trois types: chimiques, physiques ou perçus (Barton 2002). Il existe d'innombrables types de stresseurs chimiques, mais parmi la longue liste, mentionnons les polluants, la concentration en oxygène dissout ou le pH de l'eau. Les stresseurs physiques sont liés au confinement, à une haute densité de poissons dans un enclos (entassement), au transport, à l'émersion (exposition à l'air), mais aussi aux propriétés physiques de l'eau, telles que la vitesse ou la transparence. La présence de prédateurs, des bruits ambiants, des chercheurs ou bien des changements de luminosité constituent des exemples de stresseurs perçus.

Dans le but de déterminer les stimuli qui conduiront ultimement à un stress chronique et à des maladies et pathologies chez les poissons, il est important de définir des critères clairs pour ce qui est considéré comme étant des stresseurs pour les poissons. Malheureusement, ceci s'avère compliqué, car les conditions physiologiques qui différencient un stress léger, créé par des événements journaliers qui peuvent tout de même être stimulants, appelé « eustress », et une réponse intense à un stresseur qui menace la vie de l'organisme et mène au stress chronique, appelé «distress» (Selye 1976), sont difficiles à classer avec précision. Cette difficulté peut être expliquée par l'existence d'un continuum entre ces deux états, ce qui fait que le seuil à partir duquel une réponse devient un distress, et donc un stresseur qui menace l'intégrité de l'organisme, est arbitraire. L'état physiologique généralement accepté sur ce qui est une réponse au stress chez les poissons correspond à l'activation de deux systèmes conjoint: l'axe hypothalamique-sympathique-chromaffines (HSC) et l'axe hypothalamique-hypophysaire-interrénal (HHI).

1.2.2.1 L'axe hypothalamique-sympathique-chromaffines (HSC)

L'axe HSC est caractérisé par la libération rapide de catécholamines (CA) dans le sang, l'adrénaline et la noradrénaline. Ces hormones sont relâchées par les cellules chromaffines du rein, suite à la réponse déclenchée par les récepteurs cholinergiques activés par le système sympathique (acétylcholine), par des neurotransmetteurs non acétylcholiques et par des variables sanguines telles que la pression d'oxygène artérielle (Reid et al. 1998, Wendelaar-Bonga 1997). La hausse de CA résulte en une hyperglycémie par l'activation des récepteurs adrénergiques de type β qui, au niveau du foie, provoque la glycogénolyse (c'est-à-dire la production de glucose à partir de la lyse du glycogène; Gesto et al. 2014). De plus, l'augmentation de CA dans le sang provoque une consommation accrue en oxygène, principalement due à une hausse de la vitesse de respiration, du débit sanguin dans les branchies et de la capacité de transport de l'oxygène par le sang (Wendelaar-Bonga 1997). Ces changements métaboliques préparent l'organisme dans l'éventualité qu'il doive adopter des comportements de fuite, d'hyperactivité ou qui demandent une attention active.

1.2.2.2 L'axe hypothalamique-hypophysaire-interrénal (HHI)

La réponse rapide de l'axe HSC est accompagnée d'une stimulation des hormones impliquées dans l'axe HHI. L'axe HHI débute par la libération d'hormones corticotropes (HCR ou *CRH*) par l'hypothalamus, ce qui permet le relâchement de l'hormone adrénocorticotrope (ACTH) par les cellules corticotropiques du lobe antérieur de l'hypophyse (anté-hypophyse; Moyes et Schulte

2015). L’ACTH est un messager pour la libération des hormones glucocorticoïdes par les cellules interrénales. Chez les poissons téléostéens, l’hormone glucocorticoïde est le cortisol (Barton 2002). Le cortisol est aussi impliqué dans les voies métaboliques de glycogénolyse (le glycogène du foie est transformé en glucose) et de gluconéogenèse (synthèse de glucose à partir de substrats non glucidiques tels que le lactate), et peut donc aussi avoir un effet sur les concentrations de glucose sanguin (Laiz-Carrión et al. 2003, Mommsen et al. 1999). De récentes études ont démontré que d’autres hormones que le cortisol peuvent être impliquées dans l’axe HHI des poissons, par exemple la 1α-hydroxycorticostérone chez les Elasmobranchii (Anderson 2012). Puisque les glucocorticoïdes sont les derniers produits de la chaîne de l’axe HHI à être relâchés, il y a un décalage entre la présence du stresseur et le moment où la concentration de ces hormones augmente dans le sang (Gamperl et al. 1994). Pour cette raison, si le cortisol est échantillonné de façon convenable, il renseigne sur deux conditions physiologiques du poisson: 1) s’il est échantillonné en deçà du temps de décalage, la concentration en cortisol dans le sang indique l’état de stress du poisson avant sa capture et avant sa manipulation, ou 2) s’il est échantillonné au-delà du temps du décalage, alors la concentration en cortisol dans le sang correspond à la capacité de réponse au stress par le poisson. Les mêmes principes s’appliquent pour échantillonner le glucose (voir section 1.2.2.1) et lactate (voir section 1.2.2.3) sanguin.

1.2.2.3 Autres changements associés à la réponse au stress

De nombreux autres changements physiologiques surviennent de concert avec l’activation des axes HSC et HHI, dans le mécanisme de réponse au stress. Pour n’en citer que quelques-uns, il y a des modifications des concentrations sanguines en hémoglobine et en hématocrite, l’affaiblissement du système immunitaire et le déséquilibre des concentrations en électrolytes (sels et minéraux) dans les fluides des poissons (Wendelaar-Bonga 1997). Dans cette thèse, nous

nous concentrerons, plus particulièrement, sur les changements physiologiques liés aux effets de la nage active et de la fatigue musculaire, ainsi que de l'hypoxie. Cette stratégie consiste à cibler les composantes de la réponse au stress qui peuvent être affectées par des changements de débit. Le débit a un effet direct sur les changements de vitesse d'eau en rivières qui, à leur tour, peuvent affecter la vitesse de nage des poissons. Une des conséquences de la nage active contre une vitesse d'eau élevée consiste en des accumulations de lactate musculaire (Wood 1991). Il est principalement produit par les cellules musculaires par réduction du pyruvate par fermentation lactique, lors de la glycolyse anaérobique (Farrell et al. 1991, Kieffer 2000). De plus, le lactate joue de nombreux rôles intermédiaires dans le métabolisme glucidique. Des études ont démontré que le lactate est important dans la distribution, le transport et le stockage d'énergie entre les différents tissus de l'organisme, par exemple entre le foie et les cellules musculaires, par les réactions de la gluconéogenèse et de la glycogénèse (synthèse du glycogène à partir du glucose; Brooks 1991, Omlin et al. 2014, Philp et al. 2005).

1.2.3. Contexte de la thèse : lien entre physiologie et comportement

Au final, les processus physiologiques sont étroitement liés à la sélection des habitats par les poissons (Figure 1), qui est elle-même régie par des adaptations comportementales (Claireaux et Lefrançois 2007). Les changements dans les conditions environnantes sont tout d'abord détectés par les poissons par une série de capteurs spécialisés (e.g. température, signaux électriques, lumière; Jacqueline 2003). Ces stimuli sont par la suite transformés en signaux neurologiques qui déclenchent une série de réponses physiologiques et comportementales (Horodysky et al. 2015). Les réponses physiologiques, de concert avec les réponses comportementales, s'assurent donc que l'homéostasie interne est maintenue via des boucles de rétroaction (Ricklefs et Wikelski 2002). Les réponses neurologiques et physiologiques régissent donc la sélection de l'habitat par les poissons, et la sélection de l'habitat affecte inversement les réponses neurologiques et physiologiques. Malgré l'importance de ce lien, les physiologistes, qui ont, par tradition, étudié les mécanismes de cause à effet entre les conditions environnementales et les fonctions des cellules/tissus/organes, et les écologistes, qui eux étudient généralement l'effet des conditions environnementales sur les populations/communautés/écosystèmes, ont été lents à mettre leurs connaissances et approches en commun. Cette thèse se veut un effort pour tenter d'évaluer les effets des changements de débit par une vision intégrative des domaines physiologiques et écologiques, communément appelé réponse au stress ici. L'objectif principal de la thèse est de répondre à la question : les poissons sont-ils stressés par les changements de débit?

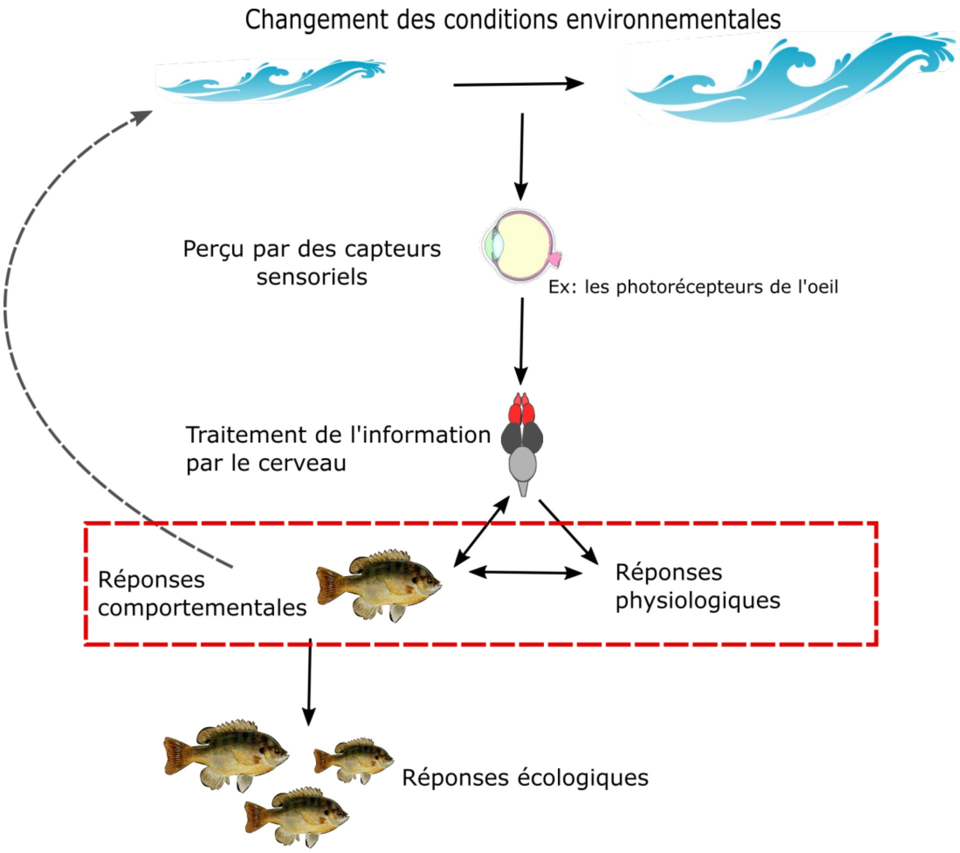

Figure 1. Conceptualisation schématique du sujet de la thèse (le rectangle pointillé rouge). Les changements environnementaux sont perçus par les récepteurs sensoriels des poissons. Cette information est traitée par le cerveau et ensuite il y a des réponses physiologiques et comportementales qui permettent de modifier les conditions environnementales dans lesquelles les poissons se trouvent. Ce mécanisme est à la base des réponses écologiques populationnelles. La figure est une adaptation de Horodysky et al. 2015.

1.3. Les effets des changements de débit sur la réponse au stress chez les poissons

1.3.1. Les effets des changements de débit sur l'axe HSC et plus particulièrement sur le glucose

La concentration de glucose sanguin en réponse à des variations de débit a été étudiée brièvement dans la littérature. Flodmark et al. (2002) ont étudié l'effet des variations journalières de débit sur des juvéniles de truite brune (*Salmo trutta*) en recréant, en laboratoire, un chenal artificiel où les poissons étaient libres de se déplacer. Ils n'ont pas observé de différence significative entre les poissons qui ont subi une diminution du débit de 80% (de 0.15 m^3 s^{-1} à 0.04 m^3 s^{-1}) et les poissons du groupe contrôle qui eux n'ont pas subi de réduction de débit. Une autre étude a évalué l'effet d'une réduction de 50% du débit hivernal, c'est-à-dire de 45 ± 5 à 22 ± 3 l s^{-1} (moyenne ± SE), d'un ruisseau situé dans les rocheuses canadiennes sur les concentrations de glucose sanguin de truites mouchetées (*Salvelinus fontinalis*) (Krimmer et al. 2011). Leurs résultats suggèrent qu'une telle diminution du débit pendant l'hiver ne cause pas de différence dans le glucose sanguin des truites mouchetées. La faible intensité des fluctuations de débit dans ces deux études pourrait expliquer l'absence de différence significative dans les concentrations de glucose sanguin. En contraste, les débits en rivières avec régime d'éclusées peuvent être 50 fois augmentés ou diminués en 3 ou 4 heures seulement, ce qui constitue une fluctuation beaucoup plus grande que celle observée dans les études précédentes. Il est donc impératif d'évaluer l'effet de fluctuations aussi importantes sur les concentrations de glucose sanguin de poissons qui vivent dans des rivières avec régime d'éclusées.

1.3.2. Les effets des changements de débit sur l'axe HHI et plus particulièrement sur le cortisol

Les effets des changements de débit sur l'axe HHI des poissons ont été examinés en laboratoire par Flodmark et al. (2002) et Arnekleiv et al. (2004). Flodmark et al. (2002) ont remarqué que les concentrations de cortisol sanguin étaient significativement plus élevées (61.3 ± 26.8 $ng\cdot ml^{-1}$, moyenne ± SD) chez les poissons qui ont subi une diminution du débit de 80% (de 0.15 $m^3\cdot s^{-1}$ à 0.04 $m^3\cdot s^{-1}$) que chez les poissons du groupe contrôle (4.9 ± 3.7 $ng\cdot ml^{-1}$). Cette diminution de débit était aussi associée à une diminution de la vitesse de l'eau de 0.26 ± 0.10 (moyenne ± S.D.), 0.33 ± 0.08 et 0.31 ± 0.09 $m\cdot s^{-1}$ dans les sections en amont, au milieu et en aval, respectivement, à 0.09 ± 0.09, 0.11± 0.07 et 0.13 ± 0.21 $m \cdot s^{-1}$ pour les sections correspondantes. Une diminution de la profondeur de l'eau (dans les sections les plus profondes, la profondeur diminuait de 40-50 cm à 30-40 cm) a aussi été observée. Puisque la diminution du débit était associée à des modifications des vitesses d'eau et de profondeur, il était difficile pour les auteurs d'affirmer quels stresseur(s) étai(en)t à l'origine de l'élévation du taux de cortisol chez les poissons. Arnekleiv et al. (2004) ont étudié les effets d'une période d'assèchement d'un chenal artificiel (débit = 0-1.9 $m^3 \cdot s^{-1}$) sur le cortisol plasmatique de truites brunes. Ils ont remarqué une augmentation significative du cortisol plasmatique de 2.3 nM, la limite de détection, à 183 ± 95 nM (moyenne ± SD) pour les poissons qui s'étaient réfugiés dans un chenal profond adjacent.

Les effets des changements de débit sur les concentrations de cortisol des poissons ont aussi été évalués en rivières naturelles. Une étude a montré qu'une augmentation du débit d'environ 2 fois, due à des pluies torrentielles, était corrélée à des concentrations corporelles de cortisol de tout le corps d'épinoches à trois épines (*Gasterosteus aculeatus*) plus élevées qu'à des moments de l'année où les conditions de débit étaient plus près des normales saisonnières (Pottinger et al. 2011). Encore une fois, la relation directe entre le stress des poissons et le débit ne pouvait pas être établie de manière irréfutable puisque d'autres conditions environnementales variaient en même temps que le débit. Taylor et al. (2012) ont aussi observé que les concentrations de cortisol sanguin du ménomini de montagne (*Prosopium williamsoni*) ont augmenté significativement en fonction du taux de changement horaire du débit dans une rivière régulée par un barrage hydro-électrique. La moyenne et l'écart-type des concentrations de cortisol observées chez les ménominis de montagne étaient respectivement de 1.60 et de 0.09 $ng \cdot ml^{-1}$, ce qui correspond néanmoins à des concentrations de cortisol pour des poissons non stressés. Ainsi, il semble que la relation observée entre la concentration de cortisol et le taux de changement du débit ne puisse s'expliquer par une réponse au stress *per se* puisque les taux de cortisol plasmatique étaient trop faibles pour que les changements de débit soient considérés comme des stresseurs. Par contre, cette étude n'avait pas de rivière contrôle avec laquelle comparer les concentrations de cortisol plasmatique chez des ménominis de montagne non stressés, c'est-à-dire la concentration plasmatique de cortisol de base, ce qui pourrait amener une importante information complémentaire sur l'effet du régime de débit sur les concentrations plasmatiques de cortisol des poissons.

1.3.3. Les effets des changements de débit sur le lactate sanguin

Très peu d'études ont quantifié les concentrations de lactate sanguin chez des poissons de rivières qui subissent des changements rapides de débit. Une étude par Taylor et al. (2012) a évalué les concentrations de lactate sanguin chez des ménominis de montage capturés à des débits variant de 556 à 1524 $m^3 \cdot s^{-1}$ (moyenne = 900 $m^3 \cdot s^{-1}$). Leurs résultats suggèrent que le lactate sanguin des salmonidés ne varie pas significativement en fonction du débit de rivière. Par contre, aucune étude n'a été effectuée sur les non-salmonidés, qui pourraient être plus susceptibles à une accumulation de lactate due à des capacités de nage restreintes (Jones et al. 1974).

1.3.4. Les effets des changements de débit sur le comportement

Les premières études sur le comportement des poissons se sont concentrées sur l'effet de la température de l'eau, de la canalisation des cours d'eau, ou de l'endiguement, sans mesurer l'effet direct du débit sur celui-ci (telles que décrites par Miller 1978). Par la suite, de nombreuses études ont porté sur la mortalité liée à l'échouage de poissons, appelé *stranding* en anglais, causée par des baisses drastiques de débit (Bradford 1995, Bradford 1997, Saltveit et al. 2001, Irvine et al. 2009). Une quantité moindre d'études a porté sur les effets sublétaux des changements de débit sur la sélection de l'habitat par les poissons, sur les déplacements journaliers qu'ils doivent effectuer dans le but de trouver des conditions environnementales souhaitables pour leur croissance, ainsi que les conséquences énergétiques liées à de tels déplacements (Scruton et al. 2005). Taylor et al. 2014a ont émis l'hypothèse que les poissons font face aux changements rapides et drastiques de débit en se relocalisant fréquemment dans le but de trouver des conditions d'habitat qui leur sont favorables, provoquant par la même occasion un accroissement de leur taux de déplacements. Par contre, les chercheurs qui ont évalué les taux de déplacement des poissons en fonction du débit ont trouvé des résultats contrastants. Cependant, ces études ont été menées sur plusieurs espèces et selon différentes méthodologies, et elles se sont concentrées sur l'analyse d'une seule rivière à la fois (Bunt et al. 2003, Bunt et al. 1999, DeGrandchamp et al. 2008, Enders et al. 2008, Robertson et al. 2004, Scruton et al. 2003, Taylor et al. 2014a). Ceci étant dit, la compréhension de l'effet des débits sur le déplacement des poissons pourrait être significativement améliorée par des études qui analysent cette relation sur la même espèce dans au moins deux rivières qui ont des régimes de débit différents et qui utilisent les mêmes méthodologies d'échantillonnage.

1.4. Espèce modèle

Le grand brochet (*Esox lucius* L), ou simplement brochet dans le reste de cet ouvrage, est un grand prédateur vivant dans les lacs, rivières et eaux saumâtres de l'hémisphère nord (Craig 2008). Le brochet chasse par embuscade; il reste immobile jusqu'à l'approche de sa proie et l'attaque par une accélération rapide (Raat 1988, Savino et Stein 1989). C'est pourquoi il sélectionne majoritairement des habitats où les vitesses d'eau sont faibles et où il peut se camoufler, soit entre des plantes aquatiques ou autres structures (tronc d'arbre, roches), et attendre ses proies (Eklöv 1997). La sélection de son habitat en fonction des vitesses d'eau faibles pourrait indiquer que cette espèce est particulièrement susceptible d'être affectée par des changements de débit en rivière. Pour cette raison, nous avons choisi cette espèce en tant que modèle pour cette thèse.

1.5. Structure générale et objectifs de la thèse

Cette thèse se veut un effort pour tenter d'évaluer les effets des changements de débit par une vision intégrative des domaines de la physiologie et de l'écologie. Le premier chapitre constitue une introduction générale aux concepts de débit de rivière et de la réponse au stress. L'approche générale adoptée pour les chapitres suivants est d'étudier les différences entre la réponse au stress des brochets qui vivent dans deux rivières qui se distinguent par leur régime de débit. La première est une rivière régulée par la méthode de gestion par éclusées et la deuxième est une rivière non régulée libre de barrages. Les sujets spécifiques abordés correspondent aux chapitres 2 à 5 et s'orientent autour de 4 axes majeurs de recherche:1) le comportement des brochets en rivière en fonction du débit, 2) la physiologie liée à une augmentation rapide des vitesses d'eau, 3) la sélection des habitats en fonction du débit et 4) les variations des niveaux de base et maximal de cortisol plasmatique, et de glucose et lactate sanguins entre des brochets qui vivent dans deux rivières avec des régimes de débit différents.

1.5.1. Chapitre 2 Les différences de mouvement entre des grands brochets qui habitent deux rivières avec des régimes de débit contrastés

Le chapitre 2 est une étude sur les mouvements des brochets en rivières. Pour se faire, 20 brochets ont été marqués avec des radio-émetteurs qui nous ont permis de les suivre sur une période de 37 jours. Les objectifs de ce chapitre sont de 1) examiner les différences inter-rivières de distance parcourue ($m \cdot h^{-1}$) par les brochets qui habitent une rivière où le débit fluctue fréquemment et une rivière où le débit est plutôt stable, 2) évaluer l'hypothèse, dans les deux rivières, selon laquelle les brochets se déplaceraient à un taux plus élevé lorsque le débit augmente et 3) comparer la portée de leurs déplacements, le type de mouvement préféré (longitudinal ou latéral) et le taux de déplacement latéral des brochets dans les deux rivières. L'hypothèse du premier objectif est que les poissons parcourent des distances significativement différentes dans les deux rivières avec des régimes de débit contrastés. De plus, puisque le débit fluctue drastiquement et plusieurs fois par jour, l'hypothèse de l'objectif 2 est que les poissons vont se déplacer à un taux plus élevé ($m \cdot h^{-1}$) dans la rivière avec les fluctuations journalières de débit. L'hypothèse de l'objectif 3 est que le régime de débit modifie la portée des déplacements des poissons, le type de mouvement préféré ainsi que les taux de déplacement latéral des poissons.

1.5.2. Chapitre 3 La réponse au stress diffère entre des grands brochets qui proviennent de rivière régulée et non régulée lorsqu'ils sont soumis à une augmentation de la vitesse d'eau

Les fluctuations de débit provoquent de nombreux changements dans les conditions abiotiques des habitats de poissons. Ce chapitre examine l'effet d'une de ces conditions, la vitesse d'eau, sur la réponse au stress chez les grands brochets. Les objectifs sont: 1) de tester l'effet d'une augmentation de la vitesse d'eau sur les concentrations de cortisol plasmatique, et de glucose et de lactate sanguin de brochets sauvages et ce, dans des tunnels de nage installés directement en rivière et 2) de tester l'hypothèse selon laquelle l'effet d'une augmentation de la vitesse d'eau sur la réponse au stress est diminuée chez des brochets qui proviennent d'une rivière régulée, lorsque comparée à la réponse de ceux qui habitent une rivière non régulée. L'hypothèse de l'objectif 1 est que les concentrations de cortisol plasmatique, de glucose sanguin et de lactate sanguin augmenteront lorsque les brochets seront soumis à une augmentation de la vitesse d'eau. De plus, l'hypothèse présentée à l'objectif 2 devrait être confirmée puisque les poissons qui sont fréquemment soumis à des augmentations rapides de la vitesse d'eau devraient présenter des mécanismes physiologiques appropriés pour faire face à ces changements.

1.5.3. Chapitre 4 Un nouveau cadre analytique pour modéliser les variables contextuelles dans la sélection de l'habitat avec des données de présences seulement

Les différences dans la réponse au stress lorsque les brochets sont soumis à une augmentation de la vitesse d'eau (chapitre 3) ont potentiellement un effet sur la sélection que ces poissons font de leur habitat. Dans le but d'explorer cette possibilité, il a été nécessaire de développer un nouveau cadre analytique qui permet d'évaluer si la sélection des vitesses d'eau par les brochets, et donc de toutes les variables physiques de leur habitat, varie en fonction des fluctuations de débits. Ce nouveau cadre analytique pourrait être utile autant en écologie terrestre qu'en écologie aquatique, et sur de nombreux taxons. Il est donc axé sur les problématiques des méthodes analytiques et statistiques dans le développement de modèles numériques d'habitat, plutôt que sur la sélection des habitats par les grands brochets. L'objectif spécifique du chapitre 4 est de développer un cadre analytique qui permet de tester et quantifier l'effet d'une variable dite contextuelle, par exemple le débit d'une rivière, et de son interaction avec les variables physiques de l'habitat (telles que la vitesse et profondeur de l'eau) sur la sélection des habitats per les animaux, pour des données récoltées par radio-télémétrie. Nous prévoyons que l'objectif sera atteint par la conception d'un nouveau cadre analytique et que ce nouvel outil permettra de montrer que le débit modifie la façon avec laquelle les poissons choisissent leur habitat.

1.5.4. Chapitre 5 Les variations des indicateurs physiologiques de base et maximaux suivant un stresseur aigu entre deux rivières qui présentent des régimes de débit contrastés

L'objectif spécifique du chapitre 5 est de comparer les niveaux de base et maximaux de cortisol plasmatique, et de glucose et lactate sanguin entre des brochets qui vivent dans une rivière régulée selon le mode de gestion par éclusées ou dans une rivière non régulée. Les niveaux de base et maximaux de ces indicateurs peuvent témoigner de la qualité de l'habitat dans lequel vivent les poissons. Les fluctuations rapides et répétées du débit dans une rivière régulée pourraient constituer un stresseur et donc un habitat de moindre qualité pour des brochets. L'hypothèse est donc que les niveaux de base de cortisol plasmatique, de glucose sanguin et de lactate sanguin seront significativement plus élevés dans la rivière avec fluctuations rapides et répétées du débit que dans la rivière où le débit est plus stable. Les niveaux maximaux en cortisol plasmatique, en glucose sanguin ainsi qu'en lactate sanguin pourraient quant à eux être réduits puisque les poissons seraient, selon notre hypothèse, dans une situation de stress chronique.

1.6. Contributions spécifiques à chacun des articles et rôles joués par les coauteurs

Harvey-Lavoie, S, Cooke, SJ, Guénard, G, Boisclair, D. 2016. Differences in movements of northern pike inhabiting rivers with contrasting flow regimes. Article publié. *Ecohydrology*. DOI: 10.1002/eco.1758.

Cet article constitue le chapitre 2 du présent document, intitulé: «Les différences de mouvement entre des grands brochets qui habitent deux rivières avec des régimes de débit contrastés». La conception de cette étude et la récolte des données ont été effectuées par S. Harvey-Lavoie. Les analyses, les interprétations et l'écriture de l'article ont été faites par S. Harvey-Lavoie, avec des commentaires de S.J. Cooke, G. Guénard et D. Boisclair. S.J. Cooke a fourni le matériel de télémétrie.

Harvey-Lavoie, S, Boisclair, D. In review. Differential stress response to an increase in water velocity in a wild top predator living in rivers with contrasting flow regimes. Submitted to: ***Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology.***

Cet article constitue le chapitre 3 du présent document, intitulé: «La réponse au stress diffère entre des grands brochets qui proviennent de rivières régulée et non régulée lorsqu'ils sont soumis à une augmentation de la vitesse d'eau». La conception de cette étude et la récolte des données ont été effectuées par S. Harvey-Lavoie. Les analyses, les interprétations et l'écriture de l'article ont été effectuées par S. Harvey-Lavoie, avec des commentaires de D. Boisclair.

Harvey-Lavoie, S, Guénard, G, Wheeland, L, Cooke, SJ, Boisclair, D. A novel analytical framework to model contextual variable in assessing habitat selection using presence-only data. In preparation for: ***Methods in Ecology and Evolution.***

Cet article constitue le chapitre 4 du présent document, intitulé: «Un nouveau cadre analytique pour modéliser les variables contextuelles dans la sélection de l'habitat avec des données de présences seulement». La conception de cette étude a été effectuée par S. Harvey-Lavoie. Les données ont été récoltées par S. Harvey-Lavoie, avec l'aide de L. Wheeland. Les modèles hydrologiques en 2D ont été effectués par S. Havey-Lavoie. Les analyses statistiques et la conception du cadre analytique ont été effectuées par G. Guénard. Les interprétations et l'écriture de l'article ont été effectuées par S. Harvey-Lavoie, avec des commentaires de G. Guénard et D. Boisclair. S.J. Cooke a fourni le matériel de télémétrie.

Harvey-Lavoie, S, Boisclair, D. Among-river variation in baseline and acute stress-induced physiological indicators of a top predator in two rivers with contrasting flow regimes. In preparation for: ***General and Comparative Endocrinology***

Cet article constitue le chapitre 5 du présent document, intitulé: «Les variations des indicateurs physiologiques de base et maximaux suivant un stresseur aigu entre deux rivières qui présentent des régimes de débit contrastés». La conception de cette étude et la récolte des données ont été effectuées par S. Harvey-Lavoie. Les analyses, les interprétations et l'écriture de l'article ont été effectuées par S. Harvey-Lavoie avec des commentaires de D. Boisclair.

Article en annexe

Senay, C, Harvey-Lavoie, S, Macnaughton, CJ, Bourque, G, Boisclair, D. Morphological differentiation in northern pike: The influence of environmental conditions and sex on body shape. Submitted to: ***Canadian Journal of Zoology***

Cet article se retrouve en annexe puisqu'il est intimement lié au sujet de cette thèse. La conception de cette étude a été effectuée par S. Harvey-Lavoie, C. Senay, C.J. Macnaughton. S. Harvey-Lavoie a coordonné le terrain et récolté les données. Les analyses et l'écriture ont été effectuées par C. Senay. G. Bourque a fourni les données de débit. D. Boisclair a participé à l'interprétation et a fourni des commentaires.

Chapitre 2 Les différences de mouvement entre des grands brochets qui habitent deux rivières avec des régimes de débit contrastés

Differences in movements of northern pike inhabiting rivers with contrasting flow regimes

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Abstract

Little is known about the effect of short-term flow changes on the movement of northern pike (*Esox lucius* L.). We conducted a comparative study in two rivers with different flow regimes (i.e. one regulated and one unregulated) to evaluate the extent to which adult northern pike movement is influenced by short-term river flow conditions. Data on northern pike hourly movement were collected in northeastern Ontario on 40 individuals in the Mississagi River, a river subjected to extreme daily flow variations associated with hydroelectric operations (i.e. hydropeaking), and the Aubinadong River, an unregulated river. Using manual tracking by radio-telemetry, we found that northern pike moved at a higher rate in the river subjected to short-term changes in river flow than in the unregulated river. Results also show that the relationship between movement of northern pike and flow can vary among rivers. In the Mississagi River, flow had a significant positive effect on northern pike activity, while the effect of flow in the Aubinadong River depended on water temperature. Moreover, fish in the Mississagi River utilized a restricted river section and travelled more laterally in comparison to fish inhabiting the Aubinadong River, where longer upstream-downstream movements were more common. The present study contributes to our understanding of the effects of short-term changes in flow on fish movement. This constitutes the first step towards assessing the effect of flow on fish habitat use, and eventually developing flow management strategies to mitigate impacts on fish.

Keywords: Fish movement, flow, telemetry, northern pike

2.1. Introduction

Fish movement is one of the most important behaviors and determines habitat selection, foraging efficiency, and predator avoidance (Kahler et al. 2001, Schreck et al. 1997). Fish movement is the individual displacements over short distances between resting, hiding, and foraging habitats, happening within the fish home range (Jacobson and Peres-Neto 2010, McMahon and Matter 2006). Movement therefore acts as a key mechanism by which fish maximize fitness endpoints such as growth, survival, and reproductive success (Barton 2002, Scherer 1992, Schreck et al. 1997).

Short-term (i.e., minutes to hours) flow changes in rivers lead to dynamic environmental conditions that have long been known to modify fish habitats (Hillyard and Keeley 2012, Scruton et al. 2003, Valentin et al. 1996). Fish have been hypothesized to cope with these short-term flow changes by moving rapidly from an original habitat to a relocated habitat of a presumed similar suitability, thereby increasing their travel rate as flow fluctuates (Taylor et al. 2014a). Studies that attempted to test the effect of short-term flow changes on fish movement, hereafter referred to as the “mobility hypothesis”, reached different conclusions. Movement of adult striped bass (*Morone saxatilis*) in the tailwater of a hydroelectric facility was significantly increased during elevated flow (Young and Isely 2007), and bull trout (*Salvelinus confluentus*) swimming muscle activity was significantly related to the hourly mean flows ranging from 0 to 1770 $m^3 \cdot s^{-1}$ (Taylor et al. 2014b). In contrast, Enders et al. (2008) and Robertson et al. (2004) found no such relationship for Atlantic salmon (*Salmo salar*) in rivers where flow ranged from 0.3 to 7.9 $m^3\ s^{-1}$, and from 1.3 to 5.2 $m^3 \cdot s^{-1}$ respectively. A number of elements (e.g. fish species or life-stage, sampling scale, river geomorphology, and flow regime) may explain the range of conclusions reached by different studies. It has also been shown that flow can affect fish movement patterns. The home range of European grayling (*Thymallus thymallus*) increased with elevated flow in a Czech Republic river (Horká et al. 2015), and lateral movements performed by the whole fish community of an Australian stream happened mainly during flow increases (Lyon et al. 2010). One element common to most studies is that they fail to include non-regulated 'control' rivers, which makes the among-river comparisons challenging (Taylor and Cooke 2012).

Northern pike (*Esox lucius* L.) is a common freshwater top predator found in lakes, rivers, and brackish marine waters of the northern hemisphere (Craig 2008). Northern pike prefer to use slow water velocity habitat where they can ambush their prey and capture them using brief anaerobic bursts (Raat 1988, Savino and Stein 1989). For that reason, pike can be more sensitive to flow fluctuations than species that prefer faster water velocities (Hontela et al. 1997). In accordance with the recognized sensitivity of pike to flow, the few studies that investigated the effect of flow on pike's seasonal and daily movement suggest that hourly movement could be affected by hourly flow changes. Masters et al. (2005) observed that extensive upstream movement of two tagged pike in the river Frome, UK, coincided with a three-fold increase in river flow, and Pauwels et al. (2014) found that the daily distances travelled by males were significantly and negatively affected by river flow.

Flow regime of regulated rivers characterized by short term (i.e. hourly) and drastic (e.g. 20-fold increase) flow changes affect a long suite of environmental variables such as dissolved oxygen (Calles et al. 2007), water temperature regime (Hillyard and Keeley 2012), wetted width, water depth and velocity (Zhong and Power 1996), substrate composition and distribution (via different erosion and sedimentation patterns; Osmundson et al. 2002), and aquatic plant diversity and abundance (Aronsuu et al. 1999). A number of these environmental variables and their interactions, all related to the flow regime, may affect fish movement in rivers. It is therefore impossible to isolate the effect of a single variable on fish movement among rivers that differ in flow regimes. However, it is possible to assess the extent to which fish movement may vary between rivers possessing different flow regimes. Radio telemetry is now a common tool in fisheries assessment and management (Cooke et al. 2016) and provides opportunity for tracking the spatial ecology of wild fish in riverine systems (Cooke et al. 2013b). Consequently, the objectives of the present study, focusing on adult pike during the summer, were: 1) to examine the inter-river differences in distance travelled by northern pike ($m \cdot h^{-1}$) in two rivers with different flow regimes; 2) to assess the "mobility hypothesis" in these two rivers by examining the intra-river relationships between flow and the distance travelled by northern pike; 3) to compare the longitudinal range, the preferred movement type (longitudinal or lateral), and the lateral travel rate performed by northern pike in the two study rivers. The present study is unique because it compares fish movements in a regulated river to fish movements in an unregulated river located nearby.

2.2. Material and methods

2.2.1. Study rivers

The study was conducted in the Mississagi River and the Aubinadong River of northeastern Ontario, Canada (Figure 1). The study area (46°54′N, 83°16′W) on the Mississagi River is a 2 km river portion (width range: 80 - 180 m), located 5 km downstream of a hydroelectric facility (Aubrey Falls Dam, average daily flow = 38 $m^3 \cdot s^{-1}$) built in 1969. The hourly flow in this study area can vary drastically within 3-4 hours (range: 6 – 307 $m^3 \cdot s^{-1}$; Harvey-Lavoie, S., unpublished data). Such important and sudden flow changes related to hydropower production are referred to as “hydropeaking”. Hourly flow data (from 2004 to 2014; Brookfield Renewable Power, Ontario) has shown that, for this period of time, the operation strategy has been consistently hydropeaking, with minor seasonal differences. The Aubinadong River (46° 55′N, 83° 26′W) is an unregulated river that flows into the Mississagi River 13 km downstream of Aubrey Falls Dam (Figure 1). The study area in the Aubinadong River is an 18 km river portion (width range: 20 - 115 m) that has an average daily flow of 15 $m^3 \cdot s^{-1}$ (range: 2 - 120 $m^3 \cdot s^{-1}$). The two study areas, one on the Mississagi River and one on the Aubinadong River, were selected based on their accessibility by canoe and their similar altitude, morphology, fish density (Table 1), and fish community (14 species being present in the Aubinadong River and 13 in the Mississagi River, with only blacknose dace [*Rhinichthys atratulus*] being absent from the latter; Macnaughton et al. 2015a). Both study areas have natural habitats in terms of riverbanks (i.e. presence of natural substrate, aquatic plants, and logs), natural sinuosity, and highly variable depths and water velocities, both spatially and temporally. There are also numerous side channels, side pools, riffle and run sequences, and small bays, in addition to the main channel. Fish captures on the Aubinadong River were situated at least 3 km upstream from its junction with the Mississagi River, thus minimizing the probability that our data include fish travelling between both rivers. During the study period, the average hourly flow was 2.4 times higher in the Mississagi River (11.8 - 258.6 $m^3 \cdot s^{-1}$; average 42.7 $m^3 \cdot s^{-1}$) than in the Aubinadong River (9 - 24 $m^3 \cdot s^{-1}$; average 17.9 $m^3 \cdot s^{-1}$). In the former, flow was overall low in the morning (11.8 to 13.0 $m^3 \cdot s^{-1}$; average 11.9 $m^3 \cdot s^{-1}$; 9:00 to 12:00 h) and higher at night (14.6 to 258.55 $m^3 \cdot s^{-1}$; average 87.2 $m^3 \cdot s^{-1}$; 17:00 to 21:00 h); a pattern absent from the Aubinadong River. Water temperatures of the studied rivers were very similar during the tracking period (Mississagi River: average 18.6 ºC, range 12 – 25 ºC; Aubinadong River: average 18.8 ºC, range 13 – 26 ºC).

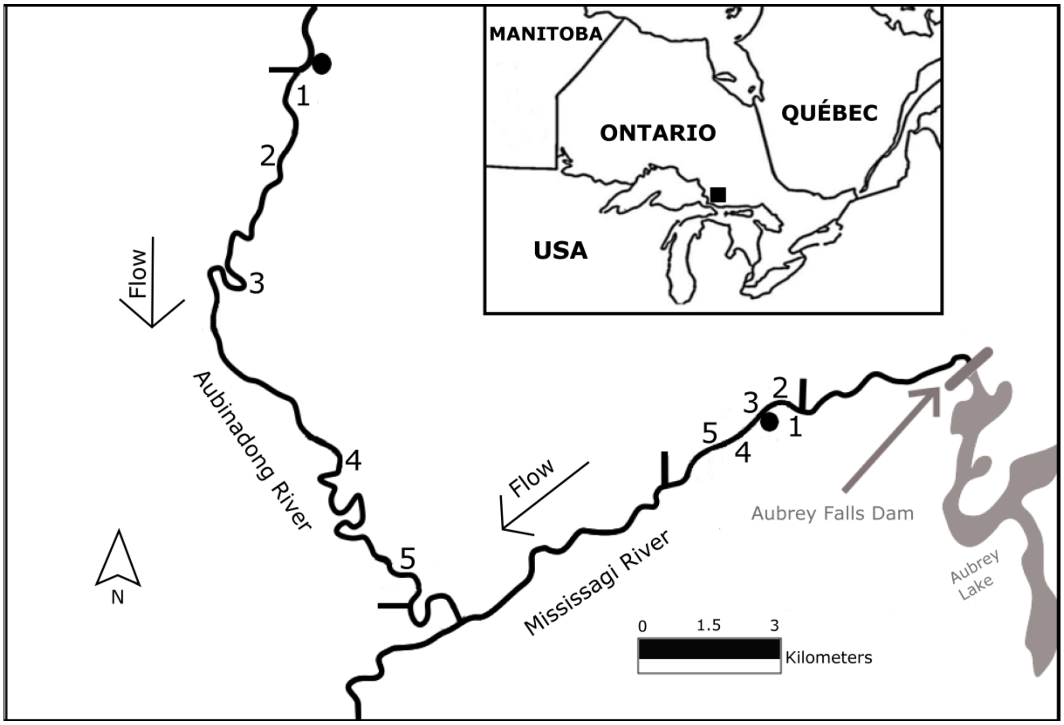

Figure 1. Map of the study rivers (the Mississagi and Aubinadong rivers; Northeastern Ontario, Canada). The black square on the inset map represents the location of the rivers in Canada. The filled black circles on the large map are the flow gauges, and the river portion in-between the two dashes, on each river, represent the area where fish tracking took place. The numbers correspond to pike catch location on each river in Table 2.

Table 1 Watershed area, altitude, hydrology, morphology and fish density of the unregulated river (Aubinadong River) and the regulated hydropeaking river (Mississagi River) at two levels: watershed and study reach.

		River and regulation type	
		Mississagi	**Aubinadong**
Level		**Hydropeaking**	**Unregulated**
Watershed	Drainage basin area (km^2)	4152.2	1580.5
	Drainage density (km·km^{-2})	0.1088	0.1317

	Median basin elevation (meters above sea level)	455	484
	Maximum Basin Elevation (meters above sea level)	590	607
	Basin Slope (Mean; %)	5.7	8.9
	Basin Slope (SD)	4.2	5.8
	Total precipitation (1961-1990; mm/year)	906	973
Study reach	Fish density (fish·m^{-2})	0.1370	0.1755
	Mean daily flow (m^{3} ·s^{-1})	38	15
	Slope (m·m^{-1})	0.0007	0.0009
	Width (range in m)	80-180	20-115
	Mean annual flood (m^{3} ·s^{-1}; months of April and May)	29	38

2.2.2. Fish capture and tagging

Fish capture and tagging took place between June 12th and July 6th 2013 (Table 2). We collected 91 northern pike (Mississagi River=56, Aubinadong River =35) by angling, from a canoe or from the shore, using barbless artificial lures and nylon lines (4.5 kg test; Figure 1). Fish were reeled in, captured using a dip net, and placed in an insulated container (990 x 480 x 480 mm) filled with well-aerated river water. The lure was removed while fish remained in the water, thus ensuring minimal handling stress and a quick recovery (Arlinghaus et al. 2009). Total length can have a positive effect on pike movement (Vehanen et al. 2006), and in order to minimize this effect, 40 adult fish with a total length of 440-655 mm were kept for the radio-telemetry. The remaining 51 fish were used to develop a length-weight relationship. Total fish mass (g wet blotted weight), total length (TL, in mm), and sex (Casselman 1974) were recorded. Movements were quantified by radio-telemetry, using externally attached individually-coded transmitters (3.2 g in air, 25 x 13 x 6 mm, 120 mm antenna, battery life 6 months, 3 seconds pulse interval; Model PD-2, Holohil Systems Inc., Carp, ON, Canada), following the method described by Arlinghaus et al. (2009). The external attachment method was rapid (few minutes) and does not require the use of anesthetics, which necessitates a long recovery and clearing period (i.e. few hours; Cooke 2003). External tagging is a suitable and commonly used method for esocids (Arlinghaus et al. 2009, Colotelo et al. 2013, Landsman et al. 2011) in short-term studies (few months). The relative mass of the transmitters was ≤ 0.6% of fish body mass. Fish were released within 5-10 minutes of capture.

Table 2 Fish ID code, longitudinal range, sex, mass, length, date tagged, catch location, number of all observations, mean of minimum distance travelled per hour ($MDPH_C$) for all observations, number of observations for travel time ≤ 24 hours and mean of $MDPH_C$ for travel time ≤ 24 hours for every fish from both the hydropeaking Mississagi River and the unregulated Aubinadong River.

River	Fish ID	Longitudinal range (m)	Sex	Mass (g)	Length (mm)	Date tagged (all in 2013)	Catch location (Fig.1)	number of all observa-tions	MDPH_C all observations mean (range)	number of observations for travel time ≤ 24h	MDPH_C for travel time ≤ 24h mean (range)
Aubinadong	A1	5660	male	756	512	14-Jun	1	26	21.3 (1-99)	16	15 (2-36)
	A2	971	female	689	511	14-Jun	1	30	8.8 (1-43)	19	9.4 (1-19)
	A3	1053	female	670	499	14-Jun	1	22	5.8 (1-17)	13	6.7 (1-17)
	A4	942	female	763	523	15-Jun	1	28	12.8 (1-115)	18	7.8 (1-60)
	A5	193	female	670	494	15-Jun	1	30	7.5 (1-29)	19	8.6 (1-27)
	A6	1041	male	959	562	21-Jun	3	27	32.0 (1-115)	16	17.3 (2-71)
	A7	704	male	1420	614	22-Jun	4	3	31.3 (6-51)	2	21.5 (6-37)
	A8	1182	female	1296	645	22-Jun	4	8	14.8 (5-42)	3	9.7 (5-17)
	A9	136	female	1244	570	24-Jun	1	30	10.7 (1-26)	19	13.8 (3-26)
	A10	7292	female	1313	610	24-Jun	5	21	26.7 (2-117)	14	15.3 (2-51)
	A11	1420	female	619	463	25-Jun	2	24	23.6 (2-57)	15	25.8 (2-54)
	A12	5626	male	1631	655	25-Jun	4	2	66.5 (11-122)	1	11 (-)
	A13	Missing	male	1581	655	03-Jul	4	0	-	0	-
	A14	2353	female	760	489	03-Jul	4	10	40.4 (4-165)	6	22.7 (4-37)
	A15	Missing	male	1142	553	04-Jul	5	0	-	0	-
	A16	486	female	1126	578	04-Jul	5	11	32.8 (8-71)	5	40.2 (8-71)
	A17	Missing	male	702	482	04-Jul	5	0	-	0	-
	A18	Missing	male	1205	563	04-Jul	5	0	-	0	-
	A19	6199	female	750	475	05-Jul	5	6	34.7 (8-70)	4	23.5 (8-55)
	A20	7939	male	950	578	06-Jul	1	27	21.1 (2-75)	18	16.6 (2-35)
Mississagi	M1	689	male	1101	556	12-Jun	2	29	60.4 (11-261)	18	53.8 (11-145)
	M2	489	female	1532	635	12-Jun	1	27	50.4 (4-188)	15	52.5 (15-126)
	M3	413	male	1419	610	12-Jun	5	31	57.0 (6-317)	19	57.0 (6-317)
	M4	672	male	1199	581	12-Jun	5	31	64.1 (2-203)	19	64.1 (3-177)
	M5	305	female	1228	593	13-Jun	2	27	53. 9 (4-171)	16	57.8 (4-171)

M6	273	male	1169	598	13-Jun	3	31	55.3 (13-120)	19	55.5 (13-120)
M7	397	male	1298	622	13-Jun	5	30	48.2 (4-144)	18	54 (11-144)
M8	232	female	1204	573	13-Jun	1	28	46.4 (11-141)	16	46.4 (11-141)
M9	611	female	526	440	15-Jun	2	9	42.3 (6-103)	4	30.5 (16-51)
M10	559	female	588	467	09-Jul	1	29	36.3 (5-179)	17	31.5 (5-94)
M11	205	female	677	481	16-Jun	2	31	34.7 (4-91)	19	38.8 (6-91)
M12	293	female	659	474	17-Jun	2	27	47.1 (8-137)	15	40.9 (9-137)
M13	305	male	1325	609	17-Jun	3	31	50.5 (3-169)	19	53.2 (3-169)
M14	342	male	631	471	17-Jun	4	27	35.6 (3-100)	15	41.4 (10-100)
M15	800	female	677	483	17-Jun	1	23	70.4 (3-155)	13	67.2 (5-155)
M16	521	female	1232	577	19-Jun	3	28	76 (4-210)	16	61.1 (4-210)
M17	523	male	1474	613	19-Jun	5	27	65.9 (9-135)	16	58.3 (10-135)
M18	436	female	595	475	20-Jun	2	33	22.8 (2-52)	21	23.5 (2-49)
M19	133	male	1349	574	20-Jun	3	28	44.8 (3-162)	19	49.1 (4-162)
M20	176	female	1199	586	20-Jun	1	26	20.4 (5-54)	15	24.6 (7-54)

2.2.3. Fish tracking

Fish were tracked between July 10th and August 16th 2013, alternating between the two rivers on a daily basis. There was therefore at least 4 days between the tagging (June 12th to July 6th 2013; Table 2) and the onset of tracking. A study by Arlinghaus et al. (2009) showed that, following a capture by angling, pike recovered and resumed their normal behaviour within 24 hours post-release. In addition, a study by Cooke (2003) showed that the attachment of external radio-transmitters did not affect the 1h or 24h post tagging parental care behaviour of rock bass (*Ambloplites rupestris*). Given these findings, the time interval of a minimum of 4 days between tagging and tracking was deemed sufficient for fish to recuperate and resume their normal behaviour. Tracking was performed at two different time periods by two different teams: in the morning (05:00 to14:00) and at night (17:00 to 02:00). Individual fish positions were therefore estimated at approximately 8-hour intervals. This strategy was adopted because flow variations in the study rivers did not present noticeable short-term periodicities (1 hour to few hours) during the day (9:00-17:00). However, in Mississagi River, because of hydropeaking happening at night (17:00-1:00), flow was consistently at its lowest at *ca* 09:00 and at its highest at *ca* 21:00. No such periodicities were noticeable in Aubinadong River. An 8-hour interval to assess fish positions was therefore considered sufficient to achieve our objective to assess the effect of flow variations on fish movement. Teams were assigned to either the morning or night shifts, and switched halfway through the sampling period (*ca* two weeks), thereby minimizing potential team bias. Fish positions were determined using a portable radio-receiver equipped with a three-element Yagi antenna (Lotek SRX 400 Telemetry Receiver, Lotek, Ontario, Canada). Pike were tracked from a canoe using the successive gain reduction technique, which consists in beginning with an elevated receiver gain and gradually decreasing it while approaching the source of the signal to pinpoint the location of the fish (Taylor et al. 2014a). Using this technique, pike could be approached within 2 m without inducing a fleeing response, a distance also reported by Klefoth et al. (2008) and Kobler et al. (2008). Repeated tracking of hidden transmitters placed at different locations in the river revealed a precision of our tracking method of ± 5 m. The geographic coordinates of fish positions were recorded using a handheld GPS instrument (Garmin 76sc, USA) with a precision of ± 5 m. Water temperature (^{o} C; Traceable thermometer, ThermoFisher Scientific, USA), date, and time were also recorded at each fish position. Hourly flow was recorded by a gauging station (Figure 1) in the Mississagi River ($m^3 \cdot s^{-1}$; Harvey-Lavoie, S., unpublished data) and the Aubinadong River (Survey of Canada, http://wateroffice.ec.gc.ca/). All fish tagged in the Mississagi River remained in the study area, but four of the fish tagged in the Aubinadong River were never located (Table 2). The 36 fish were located 0-2 times every session, which resulted in 0-4 positions per fish per day, and 2-33 positions per fish over the complete duration of the study (Table 2). A total of 858 fish positions were obtained (Mississagi: 553 positions; Aubinadong: 305 positions). The tendency of fish from the Aubinadong River to occupy more distant positions in the river, and to preferentially perform longitudinal movements is consistent with the loss of 4 tagged fish, and the small number of observations in this river.

2.2.4. Data exploration and analyses

The distance travelled per hour was estimated using the minimum distance (m) between two consecutive positions of the same fish. We assessed the shape of the relationship between the distance travelled and the time elapsed between two consecutive observations performed on the same fish. The time elapsed between consecutive fish observations was highly variable (from 3 to 105 hours), therefore the distance travelled had to be standardized with respect to travel time (e.g. in m·h^{-1}). Since the relationship must have an intercept of 0 (travelled distance must be exactly 0 when the travel time is exactly 0), and in order to account for the possibility of a non-linear relationship, we modelled the relationship between travelled distance (D; m) and travel time (ΔT; h) as a power relationship with constants a and b as:

Equation 1: $D = a \cdot \Delta T^{b}$.

The parameters of this relationship were estimated independently for each river, to account for potential inter-river differences in fish behaviour. From the parameters a and b, the relationship between the standardized distances (D_{std}; m) and the standardized travel time (ΔT_{std} ; h) was obtained as:

Equation 2: $D_{std} = a \cdot \Delta T_{std}^{b}$.

The values of D_{std} and ΔT_{std} were estimated using a rule of three (Guénard et al. 2010, Reist 1986), a method previously used in the context of morphological analysis, as follows:

Equation 3: $\frac{D_{std}}{D} = \frac{a \cdot \Delta T_{std}^{b}}{a \cdot \Delta T^{b}}$.

We used a standard travel time ΔT_{std} of 1 h, and defined the resulting D_{std} as a corrected version of the Minimal Distance travelled Per Hour (MDPH$_C$; m·h^{-1}), which, after simplification of Equation 3, was calculated as follows:

Equation 4: $MDPH_C = D \cdot \left(\frac{1}{\Delta T}\right)^{b}$.

Three explanatory models of MDPH$_C$ were developed. The first model, referred to as the "Inter-river Model", uses pooled data from both rivers, and is aimed towards reaching our first objective. The second and third models are river-specific models referred to as the “Aubinadong intra-river Model” and the “Mississagi intra-river Model”. They are aimed towards reaching our second objective. Our third objective was achieved using three descriptors of pike movement: the longitudinal range, the preferred movement type, and the lateral travel rate. The longitudinal range was calculated for every individual fish as the distance (in km) between the most upstream and the most downstream position (Bettinger and Bettoli 2002, Clapp et al. 1990). Every $MDPH_C$ corresponds to a Euclidean vector with an x component (i.e. perpendicular to shore) and a y component (i.e. parallel to shore), which form mutually perpendicular reference axes. In the case where x is longer than y, $MDPH_C$ was classified as being lateral. In the reverse situation, $MDPH_C$ was classified as being longitudinal. The preferred movement type is the most frequent type of movement performed by a fish, and was estimated by summing, for each individual fish, the occurrence of $MDPH_C$ classified as either longitudinal or lateral and taking the type having the largest sum as the preferred one. The lateral travel rate (in $m \cdot h^{-1}$) corresponds to the mean of all $MDPH_C$ described as lateral, for all fish from the same river pooled together. The lateral travel rate indicates that fish followed the lateral direction (i.e. get closer to the shore) over a short time interval (number of meters travelled laterally during one hour; lateral $MDPH_C$). Because the mean channel width of the Mississagi River is larger than that of the Aubinadong River, we divided each of the lateral travel rates observed in the Mississagi River (i.e. the $MDPH_C$) by a factor of 1.926 (i.e. the mean river width of the Mississagi River, 130 m, divided by the mean river width of the Aubinadong River, 67.5 m) to standardize them. Only fish movements with a travel time $\leq$ 24 hours (sub-daily movements; 517 observations; Table 2) were used to develop generalized linear mixed-effects models (GLMM), and to estimate the preferred movement type and the lateral travel rate. This lead to some individual fish with a very small number of observations (i.e. one observation for fish A12 and two observations for fish A7), however it is acceptable to develop GLMM with only one observation per group, for some of the groups (Gelman and Hill 2006).

Inter- and intra-river effects of flow on $\mathrm{MDPH_C}$ were analyzed using GLMM, since observations performed on the same fish could not be taken as statistically independent (Zuur et al. 2009). GLMM used fish identity (fish ID) as a qualitative variable having a random effect, whereas flow ($m^3 \cdot s^{-1}$), water temperature (°C), time of the day (h), sex (male or female), and total length (mm) were modelled as having fixed effects, on $\mathrm{MDPH_C}$. We also included a categorical variable representing the river inhabited by each individual fish in the fixed effects of the Inter-river Model, hereafter referred to as the river effect. We used the Poisson GLMM because our $\mathrm{MDPH_C}$ are counts during a standardized time interval (number of meters per hour), with a small occurrence of elevated counts and a high occurrence of small counts (Johnson et al. 2005). All GLMM were developed by backward elimination, and selected based on the smallest Akaike's Information Criterion (AIC; Zuur et al. 2009). The initial models included all the explanatory variables and the interaction terms that, based on our ecological knowledge, were likely to have a significant effect on $\mathrm{MPDH_C}$: 1) flow and water temperature, and 2) water temperature and time of the day. Generalized additive mixed modelling (GAMM) was considered in our selection of modelling methods but was not retained because there was no clear pattern in the plots of residuals against fitted values, and residuals against each explanatory variable for every GLMM developed. The presence of clear patterns in these plots is an indication of the need for GAMM modelling (Zuur et al. 2009). Our results show that the relationships between $\mathrm{MDPH_C}$ and explanatory variables are linear. We achieved our first objective by pooling observations from the two rivers, and removing the most extreme values of flow (i.e. $\geq 24\ m^3 \cdot s^{-1}$) to obtain a similar range for the explanatory variables in the two rivers. Goodness of fit of the models was analyzed using the marginal R^2 (R^2_m; the variance explained by the fixed factors) and the conditional R^2 (R^2_c; the variance explained by the entire model) described by Nakagawa and Schielzeth (2013). Inter-river variations in the longitudinal range and lateral travel rate were tested using Kruskal-Wallis rank sum tests and the preferred movement type was tested using Fisher's exact test. A linear model (LM) was developed between the log-transformed response variable fish weight and two explanatory variables: the log-transformed fish length and a categorical variable representing the two rivers. The inter-river difference in fish conditions was assessed by an analysis of variance conducted on the results of the LM. All statistical analyses were conducted with R (R Development Core Team, 2014).

2.3. Results

We found no inter-river difference in the length (Mississagi range: 440-635 mm TL; Aubinadong range: 463-655 mm TL) or the mass (Mississagi range: 526-1532 g blotted wet mass; Aubinadong range: 619-1631 g blotted wet mass) of tagged fish (Table 2; Kruskal-Wallis rank sum tests; length: $p = 0.98$; weight: $p = 0.70$). The fish length significantly explained the fish weight ($F = 607.92$, $p < 0.0001$), but we found no inter-river difference in pike condition ($F = 0.10$, $p = 0.75$).

2.3.1. Inter-river Model

The $\mathrm{MDPH_C}$ ranged from 1 to 317 $\mathrm{m \cdot h^{-1}}$, and were higher in the Mississagi River than in the Aubinadong River for all flows (Figure 3). GLMM indicated that time of the day ($z = 10.16$, $p < 0.0001$), water temperature ($z = 4.62$, $p < 0.0001$), flow ($z = 3.435$, $p < 0.0001$), river ($z = 8.45$, $p < 0.0001$), and the interaction between flow and water temperature ($z = -3.276$, $p < 0.001$) had a statistically significant effect on $\mathrm{MDPH_C}$ (Table 3). These variables explained 59% of the variation of $\mathrm{MDPH_C}$, and the random factor (fish ID) explained an additional 33%, for a total explanatory power of 92%. Sex had no effect on movements ($z = 0.603$, $p = 0.55$), nor did total body length ($z = 1.209$, $p = 0.23$). The latter may be related to the small size range used in our study (450mm<total length<650 mm). These results meant that, at the same water temperature, flow, and time of the day, a fish travelling at a rate of 11.7 $\mathrm{m \cdot h^{-1}}$ in the Aubinadong River would be travelling at 38.2 $\mathrm{m \cdot h^{-1}}$ (3.26 times faster) in the Mississagi River.

Table 3 Estimate, standard error (SE), Wald statistic (z), probability associated to z (Pr(>|z|)) of the Log-linear (Poisson) GLMM of the three models: inter-river Model, Mississagi and Aubinadong intra-river models, all calculated on $\mathrm{MDPH_C}$ with the random effect being fish IDs. R^2_m is the marginal R^2 (variance explained by the fixed factors) and R^2_c is the conditional R^2 (total variance explained by the fixed and the random factors). Variable separated by colon punctuation mark designed interaction.

Parameter	**Estimate**	**SE**	**z**	**Pr(>|z|)**	R^2_m	R^2_c
Inter-river Model						
Intercept	0.254	0.498	0.509	0.610	0.59	0.92
River Mississagi	1.186	0.140	8.452	< 0.0001		
River Aubinadong	Ref	—	—	—		
Time of the day (h)	0.020	0.002	10.155	< 0.0001		
Flow (m3/s)	0.110	0.032	3.435	< 0.0001		
Water temperature (°C)	0.101	0.024	4.169	< 0.0001		
Flow: Water temperature	-0.005	0.002	-3.276	0.001		
Mississagi intra-river Model						
Intercept	3.2244	0.5769	5.589	< 0.001	0.38	0.84
Time of the day (h)	-0.106	0.016	-6.733	< 0.001		

Water temperature (°C)	-0.063	0.015	-4.138	< 0.001		
Total body Length (mm)	0.027	0.009	2.984	0.003		
Flow (m^3/s)	0.001	0.000	6.341	< 0.001		
Time of the day: Water temperature	0.006	0.001	7.482	< 0.001		
Aubinadong intra-river Model						
Intercept	0.125	0.672	0.187	0.852	0.07	0.79
Time of the day (h)	0.009	0.003	2.654	0.008		
Water temperature (°C)	0.142	0.031	4.582	< 0.001		
Flow (m^3/s)	0.186	0.039	4.787	< 0.001		
Flow: Water temperature	-0.011	0.002	-5.575	< 0.001		

2.3.2. Mississagi intra-river Model

MDPH_C in the Mississagi River ranged from 2 to 317 $m\cdot h^{-1}$. The GLMM developed specifically for this river indicated that the variables time of the day (z = -6.733, $p < 0.0001$), water temperature (z = -0.063, $p < 0.0001$), flow (GLMM, z = 6.341, $p < 0.0001$), the interaction between time of the day and water temperature (z = -4.138, $p < 0.0001$), and total body length (z = 2.984, p=0.003) had statistically significant effects on MDPH_C (Table 3). Sex had no effect on movement (GLMM, z = 1.9, p = 0.06). The MDPH_C of the Mississagi River peaked at night from 21:00 to 1:00, following the hydropeaking schedule (Figure 2). According to the GLMM, a 55 cm fish observed at 20:00, in a water temperature of 23 °C, would have a MDPH_C of 49.7 $m\cdot h^{-1}$ at a flow of 10 $m^3\cdot s^{-1}$, but a MDPH_C of 62.8 $m\cdot h^{-1}$ at a flow of 250 $m^3\cdot s^{-1}$ (an increase of 26% in MDPH_C for a 25-fold increase in flow). The interaction between time of the day and water temperature indicated that the effect of the time of the day on MDPH_C tended to diminish as water temperature increased. That GLMM explained a total of 84% of MDPH_C variation in the Mississagi River, with 38% being associated to the environmental conditions and 46% to the random effect (fish ID).

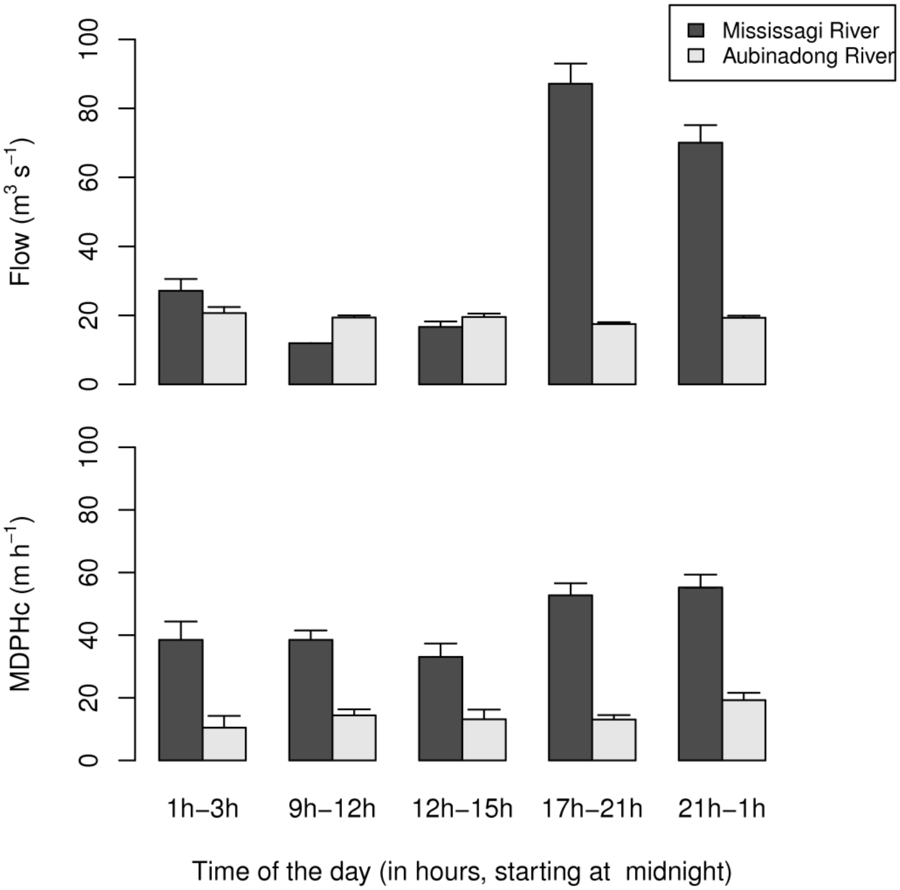

Figure 2 The flow (mean + standard error; $m^3 \cdot s^{-1}$) and the $MDPH_C$ (mean + standard error; $m \cdot h^{-1}$) of northern pike in the Mississagi River (hydropeaking) and the Aubinadong River (unregulated), with respect to the time of the day.

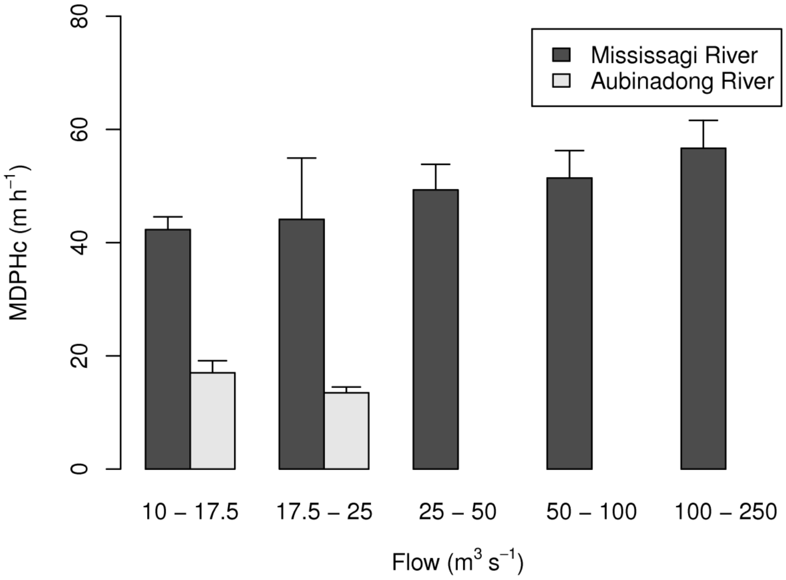

Figure 3 The MDPH$_C$ (mean + standard error; m·h^{-1}) of northern pike at different flows (mean + standard error; m^3·s^{-1}) in the Mississagi River (hydropeaking) and the Aubinadong River (unregulated). The maximum flow value observed in Aubinadong River was 24 m^3·s^{-1}.

2.3.3. Aubinadong intra-river Model

MDPH$_C$ in the Aubinadong River ranged from 1 to 165 m·h^{-1}. The GLMM developed for the Aubinadong River indicated that water temperature ($z = 4.58$, $p < 0.0001$), flow ($z = 4.79$, $p < 0.0001$), the interaction between flow and water temperature ($z = -4.138$, $p < 0.0001$), and time of the day ($z = 2.65$, $p = 0.008$) had a statistically significant effect on MDPH$_C$ (Table 3). Neither sex ($z = 0.488$, $p = 0.63$) nor body mass ($z = -0.31$, $p = 0.75$) had a statistically significant effect on the MDPH$_C$. The effect of flow on MDPHc depended on water temperature: the relationship was positive below 16.9 °C and negative above 16.9 °C. Hence, a 55 cm fish observed at 12:00 at a flow of 20 m^3·s^{-1} would have a MDPH$_C$ of 16.6 m·h^{-1} at a water temperature of 13 °C, but a $MDPH_C$ of 6.0 $m \cdot h^{-1}$ at a water temperature of 26 °C (a decrease of 64% in $MDPH_C$ for a 2-fold increase in water temperature). While the GLMM explained a total of 79% of $MDPH_C$ variation in the Aubinadong River, 72% was associated to the random effect (fish ID), and only 7% of the variation was associated to environmental conditions.

2.3.4. Longitudinal range, preferred movement type, and lateral travel rate

The longitudinal range of fish was significantly smaller in the Mississagi River (mean: 419 m; range: 133-800 m) than in the Aubinadong River (mean: 2700 m; range: 136-7939 m; $\chi^2 = 13.1733$, $p < 0.001$).The relative frequency for fish longitudinal and lateral preference was statistically different between the Mississagi River and the Aubinadong River (Fisher test, $p = 0.03$), an equal number of fish preferred to move longitudinally (10 fish) as laterally (10 fish) in the former, while fish preferred to move longitudinally in the latter (preferred movement type of 14 out of 16 fish; Figure 4). The lateral travel rates in the Mississagi River were, on average, 18 $m \cdot h^{-1}$ (range: 3-30 $m \cdot h^{-1}$), and were significantly higher than the average of 7 $m \cdot h^{-1}$ observed in the Aubinadong River (range: 3-22 $m \cdot h^{-1}$, χ^2 =81.98, $p < 0.001$).

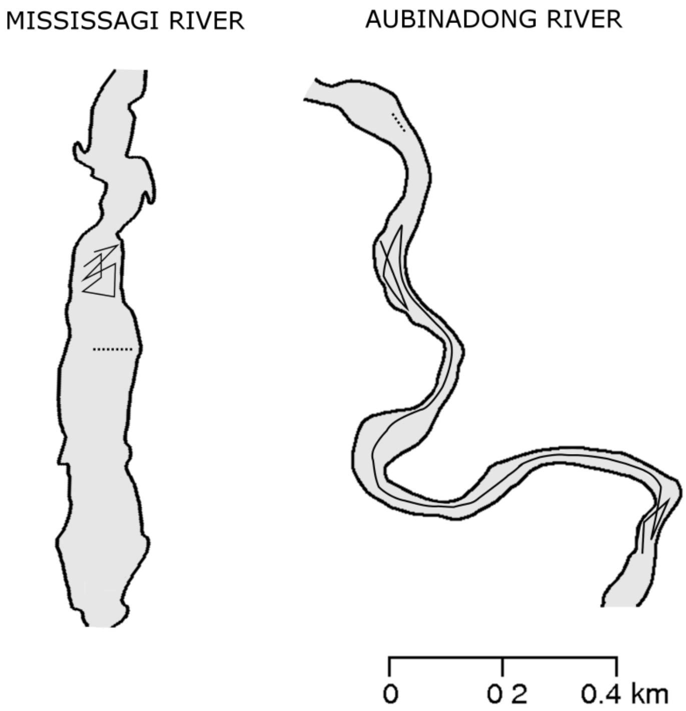

Figure 4 The northern pike movement patterns in the Mississagi River and the Aubinadong River. The single dashed line in each river represent the mean $\mathrm{MDPH_C}$ (Mississagi River = 48 $\mathrm{m \cdot h^{-1}}$; Aubinadong River= 15 $\mathrm{m \cdot h^{-1}}$) of the preferred movement type in Aubinadong River (i.e. lateral) and the movement type preferred by half of the pike in Mississagi River (i.e. longitudinal). The solid line in each river is a 4 consecutive days track of the fish M14 and the fish A11. It is important to note that the tracks are raw data and not $\mathrm{MDPH_C}$; the solid lines cannot be taken as a measure of movement rate.

2.4. Discussion

The distance travelled by fish per hour ($\mathrm{MDPH_C}$; $\mathrm{m \cdot h^{-1}}$) in the Mississagi River was significantly higher than in the Aubinadong River. This finding is consistent with the “mobility hypothesis” that suggests that fish can cope with increasing or decreasing flow by either remaining still, or changing their positions in order to find new suitable environmental conditions. Since the tendency to either hold a position or to move is related with the studied species' preference for velocity conditions, it is possible that pike moved to habitat with slower water velocity as flow changed in the Mississagi River. This pattern was not observed in the Aubinadong River, and thus leads to significantly greater $MDPH_C$ in the former. Electromyogram telemetry revealed that bull trout maintain similar focal velocities across flows ranging from 0 to 920 $m^3 \cdot s^{-1}$ in a hydropeaking river (Taylor et al. 2014b). Bull trout held a position using fine-scale adjustments, yet it is unclear if non-salmonids are able to do the same. While understanding the tendency to preferably hold a position or to preferably move as flow increases, it is also important to consider the experience of fish to previous fluctuating flows (Scruton et al. 2003). The Mississagi River pike in this study were exposed to daily flow fluctuations for a prolonged period of time (near continuously since 1969).

One of the main concerns about short-term changes in river flow is the additional energetic cost for fish to frequently find alternate locations with suitable environmental conditions (Scruton et al. 2005). Fish need to obtain energy reserves during the summer to grow and withstand or survive the winter period of diminished food availability (Johnson and Evans 1991, Miranda and Hubbard 1994). For Mississagi River pike, the energy loss associated with the extra cost of activity can be roughly estimated using fish mass and swimming speed in calculations of the net energetic costs of routine swimming (Boisclair and Tang 1993). The total net energetic cost associated to routine swimming for a 5 months period (May 1st to September 31st) and a 1000g pike were estimated at 336 kJ for a fish travelling half the time (12h by day) at 42.6 $m\ h^{-1}$ (mean $MDPH_C$ at low flow: $\leq 24\ m^3 \cdot s^{-1}$) and half the time at 52.7 $m \cdot h^{-1}$ (mean $MDPH_C$ at high flow: $> 24\ m^3 \cdot s^{-1}$) in the Mississagi River, and at 92 kJ for a fish travelling all the time at 14.7 $m \cdot h^{-1}$

(mean $MDPH_C$ at low flow < 24 $m^3 \cdot s^{-1}$, as high flows were absent) in the Aubinadong River. Based on the work of Diana (1979), we were able to approximate the among-river difference in the net energy available for growth and reproduction of a fish swimming in a water temperature of 19 °C (Diana 1983); an increase in the swimming of the Mississagi River fish led to a decrease of 16% in the net energy available. This is a rough estimate and it is, by no means, the exact net energy available to pike in the study rivers. This estimate nevertheless suggests that Mississagi River pike could be losing a significant amount of energy (16%) by travelling more than fish in the Aubinadong River. However, our length-weight relationships suggest that there is no inter-river difference in pike conditions, thus indicating that another mechanism (e.g. increased food intake), or a combination of mechanisms, may allow pike to overcome the increased activity in Mississagi River. One hypothesis is that the water mixing, created by flow fluctuations in the Mississagi River, could have made food more available to pike. While our data does not allow us to substantiate this idea, it is tempting to speculate that the potential increase of prey catchability in the regulated river may help to explain the lack of difference in pike condition between the regulated and the unregulated rivers. Growth limitations were not assessed herein and further research is needed to assess whether increased activity levels could be detrimental to the growth of non-salmonid fishes.

A meta-analysis on the effect of flow on fish movement has revealed that a 40-fold flow increase (2-332 $m^3 \cdot s^{-1}$) had a significant positive effect on the distance travelled by fish (Taylor and Cooke 2012), which is consistent with the results of the Mississagi intra-river Model. However, our results suggest that findings from regulated rivers studies do not apply to unregulated rivers. The effect of flow on movement in the Aubinadong River depended on water temperature, with no discernible effect of flow when the water temperature reached 17 °C, which are close to the temperatures associated with pike optimal activity (19-20 °C; Casselman 1978). The differences in the effect of flow between the intra-river models indicate that the interaction of water temperature with flow could potentially only take place at conditions of low flow ($< 24\ m^3 \cdot s^{-1}$). In the Mississagi River, the flow can increase 22-fold in 3-4 hours, while the range of flow observed in the Aubinadong River was 9.7 – 24.0 $m^3 \cdot s^{-1}$, with a maximum daily fluctuation of 2 $m^3 \cdot s^{-1}$. The absence of an interaction between flow and water temperature in the Mississagi River suggests that high flows (24-258.6 $m^3 \cdot s^{-1}$) trigger pike movement, irrespective of water temperature, and that high flows in an unregulated river caused, for instance, by storms or spring floods, could also affect $MDPH_C$ (e.g. 26% increase). However, only 7% of the variation was explained by environmental conditions in the Aubinadong River, which could indicate that fish moved in a more 'random walk' fashion in this river than in the Mississagi River (Codling et al. 2008).

We found the longitudinal range for Mississagi River fish to be 6-fold smaller than that of Aubinadong River fish. Such a difference in pike's longitudinal range was unexpected because studies on pike movement have reported mostly sedentary behaviour during the summer period (Koed et al. 2006, Vehanen et al. 2006). This had a major influence on the sampling design of our study: in order to locate every fish (or try locating) at every session, the river portion covered in the Aubinadong River during the tracking session needed to be longer (18 km) than anticipated. In comparison, pike from the Mississagi River stayed in a longitudinal segment of 2 km. The length of the river surveyed should not be taken as a bias of our survey design, but as a result of fish behaviour. The general tendency of pike to be mostly sedentary during summer is consistent with the results from Mississagi River, but not with that of Aubinadong River.

A study by Jepsen et al. (2001) found intra-specific heterogeneity in the dispersion of pike populations; they had a larger home range in a clear water lake than in a turbid reservoir. They also found prey density differences between the lake and the reservoir that could have caused the dissimilarity in home ranges. However, fish density, which may be taken as a proxy for prey density, is almost equivalent in the Mississagi and Aubinadong rivers (Table 1). This minimizes the potential role of prey density in the between-river movement differences observed in the present study. For salmonids species, Hillyard and Keeley (2012) found that the total distance (m) moved per week by Bonneville cutthroat trout (*Oncorhynchus clarki utah*) during the summer in a regulated river (average of 701 m; sedentary) was 11-fold smaller than in an unregulated river (average of 7964 m; mobile); a movement pattern also observed in the Mississagi and Aubinadong rivers. Hillyard and Keeley (2012) attributed the difference in mobility to small, infrequent, and widely distributed hospitable patches of cold water during warm summer months in the regulated river. Water temperatures exceeded the upper thermal limit of the Bonneville cutthroat trout (24.2 °C; Johnstone and Rahel 2003) in the study by Hillyard and Keeley (2012). However, this situation was not observed in either the Mississagi River (water temperature range: 12 – 25 ºC) or the Aubinadong River (water temperature range: 13 – 26 ºC), because the upper thermal limit of the pike is 29.4 °C (Casselman 1978). It is therefore unlikely that the difference in pike longitudinal range could be attributed to the water temperature of spatially variable, hospitable habitat patches. Lee and Berejikian (2008) have found that juvenile steelhead (*Oncorhynchus mykiss*) reared in stable environmental conditions were more inclined to have an exploratory behaviour than fish held in unstable environments where structures (rocks and plants) in aquaria were repositioned every 2-3 days. The environment in the Mississagi River can be characterized as unstable, where 22-fold daily flow changes affect velocity conditions and water depth, thus leading to losses or gains in habitats. The habitat changes in the Aubinadong River happen on a longer time-lapse (2 $m^3 \cdot s^{-1}$ maximum daily flow fluctuations during the tracking period), making it more stable on a daily basis. Rodríguez (2002) demonstrated that intra-specific heterogeneity exists in the length of river sections used by salmonids. The present study demonstrates that intra-specific behaviour heterogeneity also exists for non-salmonids fishes, and that the stability of flow conditions in which juvenile pike were reared is the most probable explanation of the difference observed in the longitudinal range of fish inhabiting both rivers.

In addition, fish preference for lateral movement and fish lateral travel rate were both higher in the Mississagi River than in the Aubinadong River. This behaviour may help fish to avoid high water velocities by reaching flow refuges (off-channel habitats like floodplains, tributaries, inundated grassland, side channels, and backwaters; Cucherousset et al. 2007, DeGrandchamp et al. 2008, Gardner et al. 2013, Gorski et al. 2014, Nunn et al. 2010). The increased preference for lateral movement for fish subjected to elevated discharge in the Mississagi River is consistent with findings from Kwak (1988), where the number of fish per day that travelled laterally to a floodplain was positively correlated to mean daily flow. As flow increases, fish can move either longitudinally (i.e. upstream or downstream) or laterally (towards the shoreline). Since no extended downstream movement was observed in the Mississagi River, pike could have been moving laterally because the other remaining choice in the type of movement (i.e. moving upstream against an increasing flow), would correspond to a high-energy demand upon the fish.

Our results demonstrate that pike respond to short-term changes and elevated flows (> 24 m^3s^1) by increasing the $MDPH_C$ in the regulated river. Under natural flow conditions and low flows (< 24 m^3s^{-1}), the importance of the flow on the $MDPH_C$ depended on the water temperature.

Therefore, the way that $MDPH_C$ varied with flow depended on the river itself, because flow regulation was completely different between the study rivers (regulated vs. unregulated river). This emphasizes the need for further work on net energy available for growth and reproduction in rivers subjected to short-term changes in flow. Differences in pike movement patterns were observed between the Mississagi and Aubinadong rivers. The flow regime affects many environmental conditions that could be the cause of such differences and identifying the sole environmental condition responsible of these differences was beyond the scope of the present study. Moreover, our findings only apply to the size class of pike studied (440 to 655 mm TL), to summer months (July and August at a latitude of 46° north), and to movement performed over a temporal scale of approximately 8 hours (i.e. the average time between two consecutive fish positions included in all the analyses, except for the longitudinal range, were 8.36 hours in Mississagi River and 8.35 hours in Aubinadong River). To date, most studies on the effect of short-term flow changes on fish behaviour were conducted on single systems (e.g. Gorski et al. 2014, Pauwels et al. 2014, Piper et al. 2013, Taylor et al. 2014a, Tripp et al. 2014), thus making it difficult to assess the indirect effects of flow regulation on fish populations. The approach chosen in the present study, which allows among-river comparisons of fish movement, enhances our understanding of the potentially adverse effects of flow regulations on fish.

2.5. Acknowledgements

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Council of Canada, (NSERC) HydroNet. All work reported herein was conducted in accordance with the guidelines of the animal care committee of the Université de Montréal and was approved by Ontario Ministry of Natural Resources and Ontario Parks.

Chapitre 3 La réponse au stress diffère entre des grands brochets qui proviennent de rivières régulée et non régulée lorsqu’ils sont soumis à une augmentation de la vitesse d’eau

Differential stress response to an increase in water velocity in a wild top predator living in rivers with contrasting flow regimes

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Abstract

The fish physiological responses to specific environmental challenges may vary depending on the previous experience that fish acquire in the ecosystem in which they live. The effect of water velocity variations *per se* on the stress response of wild fish inhabiting rivers subjected to natural and /anthropogenic perturbations remains unclear. This study elucidates the stress response (plasma cortisol, blood glucose and blood lactate) of wild northern pike (*Esox lucius* L.) to a water velocity variation (from 0 $m \cdot s^{-1}$ to 0.20 $m \cdot s^{-1}$) in a common garden experiment, using swimming tunnels installed directly in rivers. Pike were collected in two rivers with contrasting flow regimes located in northeastern Ontario, Canada: the Mississagi River, a river subjected to extreme daily flow variations (6 to 307 $m^3 \cdot s^{-1}$ within 3-4 hours) associated to hydroelectric operations (i.e., hydropeaking), and the Aubinadong River, an unregulated river. Our results show that fish inhabiting the two rivers respond differently when exposed to an increase in water velocity. Our study also suggests that the blood glucose concentration may be a more predictable and reliable indicator of fish stress than plasma cortisol in common garden experiments. These findings demonstrate that a change in the water velocity can stress wild fish, but that they have the capacity to modulate their stress response to conditions that prevail in their natural environment.

Key words: physiology, cortisol, glucose, lactate, stress response, northern pike

3.1. Introduction

Fish typically face many biotic and abiotic challenges that vary in nature and intensity depending on the ecosystem from which they originate. Challenges that threaten fish homeostasis, the stability of the organism's physiological parameters (e.g. blood glucose, Cannon 1932), are defined as stressors (Koolhaas et al. 2011). In response to stressors, fish activate two pathways: the hypothalamic-sympathetic-chromaffin cells (HSC) and the hypothalamic–pituitary–interrenal (HPI) axes (Wendelaar-Bonga 1997). Fish HSC axis corresponds to a prompt release of plasma catecholamines (CA), the epinephrine and the norepinephrine, *via* the chromaffin cells located in the head kidney (Gesto et al. 2014). The increase of plasma CA results in the activation of hepatic β-adrenoceptors and subsequently to hyperglycemia through glycogenolysis (Fabbri et al. 1998). The response by the HPI axis leads to the secretion of glucocorticoids, cortisol in teleostean fish, by the interrenal cell located in the head kidney (Donaldson 1981, Randall and Ferry 1992, Romero 2004). An increase in cortisol can also promote gluconeogenesis and glycogenolysis metabolic pathways, thus resulting in an increase in fish blood glucose (Laiz-Carrión et al. 2003, Mommsen et al. 1999). The accumulation of blood lactate is another metabolic consequence happening conjointly during the stress response, caused by fish hyperactivity (i.e. intense swimming) or hypoxia. Blood lactate is also a dynamic intermediate involved in carbohydrate metabolisms, particularly in gluconeogenesis and glycogenolysis pathways (Omlin et al. 2014, Philp et al. 2005).

Laboratory studies on fish stress response have found that an increase in water velocity results in an increase in plasma cortisol (Nielsen et al. 1994, Zelnik and Goldspink 1981), blood glucose (Nielsen et al. 1994), and blood lactate (Van Ginneken et al. 2002). It has also been shown that fish stress response can be modulated through repeated sessions of sustained swimming (*via* water velocity increases), a practice that results in exercise conditioning (Palstra and Planas 2011). Woodward and Smith (1985) found that the plasma cortisol and glucose were significantly decreased for fish that have been exercised at 1.5 bl (body length) s^{-1} when compared to fish that were kept in still water. A lower increase in blood lactate concentrations for exercise conditioned fish than for non-exercised control has been reported by laboratory studies on rainbow trout (*Oncorhynchus mykiss*; Hernández et al. 2002, Pearson et al. 1990), striped bass (*Morone saxatilis*;Young and Cech Jr 1993), and common carp (*Cyprinus carpio*; He et al. 2013).

The modulation of the stress response capacity by exercise conditioning in laboratory indicates that fish could also be capable of such modulation in the wild. Water velocity has long been known to affect fish habitat use in rivers (Guay et al. 2000, Jackson et al. 2001, Senay et al. 2015). The spatial variability of water velocity is a key element of habitat heterogeneity in rivers (Lin et al. 2015). Understanding the mechanisms that determine fish habitat use or shift in a heterogeneous environment is essential to predict their spatial distribution (Aarts et al. 2008). Fish stress response to environmental conditions constitutes a mechanism by which a fish remains in a particular habitat or shifts from one habitat to another (Homyack 2010). Identifying the effects of specific environmental conditions on wild fish stress response is crucial to elucidate this mechanism, particularly because the habitat selection can result in elevated costs associated to the maintenance of homeostasis in challenging environment(King et al. 2016), which in turns can affect fish survival and reproduction (Romero et al. 2009).

Water velocity in a river habitat can be temporally very dynamic with hourly to annual variations due to flow ($m^3 \cdot s^{-1}$) modifications related to natural (e.g. rain, ice melt, drought) and/or anthropogenic perturbations (e.g. hydropower, irrigation: Bunt et al. 1999, Scruton et al. 2003, Valentin et al. 1996). In particular, hydropeaking is an operational strategy that implies repeated (once or twice per day), rapid (within minutes to hours) and important (many-fold) changes to river flow downstream of the dam to produce electricity when it is most needed (Cushman 1985). Northern pike (*Esox lucius* L.) is a top predator found in lakes, rivers, and brackish waters of the northern hemisphere (Craig 2008). Pike tend to prefer habitats having low water velocities where they ambush their prey and capture using brief anaerobic bursts (Raat 1988, Savino and Stein 1989). In a hydropeaking river, a pike can be suddenly exposed to a rapid increase in water velocity due to many-fold changes in river flow. Pike can cope with an increasing water velocity by either holding its position, or moving to find suitable new environmental conditions. Both situations would result in an increased swimming speed, a mechanism that could lead to exercise conditioning. We, therefore, hypothesized that the stress response to an increase in water velocity of pike originating from a hydropeaking river is diminished when compared to that of pike originating from an unregulated river.

Field studies may permit to test the effect of flow conditions on the stress response of wild fish. However, field studies are subjected to the effects of confounding factors (other environmental conditions often co-varying with water velocity) that complicate the assessment of the linkage between fish stress response and water velocity variations (Pottinger et al. 2011). One strategy that would allow researchers to assess the effect of water velocity variations *per se* on the stress response of wild fish is to design swimming tunnels installed directly in the river in a common garden experiment. This novel experimental setting would allow an increasing number of studies to be conducted on wild fish in remote locations, without the elevated cost of transporting and keeping fish in laboratory tanks and swimming tunnels.

The objectives of this study are 1) to test, using swimming tunnels installed directly in rivers, the existence of an increase in plasma cortisol, blood glucose and blood lactate concentrations, following an increase in water velocity, and 2) to test the hypothesis that the stress response of fish originating from a regulated river (hydropeaking: fish subjected to frequent, rapid, and important flow variations) differs from that of fish originating from an unregulated river.

3.2. Methodology

3.2.1. Ethical procedures

All work reported herein was conducted in accordance with the guidelines of the animal care committee of the Université de Montréal and was approved by Ontario Ministry of Natural Resources and Ontario Parks.

3.2.2. Study rivers

Our study was conducted in two rivers in northeastern Ontario (Canada) having contrasting flow regimes (Figure 1). The Mississagi River is regulated by Aubrey Falls Dam, a hydroelectric installation operated as a hydropeaking facility, since its construction in 1969. Consequently, on any given day, flow in the Mississagi River can change from 6 $m^3 \cdot s^{-1}$ (minimal flow) to 307 $m^3 \cdot s^{-1}$ (maximum flow; a 500 % increase) within 3-4 hours (average daily flow = 38 $m^3 \cdot s^{-1}$). Hourly flow data provided by Brookfield Renewable Power, which operates Aubrey Falls dam, has shown that, from 2004 to 2014, the operational strategy has been consistently hydropeaking with minor inter-seasonal and -annual differences. The Aubinadong River is an unregulated river that flows into the Mississagi River 15 km downstream of Aubrey Falls Dam (Figure 1). The flow of the Aubinadong River (average daily flow = 15 $m^3 \cdot s^{-1}$; Government of Canada 2014) can change at most by 30 % (went from 97 to 126 $m^3 \cdot s^{-1}$ in 4 hours at the fall of 2013). Mississagi and Aubinadong rivers are similar in terms of watershed area, altitude, morphology, fish densities (Harvey-Lavoie et al. 2016), and fish community (14 species being present in the Aubinadong River and 13 in the Mississagi River, with only blacknose dace [*Rhinichthys atratulus*] being absent from the latter; Macnaughton et al. 2015a).

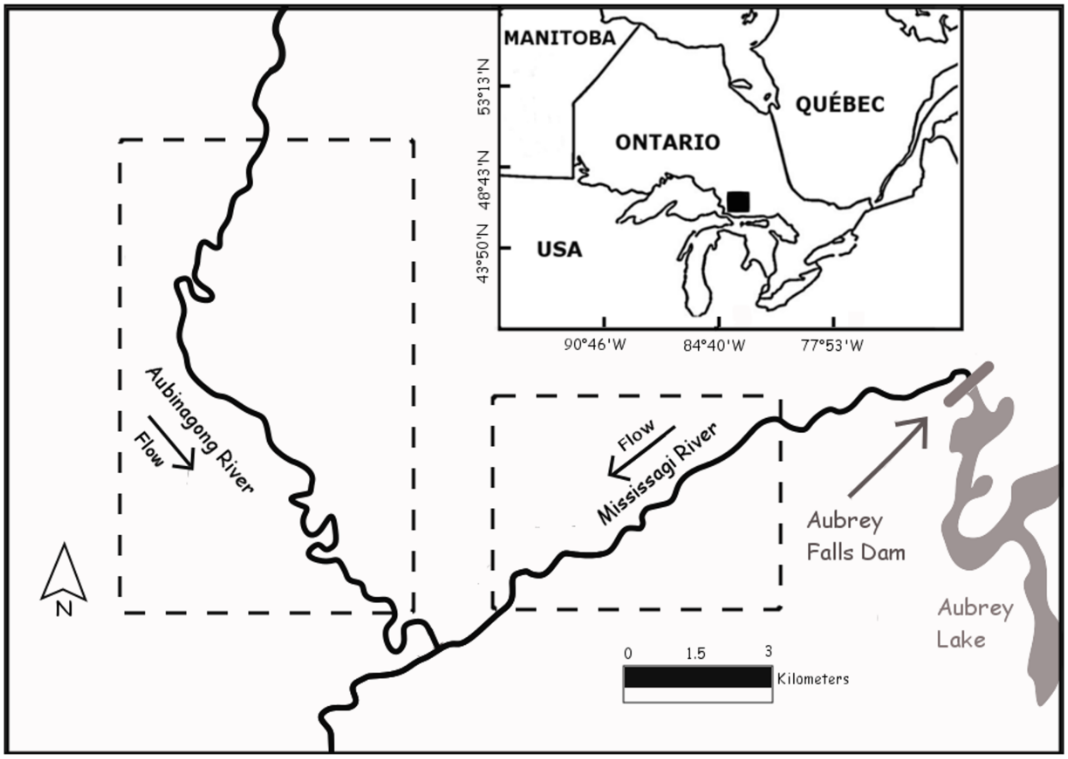

Figure 1 Map of the study rivers (the Mississagi and Aubinadong rivers; northeastern Ontario, Canada). The black square in the inset represents the location of the study area in Canada. The dashed-line squares correspond to the study segments where fish were captured.

3.2.3. Fish capture and experimental design

We achieved our objectives by exposing fish originating from the regulated and unregulated rivers to two water velocities and by estimating concentrations of plasma cortisol and blood glucose and lactate in these fish. Exposing one fish to one particular water velocity (hereafter referred to as an experiment) was conducted only in the unregulated river because flow and water velocity at any given location, in the regulated river were too variable to conduct experiments. This situation implies that, in addition to our two objectives, we also had to assess and confirm that the transfer of fish from the regulated to the unregulated river had no effect on their stress response.

Experiments were conducted between July 5th and August 13th 2012 (32 experiments with 17 individuals from the Mississagi River and 15 individuals from the Aubinadong River) and between August 4th and 28th 2013 (15 experiments with 10 individuals from the Mississagi River and 5 individuals from the Aubinadong River). Fish from Mississagi River were captured on an 8 km segment (80 m<river width<180 m) located from 5 km (46° 53′ 57″ N, 83° 16′ 9″ W) to 13 km (46° 51' 44"N, 83° 20' 49"W) downstream Aubrey Falls Dam. Fish from Aubinadong River were collected over a 19.5 km segment (20 m<river width<115 m) located from 21.5 km (46° 57' 12"N, 83° 25' 14" W) to 2 km (46° 51' 48"N, 83° 22' 40" W) upstream from the junction of the Aubinadong and Mississagi rivers.

Fish were captured by angling from a canoe or from the shore using a variety of barbless artificial lures and nylon monofilament lines (4.5 kg test). To minimize capture stress, fish were swiftly reeled near the canoe or the shore, taken using a rubber dip net, and placed in an insulated container (990 x 480 x 480 mm) filled with well-aerated river water. The lure was removed using pliers, while the fish remained in the water to ensure minimal handling stress. Such handling practices promote high survival and rapid physiological recovery in pike (Arlinghaus et al. 2009). Fish were individually kept in the insulated container and brought to either of the two experimental sites. These sites consisted in a 200 m x 5 m river section adjacent to shore of the

Mississagi River where depth averaged 1.5 m (range = 0.00 – 3.00 m) and water velocity averaged 0.10 $m \cdot s^{-1}$ (range = 0.00 – 0.27 $m \cdot s^{-1}$) and a 200 m river segment of the Aubinadong River where depth averaged 1.00 m (range = 0 - 1.75 m) and water velocity averaged 0.15 $m \cdot s^{-1}$ (range = 0 - 0.30 $m \cdot s^{-1}$).

An experiment consisted in introducing a single fish from either the Mississagi or Aubinadong River in a cylindrical swimming tunnel placed in an experimental site to subject the fish to a particular treatment (i.e. experimental condition). The three swimming tunnels used for experiments consisted in poly-vinyl chloride cylinders having a diameter of 0.30 m and a length of 1.15 m. Three cm grids were affixed to both extremities of the swimming tunnels to allow the presence of flow in, and to prevent fish from escaping from, the swimming tunnels. Removable wood panels were fitted on the grids to decrease water velocity into the swimming tunnels to 0.00 $m \cdot s^{-1}$. The swimming tunnels were perforated by 30 holes (diameter of 0.01 m) evenly distributed on their surface to allow the entry of fresh river water throughout the experiments (particularly when the wood panels were closed). A rectangular flap (60 cm x 20 cm) was cut on one side of the swimming tunnels (the side facing upward during experiments) to permit fish introduction to, or retrieval from, the swimming tunnel.

The experiments encompassed 3 treatments: the resting control (water velocity in the swimming tunnel = 0.00 $m \cdot s^{-1}$; no opening of the wood panels), the negative control (water velocity in the swimming tunnel = 0.00 $m \cdot s^{-1}$; wood panels opened for 20 minutes), and the swimming trial (water velocity in the swimming tunnel = 0.20 $m\ s^{-1}$; wood panels opened for 20 minutes). Preliminary sampling indicated that it was impossible to maintain a particular water velocity in swimming tunnels installed in the Mississagi River when wood panels were open because of the hydropeaking taking place at Aubrey Falls Dam. Consequently, negative controls and swimming trials could be conducted only in the Aubinadong River. Fish from the Mississagi River had to be transported from this river to the experimental site of the Aubinadong River to conduct these experiments (i.e. resting controls were the only experiments conducted in the Mississagi River and only for some Mississagi fish). In the Aubinadong River, the resting and negative controls were conducted by placing the swimming tunnels in a low flow area of the experimental sites that was surrounded by a rock wall that decreased water velocity in this area to $0.00\ \mathrm{m \cdot s^{-1}}$. The swimming trials were conducted by placing the swimming tunnels in an area of the experimental site that had a water velocity of $0.20\ \mathrm{m \cdot s^{-1}}$.

Water velocity in a swimming tunnel used for any given treatment was taken at ten locations inside this swimming tunnel using a Marsh-McBirney Flo-Mate2000 flow meter (Hach Company, Loveland, CO, USA). The ten locations were evenly distributed along three axes located at the top third (3 locations), the middle (4 locations), and the bottom third (3 locations) of the swimming tunnel when positioned horizontally (as installed in the river). This operation was repeated prior to each experiment, and the swimming tunnel was eventually repositioned, until the mean water velocity inside it was equal to that targeted for the treatment ($0.00\ \mathrm{m \cdot s^{-1}}$ or $0.20\ \mathrm{m \cdot s^{-1}}$ with a standard deviation $\leq 0.02\ \mathrm{m \cdot s^{-1}}$). Fish were allowed to rest for 24 hours following their introduction in a swimming tunnel. Previous studies on pike have shown that physiological indicators return to basal values within 12 hours post-handling (Arlinghaus et al. 2009, Schwalme and Mackay 1985). For this reason, a 24 hours period was deemed sufficient for pike to fully recover from the capture by angling. Fish used as resting controls were blood sampled immediately after this 24 h period.

For negative control and swimming trial treatments, the swimming tunnels containing the fish were approached laterally such that the fish could not see the experimenters, and the wood panels were carefully removed to minimize fish stress. These fish were subjected to water velocities of 0.00 m s^{-1} or 0.20 m s^{-1} for 20 minutes before being blood sampled. Fish were blood sampled within three minutes after their retrieval from a swimming tunnel to avoid responses in plasma cortisol, blood lactate and blood glucose related to fish handling (Gamperl et al. 1994, Sumpter 1997). Each blood sample (0.5-1.0 mL) was taken by puncture of the caudal vessel with a 21G Precision Glide BD Vacutainer® needle fitted to a 2 mL BD Vacutainer® tube coated with 37 USP lithium heparin (Ostrander 2000). Fish were subsequently placed in an insulated container (990 x 480 x 480 mm) filled with well-aerated river water. Fish total length (TL, in mm), sex (external examination; Casselman 1974), river water temperature (°C; Traceable thermometer, ThermoFisher Scientific, USA), swimming tunnel identity (number associated to a particular swimming tunnel; 1-3), and time of day were recorded at the end of each experiment (time at which a fish was retrieved from a swimming tunnel). Ectoparasite load (number of trematode grubs on the skin taking the form of black dots probably corresponding to *Uvulifer ambloplitis*; Lemly and Esch 1984) was recorded for every fish because of its anticipated effect on fish stress (Tveiten et al. 2010). Fish were returned to their point of capture immediately after data collection.

3.2.4. Blood sample analysis

Immediately after blood sampling, two portable handheld meters were used to estimate the blood glucose ($mmol \cdot L^{-1}$; Accu-Check, Roche, Canada; detection limit: 0.6 - 33.3 $mmol \cdot L^{-1}$) and lactate ($mmol \cdot L^{-1}$; Lactate Pro, Arkray Inc., Japan: detection limit: 0.8 to 23.3 $mmol \cdot L^{-1}$) concentrations. A small amount of whole blood (Accu-check: 0.001 mL; Lactate Pro: 0.001 mL) was transferred to a meter specific test strip, previously inserted in either the Accu-Check or Lactate Pro. Validation of these portable instruments to estimate blood glucose and concentrations in the field was done, respectively, by Cooke et al. (2008) and by Brown et al. (2008). The remaining blood from any given fish was transferred with a pipette in a micro-centrifuge tube (1.5 mL with screw cap, Fisher Scientific, USA), and immediately centrifuged (3000 rpm, 5 min.) with a micro-centrifuge (model Lx100, Chang Bioscience, CA, USA). The supernatant was transferred to a second micro-centrifuge tube and stored in liquid nitrogen for further analyses. Plasma cortisol concentration ($ng \cdot mL^{-1}$) analyses were conducted at Université de Montréal on March 15 2013 for samples collected in 2012 and on October 23 2014 for samples collected in 2013. Duplicates of diethyl ether ($(C_2H_5)_2O$) extracted plasma samples were analyzed by enzyme-linked immuno-sorbent assay (ELISA) quantification (cat # 402710, Neogen corp, KY, USA), a method previously validated for measurement of total plasma cortisol in teleostean fish (Hosoya et al. 2007, Velasco-Santamaría and Cruz-Casallas 2007). In the present study, intra- and inter-assay coefficients of variation obtained using this method are, respectively, 7% and 8%.

3.2.5. Statistical analyses

The effect of transporting fish from Mississagi River to Aubinadong River was tested using the stress indicators of Mississagi fish subjected to the resting control treatment in the Mississagi River and those of Mississagi fish subjected to the resting control treatment in the Aubinadong River. Using multiple linear regression (MLR; Zuur et al. 2007), plasma concentration in cortisol and blood concentrations in lactate and glucose were taken as a quantitative response variables and the effect of the river where the resting control was performed (Mississagi or Aubinadong River) was taken as a categorical explanatory variables. To control for other explanatory variables that could have an effect on the stress indicator of pike, mass, total length, water temperature and ectoparasite load were added to the MLR as quantitative explanatory variables, and swimming tunnel number and sex were added to the MLR as qualitative exploratory variables. It has been shown that daily rhythms such as feeding behaviour or activity patterns (López-Olmeda and Sánchez-Vázquez 2010) or circadian (endogenous) rhythm (Olivera et al. 2013) can affect fish plasma cortisol concentrations. The potential bias from daily or circadian rhythms on plasma cortisol concentrations was controlled by adding the time of the day at which sampling took place to the MLR as a qualitative explanatory variable. Moreover, a visual observation of the plot of plasma cortisol concentrations against time of the day was conducted, and the absence of a clear pattern in the data confirmed that there was no bias associated to this variable.

The objectives of the study were assessed by developing one MLR for every three stress indicators. In this analysis, plasma concentration in cortisol and blood concentrations in lactate and glucose were taken as a quantitative response variable, total length, water temperature, ectoparasite load and time of the day were taken as quantitative explanatory variables, and swimming tunnel number, sex, treatment and river of origin (Mississagi River or Aubinadong River) were taken as categorical explanatory variables.

MLR were developed using a backward elimination, beginning with a model including all explanatory variables and the interactions between two categorical variables: treatment and river of origin. This strategy was adopted because it is our objective to test the hypothesis that the stress response of fish originating from a regulated river differs from that of fish originating from an unregulated river (i.e. the interaction between response and river of origin). Explanatory variables and interactions terms that had no statistically significant effects on a stress indicator were removed successively, beginning with the variable or interaction term having the largest P-value found by an analysis of variance test (ANOVA with F-test; Zuur et al. 2009). When statistically significant interactions were found, the dataset was subdivided by river of origin so that the treatment effect could be analyzed by its own. Goodness of fit was represented by the adjusted R-squared (R^2_{adj}; Zuur et al. 2007). To find which experimental treatments were significantly different from each other, Tukey's multiple comparisons (TMC) of the means were conducted on each of the MLR, but only when the experimental treatment effect was significant. All statistical analyses were conducted with R (R Development Core Team, 2014).

3.3. Results

Stress indicators of Mississagi fish (n=8) used as resting controls in Mississagi River did not vary significantly from those of Mississagi fish used as resting controls in the Aubinadong River (n=6; Table 1). Transporting fish from the Mississagi to the Aubinadong River therefore had no statistically significant effect on plasma cortisol concentrations (p = 0.946), and blood concentrations in glucose (p = 0.588) and lactate (p = 0.590). Consequently, all Mississagi fish used as resting controls (either in Mississagi or in Aubinadong rivers) were pooled for further analysis.

Table 1 Concentrations in plasma cortisol ($ng \cdot mL^{-1}$), blood glucose ($mmol \cdot L^{-1}$) and blood lactate ($mmol \cdot L^{-1}$) of fish originating from Mississagi River, following a 24 hours resting period in either Aubinadong or Mississagi rivers.

		Cortisol ($ng \cdot mL^{-1}$)	**Glucose** ($mmol \cdot L^{-1}$)	**Lactate** ($mmol \cdot L^{-1}$)
Resting in Aubinadong River	***Mean ± SE***	139.65 ± 36.47	5.47 ± 1.21	1.13 ± 0.17
	Min-Max	68.1-309	3.6-11.4	0.9-1.9
	n	6	6	6
Resting in Mississagi River	***Mean ± SE***	142.45 ± 20.41	4.56 ± 0.38	1.29 ± 0.17
	Min-Max	23.1-207.6	2.3-6	0.9-2.3

n	8	8	8

A total of 47 experiments (21 resting controls, 12 negative controls, and 14 swimming trials), each involving a particular fish, were used for analyses (Table 2). 27 of these experiments involved fish from the Mississagi River (14 resting controls, 6 negative controls, and 7 swimming trials), whereas 20 involved fish from the Aubinadong River (7 resting controls, 5 negative controls, and 8 swimming trials). Fish total length ranged from 444 to 645 mm (average = 553 mm), ectoparasite load ranged from 0 to 28 grubs/fish (average = 5 grubs/fish), experiments were conducted at water temperature that ranged from 17.9 to 26.7 °C (average = 21.6 °C) and took place throughout all daytime from 7:23 to 17:20 (average = 11:44; Table 2). In total, 28 pike were females, 19 pike were males and fish were placed 18 times in swimming tunnel number 1, 18 times in swimming tunnel number 2 and 11 times in swimming tunnel number three (Table 2).

Table 2 The number of replicates (*n*), mean (range) fish total length, mean (range) water temperature, mean (range) ectoparasite load, mean (range) time of the day, number of females/number of males, number of fish place in each individual swimming tunnel (ST), and mean (range) plasma cortisol, blood glucose and blood lactate concentrations in fish, by treatment and river of origin.

		River of origin	
Treatment		**Mississagi**	**Aubinadong**
Resting control	*n*	14	7
	Total length (mm)	559 (486-634)	540 (446-615)
	Water temperature (°C)	20.7 (18.5-24.3)	22.9 (21.7-24.7)

	Ectoparasite load (number of grubs)	5 (0-25)	4 (0-9)
	Time of the day (hours: minutes)	11:20 (7:23-16:30)	10:19 (7:36-13:00)
	Sex (number of female/number of male)	9 F/ 5 M	2 F/ 5M
	ST (number of fish placed in: ST 1/ST 2/ST 3)	8/4/2	2/4/1
	Cortisol concentration (ng·mL^{-1})	141.25 (23.1-309.0)	198.5 (60.7-370.2)
	Glucose concentration (mmol·L^{-1})	4.95 (2.3-11.4)	4.5 (3.4-5.3)
	Lactate concentration (mmol·L^{-1})	1.22 (0.9-2.3)	2.14 (0.9-5.9)
Negative control (0.00 m/s)	*n*	7	5
	Total length (mm)	550 (444-645)	548 (488-576)
	Water temperature (°C)	20.6 (17.9-23.4)	21.7 (18.9-23.3)
	Ectoparasite load (number of grubs)	7 (0-28)	6 (0-12)
	Time of the day (hours: minutes)	12:58 (9:11-16:50)	14:17 (9:00-17:20)
	Sex (number of female/number of male)	6 F/ 1 M	4 F/ 1M
	ST (number of fish placed in: ST 1/ST 2/ST 3)	3/2/2	1/2/2
	Cortisol concentration (ng·L^{-1})	173.6 (36.6-323.4)	133.3 (94.7-190.2)
	Glucose concentration (mmol·L^{-1})	5.1 (3.2-9.3)	5.02 (4.4-5.7)
	Lactate concentration (mmol·L^{-1})	4.56 (0.9-11.9)	2.12 (0.9-5.6)
Swimming (0.20 m/s)	*n*	6	8
	Total length (mm)	547 (490-604)	506 (445-603)
	Water temperature (°C)	23.9 (18.6-26.3)	24.0 (19.0-26.7)
	Ectoparasite load (number of grubs)	6 (0-19)	4 (0-18)
	Time of the day (hours: minutes)	11:09 (8:14-14:45)	11:05 (8:05-14:45)
	Sex (number of female/number of male)	3 F/ 3 M	4 F/ 4 M
	ST (number of fish placed in: ST 1/ST 2/ST 3)	2/2/2	2/4/2
	Cortisol concentration (ng·mL^{-1})	169.4 (98.5-274.6)	266.75 (161.1-370.2)
	Glucose concentration (mmol·L^{-1})	5.6 (4.1-7.4)	8.31 (4.6-13.6)
	Lactate concentration (mmol·L^{-1})	4.53 (3.7-7.1)	7.44 (2.8-11.3)

3.3.1. Plasma cortisol concentrations

Plasma cortisol concentrations ranged from 23 to 370 ng·mL^{-1} (average = 178.7 ng·mL^{-1}; Figure 2) across experiments. The ectoparasite load (F = 6.87, p = 0.012), the treatment (F = 3.93,

$p = 0.027$), and the river of origin (F = 4.82, p = 0.034) explained 25% (R^2_{adj}) of this variation (Table 3). It is noticeable that the interaction between water velocity and the river of origin approached the level of statistical significance (F = 3.06, p = 0.058; Table 3). Plasma cortisol concentrations in pike swimming at 0.20 m·s^{-1} were significantly different than that of negative controls (p = 0.043), and only marginally significantly different than that of resting controls ($p = 0.077$). No significant difference in plasma cortisol concentrations was detected between negative and resting controls ($p = 0.975$).

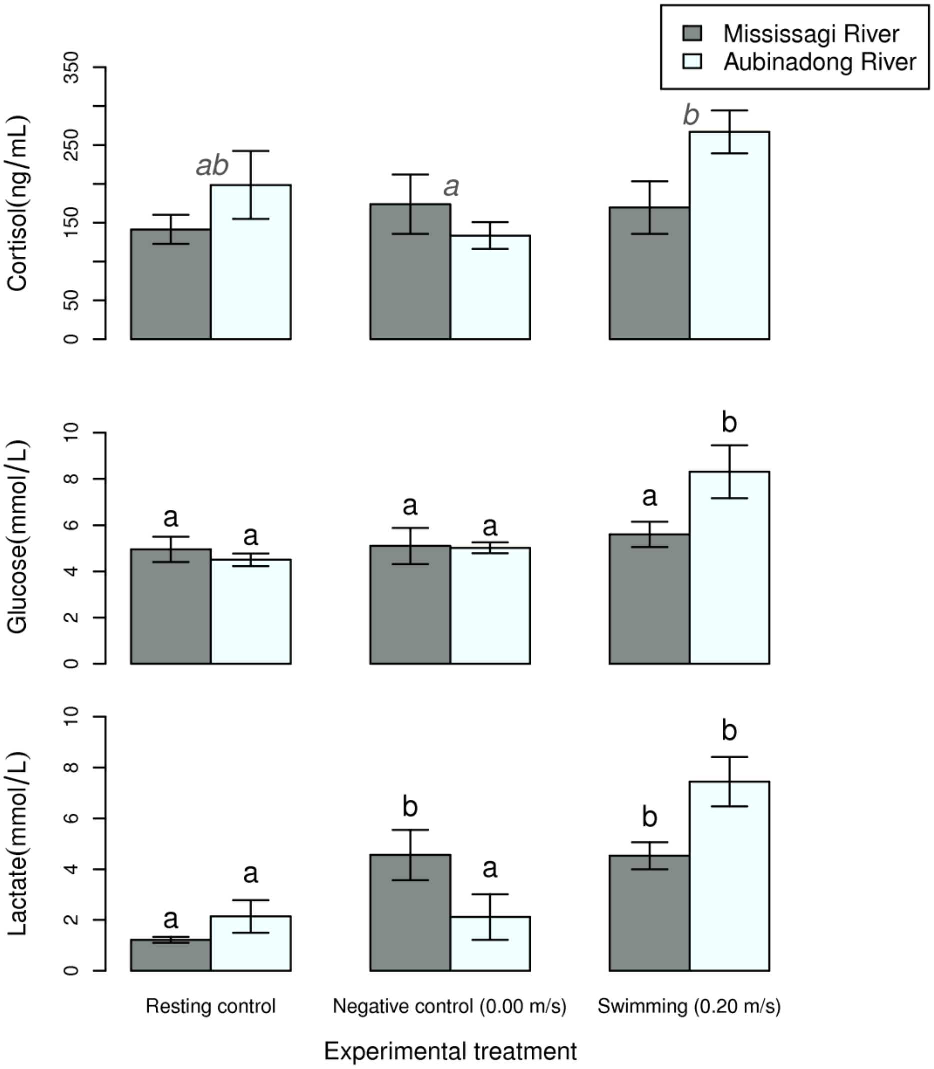

Figure 2 Mean ± SEM concentrations of plasma cortisol, blood glucose, and blood lactate of northern pike subjected to the resting control (Mississagi River = 14 fish, Aubinadong River = 7 fish), the negative control (Mississagi River = 7 fish, Aubinadong River = 5 fish), or the swimming treatment at 0.20 $m \cdot s^{-1}$ (Mississagi River = 6 fish, Aubinadong River = 8 fish). In the case when no significant interaction term was found for a specific physiological indicator (i.e. plasma cortisol, blood glucose or blood lactate), MLR were conducted for both rivers pooled together and the different grey italicized letters represent among-experimental treatment differences for both rivers together. In the contrary, when a significant interaction was found for a specific physiological indicator, MLR were conducted separately for each river and therefore the black letters in the figure represent among-experimental treatment differences within each river.

3.3.2. Blood glucose concentrations

Blood glucose concentrations ranged from 2.3 to 13.6 $mmol \cdot L^{-1}$ (average = 5.57 $mmol \cdot L^{-1}$; Figure 2) across experiments. The ectoparasite load (F= 11.04, p = 0.002), the treatment (Figure 2; F = 7.80, p = 0.001), and the interaction between the treatment and the river of origin (F = 3.81, p = 0.031) explained 39% (R^2_{adj}) of the variation in blood glucose concentrations (Table 3). Given the statistical significance of the interaction term between the treatment and the river of origin, a specific MLR was developed for each river to test the effect of the treatment alone on the blood glucose concentrations. For fish originating from the Mississagi River, the ectoparasite load (F = 18.37, p < 0.001) explained 40 % (R^2_{adj}) of the variance in blood glucose concentrations (Table 3). No TMC was conducted on this MLR because the treatment did not significantly affect glucose concentrations. In contrast, for fish originating from the Aubinadong River, the treatment (F = 8.66, p = 0.003) and the sex (F = 5.60, p = 0.031) explained a total of

51% (R^2_{adj}) of the variance of this stress indicator (Table 3). Blood glucose concentrations in Aubinadong River pike swimming at 0.20 $m \cdot s^{-1}$ were significantly different than that of the resting controls ($p = 0.004$) and the negative controls ($p = 0.006$). For this same river, no significant difference was detected in blood glucose concentrations between negative controls and the resting controls ($p = 0.976$).

Table 3 The parameters, type II sums of squares (Type II SS), *F*-value (F) and probability associated to *F* (*P*-value) of the analysis of variance conducted on the multiple linear regression (MLR) of the models built on plasma cortisol, blood glucose and blood lactate concentrations of fish originating from Mississagi and Aubinadong rivers, with the adjusted R^2 (R^2_{adj}; variance explained by the explanatory variables in the MLR).

		Cortisol (ng·mL^{-1})			**Glucose (mmol·L^{-1})**			**Lactate (mmol·L^{-1})**		
Model	**Parameters**	**Type II SS (d.f)**	***F***	**P-value**	**Type II SS (d.f)**	***F***	**P-value**	**Type II SS (d.f)**	***F***	**P-value**
1-Both rivers	**Ectoparasite (counts/fish)**	**42802(1)**	**6.87**	**0.012**	**35.70(1)**	**11.04**	**0.002**	0.20(1)	0.04	0.836
	River	**30022(1)**	**4.82**	**0.034**	**4.41(1)**	**1.36**	**0.250**	**4.64(1)**	**1.00**	**0.323**
	Treatment	**49006(2)**	**3.93**	**0.027**	**50.44(2)**	**7.80**	**0.001**	**182.94(2)**	**19.74**	**< 0.001**
	Treatment : River	34762(2)	3.06	0.058	**24.64(2)**	**3.81**	**0.031**	**45.56(2)**	**4.92**	**0.012**
	Length (mm)	10224(1)	1.80	0.188	3.60(1)	1.12	0.298	2.15(1)	0.48	0.493
	Sex	1476(1)	0.26	0.616	1.72(1)	0.52	0.475	1.87(1)	0.41	0.526
	Swimming tunnel number	2498(2)	0.20	0.822	8.00(2)	1.26	0.308	9.64(2)	1.08	0.349
	Time of the day (h)	1962(1)	0.33	0.568	1.19(1)	1.22	0.555	12.19(1)	2.66	0.111
	Wat. Temp. (°C)	449(1)	0.07	0.787	5.48(1)	1.68	0.203	0.53(1)	0.12	0.736
	Residuals	**261679 (42)**	**-**	**-**	**129.36(40)**	-	-	**190.02(41)**	**-**	**-**
	R$^2_{adj}$	0.25			0.39			0.50		
2- Mississagi River	**Ectoparasite (counts/fish)**	NA			**38.68(1)**	**18.37**	**< 0.001**	3.20(1)	0.88	0.360
	Treatment				1.79(2)	0.40	0.674	**74.51(2)**	**8.65**	**0.001**
	Length (mm)				2.36(1)	1.06	0.314	1.77(1)	0.50	0.489
	Sex				0.16(1)	0.06	0.807	8.02(1)	2.20	0.153
	Swimming tunnel number				4.59(2)	1.04	0.372	18.93(2)	2.46	0.108
	Time of the day (h)				0.23(1)	0.10	0.757	0.01(1)	0.00	0.962
	Wat. Temp. (°C)				0.20(1)	0.08	0.779	0.01(1)	0.00	0.953
	Residuals				**52.64(25)**			**103.41(24)**	**-**	**-**
	R$^2_{adj}$				0.40			0.37		
3- Aubinadong River	**Ectoparasite (counts/fish)**	NA			2.26(1)	0.53	0.482	**26.26(1)**	**9.04**	**0.009**
	Treatment				**62.85(2)**	**8.66**	**0.003**	**136.07(2)**	**23.42**	**< 0.001**
	Length (mm)				0.11(1)	0.03	0.877	0.72(1)	0.22	0.648
	Sex				**20.32(1)**	**5.60**	**0.031**	0.004(1)	0.00	0.975
	Swimming tunnel number				9.94(2)	1.27	0.316	2.92(2)	0.40	0.679
	Time of the day (h)				4.54(1)	1.11	0.310	**16.24(1)**	**5.59**	**0.032**
	Wat. Temp. (°C)				4.82(1)	1.26	0.280	5.93(1)	1.92	0.188
	Residuals				**58.06(16)**			**43.58(15)**	**-**	**-**
	R$^2_{adj}$				0.51			0.75		

Variables separated by colon punctuation mark design interaction.

Explanatory variables in bold character were included in the final MLR models.

Wat.Temp. is the water temperature and length is the total fish length.

3.3.3. Blood lactate concentrations

Blood lactate concentrations ranged from 0.9 to 11.9 mmol·L^{-1} (average 3.43 mmol·L^{-1}; Figure 2) and were explained by the treatment (F = 19.74, $p < 0.001$) and the interaction between the treatment and the river of origin ($F = 4.92$, $p = 0.012$). The treatment and the interaction explained a total of 50% of the variation in blood lactate concentrations ($R^2_{\text{adj}} = 0.50$; Table 3). A specific MLR was developed for each river to tease apart the interaction between treatment and river of origin and therefore test the effect of the treatment alone on blood lactate concentrations. For fish originating from the Mississagi River, the variance in blood lactate concentrations was explained ($R^2_{\text{adj}} = 0.37$; Table 3) by the treatment ($F = 8.65$, $p = 0.001$). For this river, no statistical difference was observed between blood lactate concentrations of pike swimming at 0.20 m·s^{-1} and the negative controls ($p = 0.852$). However, blood lactate concentrations of resting controls were significantly different than that of negative controls ($p = 0.004$), and that of pike swimming at 0.20 m·s^{-1} ($p = 0.003$). For fish originating from the Aubinadong River, the variance in blood lactate concentrations was explained by the treatment ($F = 23.42$, $p < 0.001$), the ectoparasite load ($F = 9.04$, $p = 0.009$), and the time of the day ($F = 5.59$, $p = 0.032$). These variables explained 75% (R^2_{adj}) of the variation in blood lactate concentrations (Table 3). Blood lactate concentrations of Aubinadong River pike swimming at 0.20 m·s^{-1} were significantly different than that of the negative controls ($p < 0.001$), and resting controls ($p < 0.001$). No significant difference in blood lactate concentrations was detected between negative controls and resting controls, for the Aubinadong River ($p = 0.958$).

3.4. Discussion

Our results suggest that an increase in water velocity can stress wild fish, but that the way fish respond to this stressor can differ among rivers. The present study found that plasma cortisol concentrations of wild pike were significantly elevated following a 0.20 m s^{-1} increase in water velocity compared to that of fish maintained at a constant water velocity of 0.00 m s^{-1}. Previous findings showed that plasma cortisol concentrations of rainbow trout held in laboratory conditions increased by 70 % after swimming velocity was augmented from 0 to 1.0 $bl \cdot s^{-1}$ for 15 minutes (Zelnik and Goldspink 1981). Another laboratory study conducted on rainbow trout found that plasma cortisol concentrations showed no increase when swimming velocity was raised from 0 to 0.5 $bl \cdot s^{-1}$, but that this stress indicator increased by 171% when swimming velocity was raised from 0 to 1.5 $bl \cdot s^{-1}$ (Nielsen et al. 1994). In the present study, northern pike subjected to the 0.20 $m \cdot s^{-1}$ treatment were swimming at velocities ranging from 0.31 to 0.45 $bl \cdot s^{-1}$, depending on their total length. Plasma cortisol concentrations in pike swimming at velocities ranging from 0.31 to 0.45 $bl \cdot s^{-1}$ were 36 % higher than in negative controls. The fact that a swimming velocity of 0.5 $bl \cdot s^{-1}$ does not trigger an increase in plasma cortisol concentrations in rainbow trout but does in pike is consistent with the poor aerobic swimming capacities of the latter species (Jones et al. 1974). The difference between plasma cortisol concentrations of pike swimming at 0.20 $m \cdot s^{-1}$ and that of resting controls was only marginally significant. This situation is likely due to the highly variable cortisol concentrations among individuals. For this reason, further studies should consider an elevated sample size when comparing fish plasma cortisol concentrations in common garden experiments.

The response in plasma cortisol concentrations significantly differed between-river (significant effect of the river of origin in the cortisol MLR); the concentration was 34 % lower in the Mississagi River (hydropeaking) than in the Aubinadong River (unregulated). Previous studies have found a diminished plasma cortisol response for fish living in polluted environmental conditions (Blevins et al. 2014, Hontela et al. 1992, Norris et al. 1999) and in low quality habitats (degraded habitat due to lower percentages of wetland areas; King et al. 2016). An assessment of the indicators of water quality and pollutant (i.e. alkalinity, molybdenum, zinc, chromium, copper, dissolved oxygen, mercury, nickel, reactive chloride, reactive total nitrates, iron, lead, phosphorus, sodium, pH; Government of Canada [http://www.yourenvironment.ca/ontario-rivers.php]) in the Mississagi River indicated that for the years 2003-2005, the indicators have been consistently within the Canadian guidelines for stream water quality and pollutant (Gouvernement du Canada 2011). Therefore, it is very unlikely that the diminished HPI response in fish from the Mississagi River could be attributed to water pollutant or quality. Data on water quality and pollutants are not available for Aubinadong River, but fish in Aubinadong have an augmented HPI response in comparison that of Mississagi River pike, which is very unlikely to be caused by the water quality or pollutant. Both study rivers are also characterized by riverbanks typical of alluvial ecosystems, by an elevated sinuosity and number of wetlands. Still, a regulated river can differ from an unregulated river in a long suite of environmental variables such as wetted width, water depth and velocity (Zhong and Power 1996), substrate composition and distribution (via different erosion and sedimentation patterns; Osmundson et al. 2002), and aquatic plant diversity and abundance (Aronsuu et al. 1999). A number of these environmental variables and their interactions, all related to flow conditions, could be the cause of the diminished cortisol response of fish originating from the Mississagi River, but isolating the single variable (or a combination of variables) responsible for this difference was beyond the objective of this study. Nevertheless, our findings are novel because they demonstrate that the HPI response of wild fish living in rivers with contrasting flow regimes can significantly differ. Moreover, our findings add evidence that fish living in rivers subjected to anthropogenic activities have diminished cortisol response, which is consistent with previous studies (Blevins et al. 2014, Hontela et al. 1992, King et al. 2016, Norris et al. 1999). It is also the first mention, to our knowledge, that a hydropeaking flow regime, a type of anthropogenic activity, can affect the HPI axis response in fish.

The treatment effect on blood glucose concentrations depended on the river of origin. Increasing the water velocity from 0 to 0.20 $m \cdot s^{-1}$ had a significant effect on blood glucose concentrations in pike originating from the Aubinadong River, but had no effect on fish from the Mississagi River. Hammond and Hickman Jr. (1966) obtained similar results by conducting laboratory experiments with exercise-trained rainbow trout. One group of rainbow trout was held in still water for 16 days while two other groups of fish were conditioned, respectively, to a water velocity of 0.16 $m \cdot s^{-1}$ or 0.40 $m \cdot s^{-1}$. After 16 days of exercise conditioning, rainbow trout were forced to swim at 0.53 $m \cdot s^{-1}$ for 15 minutes. The authors found that blood glucose concentrations in fish held in still water was greater than in fish conditioned to 0.16 or 0.40 $m \cdot s^{-1}$. These results suggest that exercise conditioning could explain the different blood glucose concentrations in fish originating from Mississagi and Aubinadong rivers. Indeed, in the Mississagi River, the water velocities can vary many-fold due to drastic flow increases (e.g. from 6 to 307 $m^3 \cdot s^{-1}$ in 3−4 hours). In this river, it is expected that while holding a position in a given habitat, pike may experience important increases in water velocity (e.g. an increase from 0.10 to 0.40 $m \cdot s^{-1}$ in only 3−4 hours). Such an increase in water velocity would force pike to either hold location in this habitat or to change its location by seeking a flow refuge. Under both scenarios, pike are confronted to frequent and important increases in water velocity that may contribute to train them to this kind of challenge and to decrease their stress response when they face flow increases.

Recent stress studies indicate that our findings on blood glucose concentrations can be explained by the extent to which the applied challenge is controllable or predictable (Koolhaas et al. 2011). Pike originating from the regulated river are confronted to daily increases in water velocity due to important and drastic flow fluctuations. Accordingly, these predictable flow changes are part of the range of conditions to which pike in the Mississagi River have optimized behavioural and physiological mechanisms (a process that is called exercise training in laboratory studies). The variation in the physiological indicators' values over a set of normal ranges in environmental conditions experienced by an animal in its habitat is called the predictive homeostasis (Romero et al. 2009). Within these normal environmental conditions, called the regulatory ranges, optimized physiological and behavioural mechanisms developed for predictable variations provide the animal with a perception of control (Koolhaas et al. 2011). In the unregulated river, flow fluctuates over a much longer time lapse, and fluctuations are less important than that in the regulated river. The increase in water velocity experienced by pike in the swimming tunnel could be seen as an uncontrollable and unpredictable situation for pike originating from the unregulated river, but not for pike originating from the regulated river. In other words, such a change in water velocity would be outside the regulatory ranges of pike from the unregulated river only. A previous study showed that a repeated exposure to a stressor leads to a decrease in HSC axis activation, thus resulting in a decreased release in noradrenalin, a catecholamine that directly affects glucose mobilization (Scheurink et al. 1989). In agreement with this study, the increase in water velocity resulted in a HSC axis response (i.e. increase in blood glucose concentrations) for pike from the unregulated river, but not for pike from the regulated river. The stress physiology concepts presented by Koolhaas et al. (2011) and Romero et al. (2009) were mostly demonstrated using mammals (Ferrari et al. 2003, Fokkema et al. 1995, Sapolsky 1995). Studies on the extent to which stressors are controllable or predictable for fish in the wild are rare, although understanding these mechanisms is crucial to predict wild fish habitat selection and therefore, their survival and reproduction.

The treatment effect on blood lactate concentrations followed the same trend as blood glucose concentrations and also depended on the river of origin. Blood lactate concentrations for fish from the Aubinadong River swimming at 0.20 $m \cdot s^{-1}$ were respectively 247% and 250% higher than the values observed for resting and negative controls. In contrast, fish from the Mississagi River did not show an increase in blood lactate concentrations after swimming at 0.20 $m \cdot s^{-1}$ for 20 minutes (i.e. 4% difference for this stress indicator between the negative controls and the swimming treatment). Exercise conditioning can explain between-river differences in stress responses given that this mechanism promotes higher metabolic response capacity and increases intra-specific critical swimming speed in fish (Davison 1989, 1997, He et al. 2013, McClelland et al. 2006, Zhao et al. 2012). It has been suggested that increased swimming capacity and low blood lactate in exercise-conditioned fish are associated to an improvement of the cardio-respiratory capacity (Farrell et al. 1991), to an increase in the activity of muscle enzymes (e.g. creatine kinase, hydroxyacyl CoA dehydrogenase, phosphofructokinase, citrate synthase; He et al. 2013, Johnston and Moon 1980), to an increased capacity in plasma lactate clearance (Pearson et al. 1990), to an increased liver and glycogen storage (He et al. 2013, Johnston and Moon 1980), to an increased myonuclear number and muscle fiber hypertrophy (Hinterleitner et al. 1992, Martin and Johnston 2006) and to an increase in muscle capillaries (Davie et al. 1986). Our results suggest that Mississagi River fish have increased swimming capacities relative to

Aubinadong River fish, but further research is needed to understand the underlying physiological mechanism that could explain these differences.

Blood lactate concentrations were also significantly lower in Mississagi River pike from the resting controls than in Mississagi River pike from the negative controls. In the resting control, Mississagi River pike stayed in the closed swimming tunnel (wood panels remained on the swimming tunnel) installed in the Aubinadong River. In contrast, the swimming tunnels in the negative controls were open so that the Mississagi River fish could see the exterior of its enclosure, and thus the Aubinadong River substrate, aquatic plants, etc. This pattern was absent from the experiments conducted on Aubinadong River pike, where no blood lactate concentration differences were observed between the resting and negative controls. An increased blood lactate concentration would indicate the fish increased muscular activity in the swimming tunnel. Harvey-Lavoie et al. (2016) showed that northern pike living in the Mississagi River have an increased movement rate ($m \cdot s^{-1}$) when compared to pike living in the Aubinadong River. A potential explanation could be that the behaviour of Mississagi River pike predisposes them to be more active when they see the river in the open swimming tunnel of the negative control, than when they are in the darkness of the swimming tunnel of the resting control.

MLR indicated that blood glucose concentrations ($0.39 < R^2_{\text{adj}}$ in MLR < 0.51, average R^2_{adj} of all in MLR for blood glucose = 0.43) and lactate concentrations ($0.37 < R^2_{\text{adj}}$ in MLR < 0.75, average R^2_{adj} of all in MLR for blood lactate = 0.54) may be more predictable and reliable indicators of fish stress than plasma cortisol concentrations (R^2_{adj} in MLR = 0.19) for data obtained from in situ experiments. In this study, plasma cortisol concentrations were highly variable among individuals subjected to the same treatment (Table 3). These results could be explained by the difficulty of working in the field with such an indicator of the HPI axis. Indeed, any small disturbance can raise plasma cortisol concentrations of fish within only minutes (Olsen 1993). For field studies, the difficulty of assessing the effects of environmental conditions on plasma cortisol concentration is further increased by the difficulty of controlling the complete suite of environmental conditions. For instance, something as difficult as ambient noise to control can induce a spike in plasma cortisol levels (Smith et al. 2004).

Basal (i.e. resting control) blood glucose and lactate concentrations of fish from both rivers were comparable to published basal values for freshwater northern pike kept in captivity (glucose: 4.4−5.9 mmol L-1; lactate: 0.8−1.4 mmol L-1; Schwalme and Mackay 1985, Soivio and Oikari 1976). However, plasma cortisol concentrations for northern pike resting in the swimming tunnels for 24 hours (Mississagi: 141.2 $ng\cdot ml^{-1}$; Aubinadong: 198.5 $ng\cdot ml^{-1}$) were much higher than the previously reported basal values for wild teleost (< 10 ng mL-1; Pankhurst 2011). A study by Edeline et al. (2009) on northern pike living in 13 m^3 indoor experimental ponds reported that plasma cortisol concentrations of unstressed northern pike were, on average, 12.5 $ng\cdot ml^{-1}$. This is 11 and 16 times lower than Mississagi and Aubinadong rivers resting controls, respectively. Northern pike in the work by Edeline et al. (2009) had at least 2 days after capture to rest and return to basal level. To our knowledge, the ranges of plasma cortisol concentration for resting pike in the wild are still unknown, but according to the values reported by Edeline et al. (2009), a 24 hours resting period may not have been sufficient to allow pike to return to the basal cortisol concentration.

Pike in the swimming tunnel were exposed to multiple stressors: the capture and the velocity increase. Multiple stressors can interact on ecological responses by being additive (i.e. the response corresponds to the sum of each stressor when acting alone; Schreck 2000), synergistic (the response is greater than the sum of all stressors acting alone; Brook et al. 2008) or antagonistic (the response is smaller than the single response to an initial stressor; herein the initial capture; Oliver and Morecroft 2014). One criticism for the present study may be that, if the effect of the multiple stressors is antagonistic, it may be pointless to assess the effect of an increase in water velocity on fish plasma cortisol concentrations; fish response would not increase as the stressor is applied. However, the elevated plasma cortisol concentrations in the swimming treatment suggest that the multiple effects of the stressors applied to pike in the present study are additive or synergistic, but not antagonistic. Our findings are supported by a study by Barton et al. (1986), which found that the responses in plasma cortisol and glucose to multiple acute handling stresses were cumulative in juvenile Chinook salmon (*Oncorhynchus tshawytscha*). The possible synergistic aspect of the multiple stressors limits the interpretation of the results in the present study because the exact magnitude of the plasma cortisol concentration for pike exposed to an increase in water velocity directly in the river is still unknown. Despite this limitation, our study shows that it is possible to assess 1) the between-river differences in plasma cortisol concentrations by comparing pike exposed to the same experimental treatment and 2) the direction of the change in plasma cortisol concentration for pike subjected to an increase in water velocity. The field of stress physiology has become an eminent component of conservation physiology, focusing on understanding animal stress response to disturbances in their environment (Wikelski and Cooke 2006). The installation of swimming tunnels directly in rivers constituted a novel experimental setting that yields a promising avenue in assessing animal stress response to environmental disturbances, especially for top predators that live in habitats located in remote areas. Indeed, in these systems, the accessibility of pike habitats is often limited, which limits as well the use of the most efficient fishing gears. For example, pool-riffle-run sequences composed of shallow habitats prevent the use of an electro-fishing boat on the study rivers, especially because river accesses are limited. The backpack electro-fisher was also considered to catch large pike. However, this gear is not appropriate for large predatory fish because they often flee from the operator of the backpack electro-fisher (Macnaughton et al. 2015a). Angling was, therefore, the only practicable gear to capture pike in the present study. The capture of 47 individuals required a considerable amount of time (close to 300 hours of fishing) because the abundance of top predators in small-medium streams (river width range: 20 − 180 m) like the Mississagi and Aubinadong rivers is low. This type of research would have been impossible to conduct if pike had to be transported from those remote locations to research facilities. It would have been excessively time and money consuming.

The between-river variability in the stress response of fish to an increase in water velocity provides information on basic responses to environmental stress, which contributes to the overall scope of the potential use of stress responses to measure environmental quality (Pankhurst 2011). There is a considerable knowledge gap on physiological responses to long-term stressors of wild ectothermic vertebrate taxa like fish, to their physiological adaptations and to their energetic expenses related to the presence of a persistent stressor (Schreck 2000). By showing among-river differences in wild fish stress responses, our study contributes to the understanding of the effect of persistent stressors on fish stress physiology.

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Chapitre 4 Un nouveau cadre analytique pour modéliser les variables contextuelles dans la sélection de l’habitat avec des données de présences seulement

A novel analytical framework to model contextual variable in assessing habitat selection using presence-only data

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Abstract

Numerical habitat models quantify relationships between species or community distribution and environmental variables describing the habitat. Habitat selection by animals is affected by a wide array of environmental variables, some of which depend on the context, such as weather conditions or altitude. These contextual variables can determine the specific physical conditions found by animals in the habitat (e.g. percentage cover, temperature). The present study allows one to test and quantify the interactions of contextual conditions with physical conditions of the habitat in implementing numerical models. To achieve this, we herein propose to use a two-stepped compound analysis. The first step involves a classification model that quantifies contextual habitat suitability from tracking data using a multi-layer feed-forward artificial neural network. The second step consists in using the suitability values given by the classification model under a set of chosen contexts as an intermediate response variable in a bilinear regression models. Bilinear regression models combine the contextual variables with the habitat descriptors and thus quantify the effect of any variable taken alone or together. We exemplified the analytical framework by modelling the river habitat of northern pike (*Esox lucius* L.) in a section of a northeastern Ontario (Canada) river experiencing highly variable discharge modulated by an upstream hydropower facility. This study describes a framework that quantifies the effect of any physical variable taken alone or interacting with the contextual variable. We expect the method to be of great interest for decision makers in the field of conservation.

Key words: numerical habitat model, artificial neural network, bilinear regression, contextual variable, flow, *Esox Lucius* L., radio-telemetry, animal tracking

4.1. Introduction

Animals must find resources (e.g. food items, mating partners, shelter) that are distributed heterogeneously in space (Beyer et al. 2010, Moe et al. 2007). To understand how animals exploit their resources, researchers first have to answer fundamental questions about what motivate organisms to be at a particular location at a given time. The scientific knowledge acquired while answering these questions is also important for practical purposes such as management and conservation (Aarts et al. 2008).

Numerical habitat models quantify the relationships between species or community distribution and environmental variables describing the habitat (Guisan and Zimmermann 2000). For animals, habitat selection has traditionally been assessed using resource selection functions (RSF; Boyce and McDonald 1999, Johnson 1980, Manly et al. 2002) that compare the characteristics of the habitat used (presence data) by a species with the characteristics of the habitat that is available in the ecosystem, but not used. Preferred habitats are those used in a high proportion with respect to their availability; preference can thus be evidenced in the light of the conditions available. To what extent a particular habitat is accessible, and thus available, is often unknown because the displacement capacity of the organism is often uncertain. Researchers have dealt with this assumption in different ways. Some authors, for example Johnson (1980), used a conservative approach defining displacement capacity as the home range of the species. That approach may only represent the displacement capacity over the complete lifespan of an organism, or over a shorter observation period while a study takes place, and may thus overestimate or underestimate displacement capacity, respectively. RSF models have been developed to give the best accuracy in the availability of the habitat by animals, but discrepancies may still exist while assessing habitat availability (Aarts et al. 2008).

Avoiding the drawbacks from the RSF models has led to the development of the presence/absence models (Fielding and Bell 1997). Data sets collected for that purpose include both used sites (presence data: preferred habitat) and non-used sites (absence data: non-preferred habitat or unsuitable locations). However, in many cases, only presence data can be collected and little or no information is available about the absence of a species from sites. This is often the case in telemetry studies (radio-, acoustic, pit tags) where reliable absence data can be strenuous to obtain and are often not available (Zaniewski et al. 2002). For instance, species that hide in their habitat (e.g. bird colouration pattern resembling the tree foliage, thus improving camouflage) may not allow one to obtain reliable absence observations due to the species' ability to take cover, thereby leading to false absence and, ultimately, poor model performance. Also, data sets on species living in environmental conditions where sampling is laborious, for example fish in very large and deep rivers, are commonly presence-only data. Computer-simulated pseudo-absence data have been used to attempt to address the failure in gathering reliable absence-data (Graham et al. 2004, Zaniewski et al. 2002). The pseudo-absence data represents randomly selected positions on the study map for which environmental conditions are known or can be modelled. These pseudo-absence data facilitate the modelling of habitat selection by researchers because they allow them to use modelling methods such as logistic regression models (Johnson et al. 2006), multiple linear models (MLR; Brosse and Lek 2002) or generalized additive models (GAM; Franklin 1998, Pearce and Ferrier 2001), that are known to perform well with presence/absence data. That strategy comes at the price of allowing fallacious absence data to contaminate the set of absence data, however.

Presence-only modelling techniques can omit the simulating absence data in numerical habitat modelling. Early presence-only modelling methods comprises, among others, the probability density using kernel functions (Marzluff et al. 2004, Van Winkle 1975), the environmental envelopes (Busby 1986, Lindenmayer et al. 1991, Pearce and Lindenmayer 1998) or the ecological niche factor analysis (ENFA; Hirzel et al. 2002). Among the numerous sets of emerging statistical methods, machine learning algorithms (maximum entropy, artificial neural networks, genetic algorithms, decision trees, and support vector machines) are promising avenues in developing habitat selection model. For instance, they have been shown to outperform other traditional modelling approaches in predicting wildlife spatial use (Elith et al. 2006, McCue et al. 2014). Machine learning algorithms have been appealing statistical methods in recent ecological studies because they can model non-linear or hierarchal responses involving multiple interactions among variables. In spite of their ability to fit complex models and thus their power in explaining or predicting ecological patterns, ecologists have been slow in adopting these methods (Olden et al. 2008).

While habitat selection is a function of the animal's needs and habitat availability, a given habitat may not always suffice at fulfilling all the basic needs of species, thus leading to trade-offs between the specific costs and benefits of using a particular location (Godvik et al. 2009). Habitat selection is the consequence of these trade-offs. Habitat selection is affected by a wide array of environmental variables (e.g. weather conditions or time of the day; Chapman and Mackay 1984, Eldegard et al. 2012, Yasué et al. 2003) or factors intrinsic to the species (e.g. the animal’s behaviour, sex or age class; Beier and McCullough 1990, Marchand et al. 2015). In the present study, we will refer to these circumstantial factors affecting habitat selection as “contextual variables” (e.g. weather conditions), while the specific physical habitat conditions selected by animals will be referred to as “habitat descriptors” (e.g. percentage cover, temperature).

The acknowledgement of the variations in the selection of habitat environmental conditions due to contextual variables have led to recommendations that habitat models should be used within a narrow range in contextual conditions (e.g., within summer only, within good weather), thus allowing one to exclude these variables from the habitat model (Manly et al. 2002). Although such a cautious approach appears reasonable for specific, narrowly targeted, applications, it does not grant us much understanding about how contextual conditions affect habitat selection through their interaction with habitat descriptors. One of the difficulties in integrating contextual variables in numerical habitat modelling is that they are themselves often correlated with the habitat descriptors. This correlation may be combined to sampling constraints as the whole ecosystem may not be accessible for sampling under every value on the contextual variable, leading to certain site being sampled at given occasion and other physically different sites being sampled at another occasion with radically different context. For instance, season (the contextual variable) affects the habitat selection of the white-tailed deer in terms of snow depth and air temperature (the habitat descriptors), two important habitat descriptors of deer numerical habitat models (Beier and McCullough 1990). If one assesses whether the season is an important determinant of deer habitat selection, it would be tedious to partial out the effect of snow depth and air temperature. In river fish ecology, flow ($m^3 \cdot s^{-1}$; contextual variable) is an important determinant of the water velocity and depth of fish habitat, two habitat descriptors typically included in fish numerical habitat models (Guay et al. 2000). Researchers thus lack method to test and quantifying the effects of these contextual variables on habitat selection by animals.

The objective of this study was to develop an analytical framework using presence-only (radio-telemetry) data to test and quantify the interactions of contextual conditions with habitat descriptors in implementing numerical habitat models. To achieve this, we propose to use a two-stepped compound analysis. The first step involves quantifying contextual habitat suitability for a suite of sites from tracking data using a classification model. That model predicts the future location of an organism from its actual location and contextual variables. The second step consists in using the suitability values given by the classification model under a set of chosen contexts as an intermediate response variable in a bilinear regression model. That regression model combines the contextual variables with the habitat descriptors and thus quantifies the effect of any variable taken alone or interacting together. We then propose a Monte-Carlo (random walk) method to test the resulting habitat model for statistical significance. The method is exemplified by modelling the river habitat of northern pike (*Esox lucius* L.) in a section of a river experiencing highly variable discharge modulated by an upstream hydropower facility.

4.2. Methodology

4.2.1. Habitat characterization

The preliminary step of the analytical framework consists in partitioning the habitat into a set of discrete patches containing homogeneous habitat descriptors. That step is facultative as the study environment may be intrinsically discrete (e.g., a patchwork of forests, prairies, farmlands, and wetlands of different types). While measurements in habitat descriptors are often taken at points, the first step of the framework (the classification model, see below) needs a set of discrete locations. The bilinear regression model is expected to best perform when the within-patch habitat descriptors variation is small with respect to that of the among-patches variation. These discrete patches are meant to map the habitat descriptors at a scale of ecological relevance to the species of interest. Often, different instruments and methods are used to obtain information about the habitat descriptors, which results in different variables being sampled or estimated at different sets of points. In such a situation, all information about the habitat descriptors has to be brought on the points of a common analysis grid. Some habitat descriptors may be constant with respect to the contextual variable while others may covary. We hereafter refer to that former as an “independent habitat descriptor” and to the latter as a “dependent habitat descriptors”. For dependent habitat descriptors, a set of values is available for each and every possible value of the contextual variable. Instead of using the whole set of possible values, which may involve a very large number of variables, it is advisable to estimate relationships between the dependent and contextual variables for each node of the analysis grid. The parameters of these relationships (e.g. intercept, slope; synthetic variables) are assumed to be constant at a given node and are used as independent habitat descriptors.

For instance, the water depth at a given location in a river may be influenced by the flow magnitude. In such a scenario, and given that the river flow magnitude is used as a contextual variable, synthetic variables such as the intercept, the slope, and the residual standard deviation of the linear relationship between river flow and water depth can be implemented at each node of the analysis grid and used in the place of the raw water depths for all the different flow magnitudes.

Once a common analysis grid has been defined and a matrix of independent habitat descriptors has been obtained, habitat patches have to be delineated. To do so, we propose to use a space-constrained agglomerative clustering (constrained.clust; P. Legendre). That method consists in merging neighbouring nodes or groups of nodes on the basis of a distance metric. We chose the Mahalanobis distances (Mahalanobis 1936) for that purpose because the habitat descriptors had different physical dimensions and were correlated to one another. The number of clusters needs to be chosen to maximize the number of habitat patches, while minimizing the number of patches where organisms have never been observed. As a tentative guideline, we propose that the proportion of unused patches be ≤ 15%.

4.2.2. Habitat selection model

The first step, following the preliminary step, of the analytical framework is to quantify the contextual habitat suitability of a suite of discrete habitat patch from tracking data using a classification model. That model predicts in which habitat patch an organism is likely to be found from the value of the contextual variable, the identity of the patch in which it was observed on the last tracking event, the value of the contextual variables at that previous tracking event, and the time elapsed between the two events. As a classification model, we propose to use a multi-layer feed-forward artificial neural network (ANN) having a "softmax" (multinomial) output. That model is trained with all consecutive tracking locations (i.e. 2 sequential positions of the same individual) from the radio-tracking (Figure 1). The number of neurons in the hidden layer and the value of weight decay parameter (L_2 regularization) can both be estimated as those maximizing predictive power in cross-validation trials. Once the ANN model is properly trained, it provides probabilities of occurrence on the habitat patches after a given amount of time, given the value of the contextual variable and the initial position of the animal. These probabilities for any given set of initial and final values of the contextual variable and a given time interval can be stored in an $m \times m$ matrix of transition probability, where m is the number of habitat patch. The rows of that matrix represent the initial location of the fish, its columns, the final location of the fish, and its elements are the probability that a fish be found in a given patch at the end of the time interval. There is one such matrix for each of the values of the contextual variable. From that matrix, we defined two surrogates of habitat suitability: the mean probability of attraction (i.e. to go from any patch to certain patch: the mean of the column representing that patch, notwithstanding the element in the main diagonal of the transition probability matrix) and the probability of retention (i.e. to stay in the same patch: the element of the main diagonal of the matrix) of an animal after the standard time interval. The mean attraction probability and the retention probability are then summarized in $n \times m$ matrices, where n is the number of habitat patch and m is the number of values of the contextual variable (Figure 1).

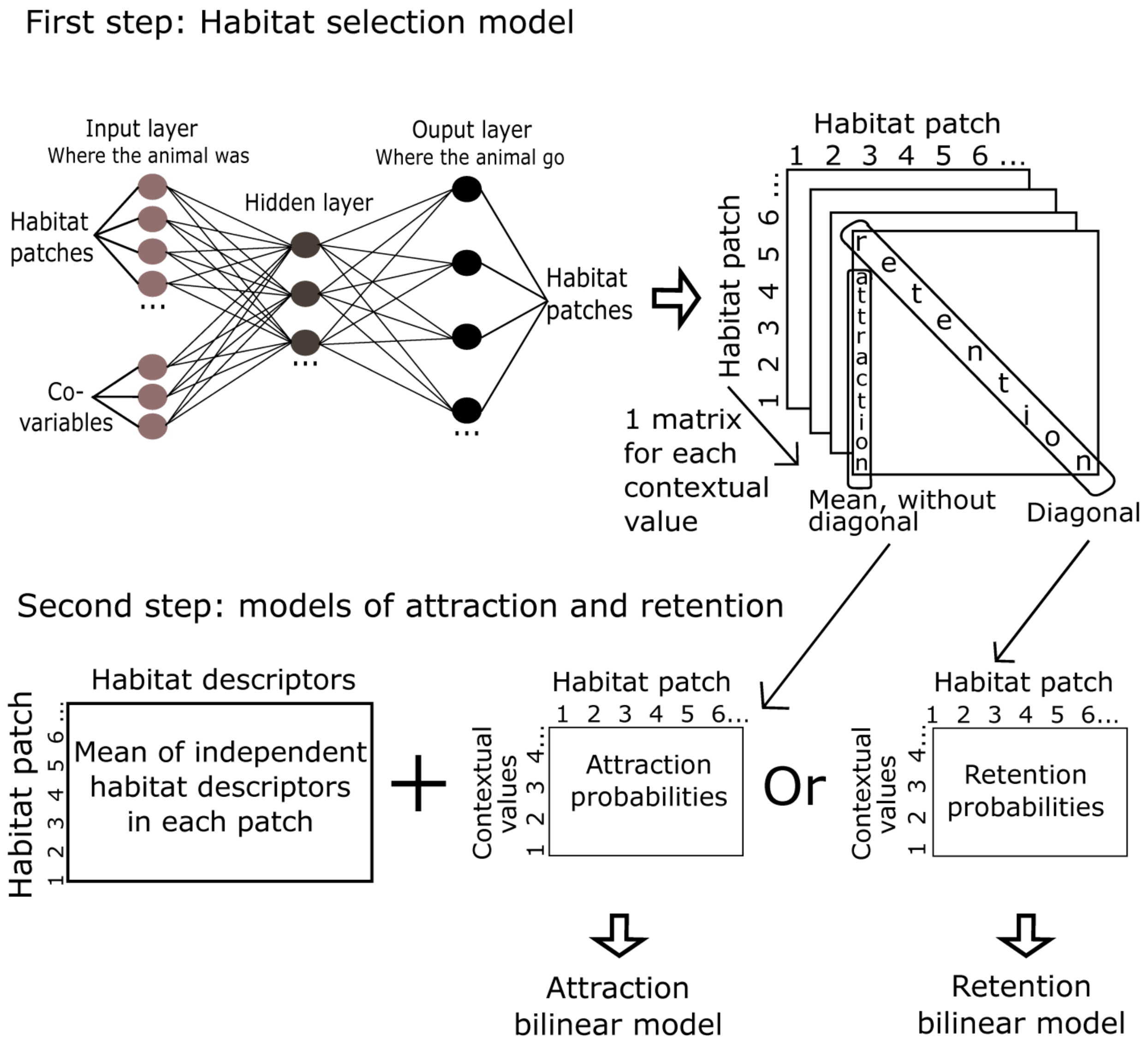

Figure 1 Two-step analytical framework in assessing the effect of the contextual variable in numerical habitat models for presence-only data.

4.2.3. Models of attraction and retention

The second step of the analytical framework is to model the attraction or retention of habitat patches using bilinear models (Gabriel 1998). It allows one to predict habitat suitability to an animal on the basis of habitat descriptors and given the value of the contextual variable. A bilinear model requires three sets of descriptors: 1) the independent descriptors, 2) the contextual variable, and 3) a response matrix of attraction or retention probabilities. Each of the two bilinear models is represented as follow:

$$\mathbf{Y} = \mathbf{X}\mathbf{B}\mathbf{Z}^{\mathrm{T}} + \mathbf{E}$$

where $\mathbf{Y} = [y_{i,j}]$ is an $n \times m$ matrix (n: number of habitat patch, m: number of contextual variable values) with response variables whose elements $y_{i,j}$ are either the probabilities that the animal be attracted by each habitat patch (the attraction model) or the probabilities that the animal retains in the same habitat they were (the retention model), $\mathbf{X} = [x_{i,k}]$ is an $n \times p$ design matrix with a constant (all ones) column vector followed by one column for each of the independent habitat descriptors of the patches, and one column representing the patch area, thus controlling for the among-difference in the habitat patch area, $\mathbf{Z} = [z_{j,l}]$ is an $m \times 2$ design matrix with one column containing all ones followed by a second column for the contextual variable, $\mathbf{B} = [b_{k,l}]$ is a $p \times 2$ matrix of bilinear regression coefficients, $\mathbf{E} = [\varepsilon_{i,j}]$ is a matrix of residuals, and $^{\mathrm{T}}$ denotes matrix transposition. Since the first columns of both $\mathbf{X}$ and $\mathbf{Z}$ are constant vectors, the leftmost column vector of $\mathbf{B}$ ($b_{k,1}$) contains the marginal effects of the habitat patch, the uppermost row vector of $\mathbf{B}$ ($b_{1,l}$) contains the marginal effects of the contextual variable, while element $b_{1,1}$, which is the common element of the latter two vectors, is the intercept of the model. All elements of $\mathbf{B}$ other than those of the first row and column are interaction terms between habitat patches and the values of the contextual variable. As mentioned previously, two such models are produced; one for the mean attraction probability and one for the retention probability. Because values of **Y** are probabilities, they were logit-transformed ($y_{i,j}^* = \log(\mathrm{y})\cdot(1-y_{i,j})$) before estimating bilinear models. The values of the independent descriptors included in the matrix **X** are the average values of the nodes of the analysis grid within the habitat patches. To control for the effect of patch size on their mean attraction probability and retention probability, we added the surface area of the habitat patch as an independent descriptor in **X**.

To ease their estimation using standard regression software, the bilinear models were transformed into a single response equation system using vectorization (i.e to transform a matrix into a single vector by stacking its column: the $\langle \ldots \rangle$ operator) and the Kronecker product ($\otimes$) as follows:

$$\langle \mathrm{Y} \rangle = (\mathrm{Z} \otimes \mathrm{X}) \langle \mathrm{B} \rangle + \langle \mathrm{E} \rangle.$$

The data used for the bilinear models were generated from an ANN and thus not real world independently sampled observations. It is not possible to ascertain how many degrees of freedom they have, and thus perform the standard hypothesis tests of the regression on them. To address this issue, the significance of each explanatory variable was tested against its distribution under a null distribution model obtained by random walk (a Monte Carlo method). The null model represents a situation whereby animals move in a random way within and among the patches, irrespective of the environmental conditions. These simulations consist in planting the organisms randomly in the study area, making them move randomly following their individual propensities at making long or small displacements and turning sharply of more gently about the centroid of their home range. To match field conditions as closely as possible, the null model is simulated at the same time of observation and for the same values of the contextual variable as in the original data set. We estimated descriptors for each tracked individual because they all have their own particularity with respect to locomotive behaviour. We begin by calculating the centroid of each tracked individual, then build individual models describing the distance travelled by the animal (*D*; m) as a function of the time elapsed since the last observation *D* (ΔT; h) as follows:

,

where *a* and *b* are constants estimated for each individual. Then, a second model is built to describe the turning angle of the individual relative to the centroid. This model uses the distance between the individual and its centroid as a descriptor to estimate the cosine and the sine of that turn angle. For simulations, the centroids are planted at random within the sampling area, from there, travel distances are drawn randomly from the time elapsed, the turn angle is drawn randomly from the previous location, and the next location is calculated while making sure it falls within the study area. When it falls outside of the study area, the simulation is retried until the next location falls within the study area. Once all steps are completed for all the organisms, a new data set is obtained. This new data set is submitted to the very same analyses as the nominal data set, producing a new set of bilinear model coefficients obtained under the null hypothesis. Under that null hypothesis, the environment as no bearing whatsoever on habitat selection, whereas the size and particularity of the study area and the possible consequences of the particular individual characters of the organisms are accounted for. This computation was repeated 100 000 times. Hypothesis tests are performed by performing two-tail comparisons of the nominal and simulated Student's *t* statistics associated with the regression coefficients. P-values were adjusted for the test of multiple comparisons using the Šidák correction (Šidák 1967).

4.3. Exemplary scenario

To exemplify our analytical framework, we used data collected on northern pike (*Esox lucius* L.), a predator fish commonly found in freshwaters (lakes and rivers), and brackish marine waters of the northern hemisphere (Craig 2008). We analyzed the habitat use of that fish in a river, with the flow as the contextual variable, and hydrological features of the channel (i.e. water depth and water velocity), substrate size and cover, as the habitat descriptors (Jackson et al. 2001, Senay et al. 2015).

4.3.1. Study area

The study area (46°54′N, 83°16′W) is a 1 km longitudinal river section located on the Mississagi River (Ontario, Canada), 5 km downstream of Aubrey Lake, a reservoir formed by Aubrey Falls Dam. Aubrey Falls Dam is a hydropeaking facility built in 1969 that regulates Mississagi River flow (average daily flow = 38 $m^3 \cdot s^{-1}$). The hourly flow on the Mississagi River can vary from 6 (minimal flow) to as much as 307 $m^3 \cdot s^{-1}$ (maximum flow) within 3-4 hours. The study area has natural habitats on its riverbanks (i.e. presence of natural substrate, aquatic plants, logs), natural sinuosity, and highly variable depths and water velocities (both spatially and temporally). Alongside the main channel, there are also numerous side channels, side pools, riffle and run sequences, and small bays.

4.3.2. Fish tagging

We collected 20 northern pike by angling from a canoe or from the shore, between the 12th and the 20th of June 2013 (Table 1), following the exact capture method describe by Harvey-Lavoie et al. (2016). Total fish mass (g wet blotted weight) and total length (TL, in mm), and sex (Casselman 1974) were recorded. Individually traceable transmitters (3.2 g in air, 25 x 13 x 6 mm, 120 mm antenna, battery life 6 months, 3 seconds pulse interval; Model PD-2, Holohil Systems Inc., Carp, ON, Canada) were attached to pike using the method described by Arlinghaus et al. (2009; see Harvey-Lavoie et al [2016] for details on the method). The relative mass of the transmitters was ≤ 0.6% of fish body mass. Fish were released within 5-10 minutes of capture.

Table 1 Identification (ID), sex, mass length, date tagged and number of observations of each radio-tagged fish in the Mississagi River.

Fish ID	Sex	Mass (g)	Length (mm)	Date tagged (all in 2013)	number of observations
M1	male	1101	556	12-Jun	31
M2	female	1532	635	12-Jun	33
M3	male	1419	610	12-Jun	34
M4	male	1199	581	12-Jun	34
M5	female	1228	593	13-Jun	29
M6	male	1169	598	13-Jun	33
M7	male	1298	622	13-Jun	32
M8	female	1204	573	13-Jun	32
M9	female	526	440	15-Jun	13
M10	female	588	467	09-Jul	31
M11	female	677	481	16-Jun	32
M12	female	659	474	17-Jun	29
M13	male	1325	609	17-Jun	36
M14	male	631	471	17-Jun	removed from analysis
M15	female	677	483	17-Jun	27
M16	female	1232	577	19-Jun	35
M17	male	1474	613	19-Jun	31
M18	female	595	475	20-Jun	34
M19	male	1349	574	20-Jun	33
M20	female	1199	586	20-Jun	removed from analysis

4.3.3. Fish tracking

Fish were tracked twice a day every two days between July 10th and August 16th 2013, at two different time periods (between 05:00 and 14:00 and between 17:00 and 02:00) and by two different teams. Fish were tracked from an electrically powered canoe using a portable radio-receiver equipped with a three-element Yagi antenna (Lotek SRX 400 Telemetry Receiver, Lotek, Ontario, Canada). Teams were trained prior to the beginning of the survey by tracking hidden transmitters placed at different locations in the river, thus revealing a precision of our tracking method of ± 5 m. The geographic coordinates of fish positions were recorded using a handheld GPS instrument (Garmin 76sc, USA) with a precision of ± 5 m. Details on fish tracking can be found in Harvey-Lavoie et al. (2016). Hourly flow was recorded by a gauging station located within the study area ($m^3 \cdot s^{-1}$). The average hourly flow magnitude was 42 $m^3 \cdot s^{-1}$ (range 11.8 - 258.6 $m^3 \cdot s^{-1}$) during fish tracking. All tagged fish remained in the study area for the complete duration of the study, except for fish M14 and fish M20 that moved 650 and 1500 m downstream of the study area, respectively, immediately after their tagging. Since they were never observed in the study area, these two fish were removed from the analysis. The data set encompassed from 13 to 36 tracking events per fish, for a total of 559 events recorded during the tracking surveys (Table 1).

4.3.4. Characterizing the habitat

We estimated a set of discrete habitat patches defined on the basis of four habitat descriptors: depth (m), water velocity ($m \cdot s^{-1}$), vegetation height (cm), and substrate type (soft or hard). To obtain these information, topography (bed elevation), submerged vegetation height (cm) and substrate data were collected on the field between the 14th and 20th of August 2013, using a scientific echosounder (BioSonics DTX; BioSonics Inc., Seattle, Washington, USA; 200 kHz downward-facing transducer) operated from an aluminum boat (Cholwek et al. 2005). Hydro-acoustic gathered 650 149 data points (1 data point = 1 ping), over a series of 80 transects perpendicular to the longitudinal axis of the river, in addition to a number ranging from 14 to 18 transects parallel to the longitudinal axis of the river. The boat was coasting at a constant 3 $m \cdot s^{-1}$. Pulse width was set to 0.4 ms in order to use the maximum ping rate achievable by the instrument (10 $ping \cdot s^{-1}$). The sampling was conducted at peak flow to ensure that flood-risk areas were included in the mapping. Data points were geo-referenced by an on-board GPS (Garmin 17x HVS; Garmin International, Olathe, Kansas, USA) with an accuracy of ±3 m. Data were edited and analyzed in Visual Habitat software (BioSonics Inc., Seattle, Washington, USA).

Every data points sampled by hydro-acoustic were implemented into a two-dimensional hydrodynamic numerical model, using an integrated software package (CCHE 2D; Jia and Wang 1999) developed by the National Centre for Computational Hydroscience and Engineering (NCCHE, University of Mississipi, USA). We used the 2D mesh generator included in that package (CCHE-MESH, V 3.0) to build an orthogonal mesh with 4462 nodes representing the bed elevations for the entire study area. The data points sampled using hydro-acoustics were imported in the mesh 2D generator to assign a value of bed elevation to each node of the mesh using interpolation by triangulation. The mesh was then implemented in a 2D hydrodynamic model for unsteady open channel flows (software CCHE 2D-GUI, V 3.0). A set of flow magnitudes were selected and for each of them, a 2D simulation was produced. Flow magnitudes were selected by transforming the range of flow magnitudes observed during fish tracking (11-258 $m^3 \cdot s^{-1}$) on a base 10 logarithmic ($\log_{10}$) scale and taking one magnitude every 0.10 on the $\log_{10}$ scale. The selection of flow magnitudes was conducted over a logarithmic scale because fish were mainly observed in low to medium flow magnitudes (11-100 $m^3 \cdot s^{-1}$; 485 fish positions out of a total of 559). Each simulation, one for each of the 16 selected flow magnitudes (11, 12, 16, 20, 25, 31, 40, 50, 63, 79, 100, 125, 134, 158, 200 and 250 $m^3 \cdot s^{-1}$) produced an output table that corresponded to 2D scalar fields of water velocities and depths for each node of the mesh.

Habitat descriptors that depend on the flow magnitude (i.e. dependent descriptors) are water velocity and depth, while the independent descriptors are the submerged vegetation height and the substrate type. Two sets of linear regressions (between each of the dependent descriptors and the flow magnitudes) were developed, with one regression for each of the 4462 mesh nodes. The intercept, slope, and coefficient of variation of the residuals were selected as synthetic variables to represent these relationships. The intercept characterizes the mean depth or velocity at a location, irrespective of the river flow, the slope describes to what extent depth or velocity is locally affected by the river flow, whereas the residual coefficient of variation assess the linearity of the relationship for a given location of the analysis grid. Habitat characterization focused on meso-scale habitat patches, which is suitable to adequately represent the physical features of the river that are important to fish (Maddock and Bird 1996). The analysis grid was composed of 15 m sided equilateral triangles, with 1223 vertexes, corresponding to the analysis nodes, separated by 15 m from one another. Kriging was used to interpolate the synthetic variables from every mesh nodes to the analysis nodes of the analysis grid. The same method was used to interpolate the data on submerged vegetation height from the data points sampled by hydro-acoustic. Since substrate data were qualitative (hard or soft) and cannot be interpolated by kriging method, we used k-nearest neighbours instead.

4.3.5. Habitat selection model

The input layer of the ANN developed to model the habitat patch selection by northern pike in function of flow magnitudes consisted in 29 neurons, i.e. one for each habitat patch and one for each of the three co-variables: flow magnitude at the initial fish position, flow magnitude at the next fish location and time elapsed between the fish initial and the next positions. The output layer had one neuron for every habitat patch, for a total of 26 neurons. The ANN was trained using the data composed of 559 fish positions, which resulted in 541 observations (559 minus the 18 initial positions) of a fish moving among the habitat patches. The best number of hidden layer nodes and value of the decay parameter were estimated by gradient descent using cross-validation. To achieve this, the radio-tracking observations were divided in 8 even groups and the ANN is trained 541 times by sequentially removing group 1, 2, 3, 4, 5, 6, 7 or 8 and predicting its observations using the remainder of the observations. The best number of nodes was searched in the range [1, 17], whereas the best decay parameter was searched in the range [10-10, 1010] and were both estimated iteratively as those maximizing the predictive power of the neural network. From our ANN model, a single 16 $m \times m$ (where m is the number of habitat patch) square matrices was produced for each of the 16 simulated flow magnitudes. The mean probability for a patch to either attract or retain an animal was predicted for a standard time of 1 hour. The information contained in the 16 matrices obtained from the ANN were then summarized in two $n \times m$ matrices, where n is the number of habitat patch (26) and m is the number of contextual variables values (16): the attraction and the retention matrices.

4.3.6. Models of attraction and retention

The bilinear models were developed using the mean of every analysis grid nodes in each habitat patch of the synthetic variables (the intercept, slope, and residual coefficient of variation) of the dependent habitat descriptors (water velocities and depths) and one of the independent habitat descriptor (submerged vegetation height). The substrate type was summarized for each habitat patch by calculating the % of hard vs soft substrate and the area of each patch was also calculated. The matrices of attraction or retention probabilities for each flow magnitude were included in the bilinear models as response matrices.

4.3.7. Calculations

All calculations other than the mesh generator for bed elevation and the 2D hydrological modelling were performed using the R language for statistical computing (R Development Core Team, 2015) with packages spdep for spatial neighbour matrices (Bivand and Piras, 2015; Bivand et al., 2013), gstat for kriging (Pebesma 2004), class for nearest neighbour analysis (Venables and Ripley, 2002), const.clust for constrained clustering (Legendre and Legendre, 2012), sp for spatial data drawings (Pebesma, 2005) and nnet for neural network (Venables and Ripley, 2002).

4.4. Results

4.4.1 Habitat characterization

The water velocities and depths obtained from the 2D hydrodynamic simulations were in average 0.13 $m{\cdot}s^{-1}$ (range: 0-1.75 $m{\cdot}s^{-1}$) and 3.13 m (range: 0-16.30 m), respectively, across all flow magnitudes and all mesh nodes. The submerged vegetation height obtained from the hydro-acoustic sampling were in average 1.22 m (range: 0-3.9 m) and the substrate type was in majority of the type soft (64 %). Linear regressions developed for each mesh nodes between the water velocities and flow magnitudes resulted in 3 synthetic variables at each mesh nodes: the intercept (mean: 0.03, range: −0.05 - 0.25), the slope (mean: 0.001, range: −0.0003 - 0.0034), and the residual coefficient of variation (mean: 0.257, range: 0.000 - 4.084). The same type of synthetic variables were found for the linear relationship between water depth and flow magnitudes: the intercept (mean: 2.28, range: −1.289506 - 14.013639), the slope (mean: 0.01, range: 0.00 - 0.01), and the residual coefficient of variation (mean: 0.26, range: 0.00 – 204.59). Therefore, a total of 6 synthetic variables were selected for each of the 4462 mesh nodes.

The habitat patches were computed using the space-constrained agglomerative clustering (Figure 2). The cluster was cut so that the number of habitat patches was set to 30. There was in total 4 habitat patches (patch number 2, 16, 21 and 25) where no fish has been observed. The areas of these patches were relatively small compared to the other habitat patches (average area of the patches 2, 16, 21 and 25 was 1072 m^2, average area of the other patches was 9516 m^2; Table 2).

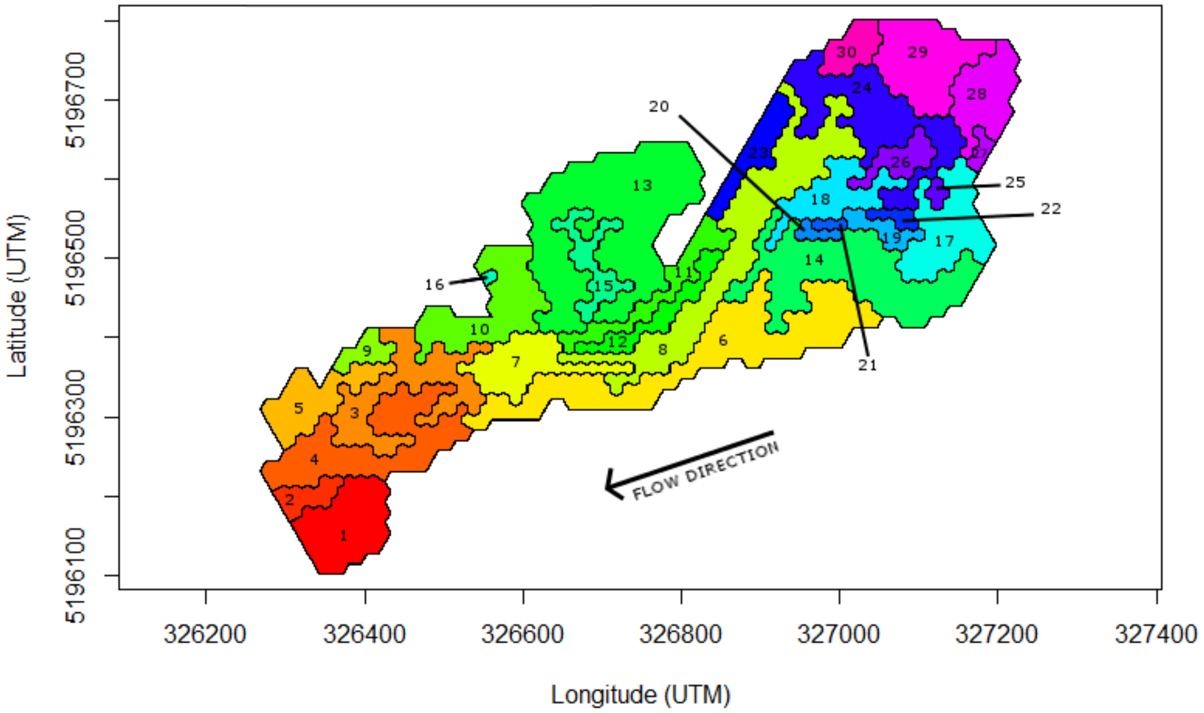

Figure 2 Map of the habitat patches defined by spatially constrained agglomerative clustering. The numbers correspond to habitat patch numbers in Table 2.

Table 2 Mean values of the habitat descriptors in the habitat patches. Prefixes Int.- Slope-, and CVR- represent the intercept, slope and coefficient of variation of the residuals, respectively, of the linear regressions between water velocity or water depth and flow magnitudes. Veg. is the submerged vegetation height, substrate is the substrate type (0=soft substrate, 1=hard substrate), area is the habitat patch's surface area and Obs. is the number of time a fish was detected in the habitat patch.

Patch number	Latitude (UTM)	Longitude (UTM)	Int.-velocity	Slope-velocity	CVR-Velocity	Int.-depth	Slope-depth	CVR-depth	Veg. (m)	Substrate (0 or 1)	Area (m^2)	Obs. (n)
1	5196165	326376	0.025	0.001	0.385	2.908	0.011	0.091	1.33	0.43	10275	2
2	5196200	326333	0.044	0.002	0.199	5.347	0.010	0.063	2.37	1.00	2632	0

3	5196270	326410	0.060	0.002	0.185	1.888	0.011	0.126	0.86	0.18	15884	30
4	5196330	326455	0.045	0.002	0.183	2.326	0.011	0.179	0.88	0.94	12766	27
5	5196321	326344	0.021	0.001	0.316	1.149	0.010	0.181	1.33	0.22	7565	25
6	5196386	326832	0.016	0.001	0.304	1.621	0.011	0.214	1.47	0.07	25153	87
7	5196365	326606	0.028	0.002	0.225	5.215	0.011	0.087	1.38	0.69	8181	6
8	5196525	326874	0.042	0.002	0.171	2.774	0.011	0.083	0.67	0.99	22703	31
9	5196379	326406	0.019	0.001	0.763	0.613	0.010	0.487	2.03	0.00	2307	6
10	5196436	326560	0.011	0.001	0.403	1.100	0.010	1.355	2.35	0.14	11698	4
11	5196458	326767	0.011	0.002	0.202	1.633	0.011	0.172	0.78	0.04	6073	28
12	5196433	326773	0.037	0.002	0.153	2.751	0.011	0.095	0.38	1.00	4678	13
13	5196533	326708	0.006	0.000	0.405	1.000	0.011	0.243	1.28	0.09	32081	64
14	5196479	327008	0.019	0.001	0.245	1.199	0.010	0.182	2.09	0.29	21434	102
15	5196495	326688	0.005	0.001	0.342	1.413	0.011	0.159	1.46	0.88	4871	17
16	5196477	326561	0.010	0.001	0.736	0.632	0.010	17.548	1.88	0.00	293	0
17	5196537	327132	0.013	0.001	0.345	0.657	0.010	-0.499	1.94	0.37	10426	42
18	5196578	326993	0.075	0.001	0.159	1.835	0.010	0.060	0.55	0.68	7213	7
19	5196536	327055	0.015	0.001	0.411	0.432	0.009	0.267	1.92	0.17	2337	7
20	5196532	326971	0.021	0.001	0.180	1.026	0.009	0.185	1.38	0.00	975	1
21	5196542	326989	0.010	0.000	0.080	0.405	0.003	0.049	0.97	0.00	584	0
22	5196551	327071	0.018	0.001	0.207	0.461	0.006	-0.162	1.62	0.00	1169	1
23	5196634	326898	0.013	0.001	0.216	1.267	0.011	0.180	1.74	0.00	4870	23
24	5196672	327046	0.060	0.001	0.230	1.152	0.011	0.022	0.66	0.09	15841	22
25	5196581	327124	0.009	0.001	0.337	0.045	0.011	-7.915	2.03	0.00	780	0
26	5196624	327077	0.131	0.001	0.125	1.170	0.011	-0.004	0.36	0.00	3507	4
27	5196640	327176	0.075	0.001	0.931	1.489	0.010	0.009	0.87	0.00	1072	1
28	5196704	327180	0.031	0.001	0.201	4.394	0.011	0.054	0.77	0.23	7823	1
29	5196743	327107	0.031	0.001	0.203	1.940	0.011	0.259	0.57	0.25	11761	4
30	5196761	327017	0.018	0.001	0.597	0.560	0.010	0.234	1.17	0.13	3694	4

4.4.2. Habitat selection model

Following cross-validation, an ANN with 6 hidden nodes and a decay parameter of 0.064 that was found to give the most accurate predictions of fish transition among patches, with a 44% correct classification rate. From that network, we calculated the (16) transition probability matrices (dimensions: 26x26; one for each flow magnitude). These matrices contain the probability that a northern pike located in any of the 26 patches either transition to another patch (probability to move towards a location; Figure 3) or stay in the same patch where it was at the previous time step (probability to hold location; Figure 4) after one hour at a steady flow magnitude.

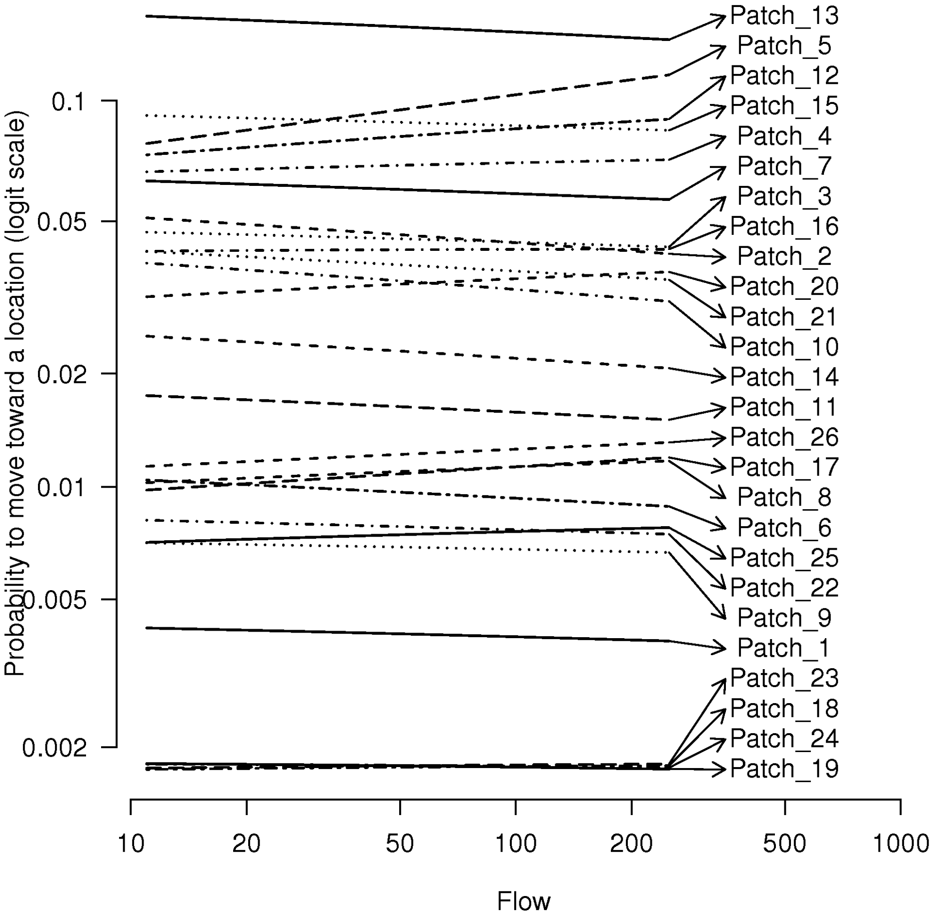

Figure 3 Probability from the ANN that a fish move towards (attraction) a specific habitat patch (logit scale) depending on the flow magnitude at which the habitat selection is performed.

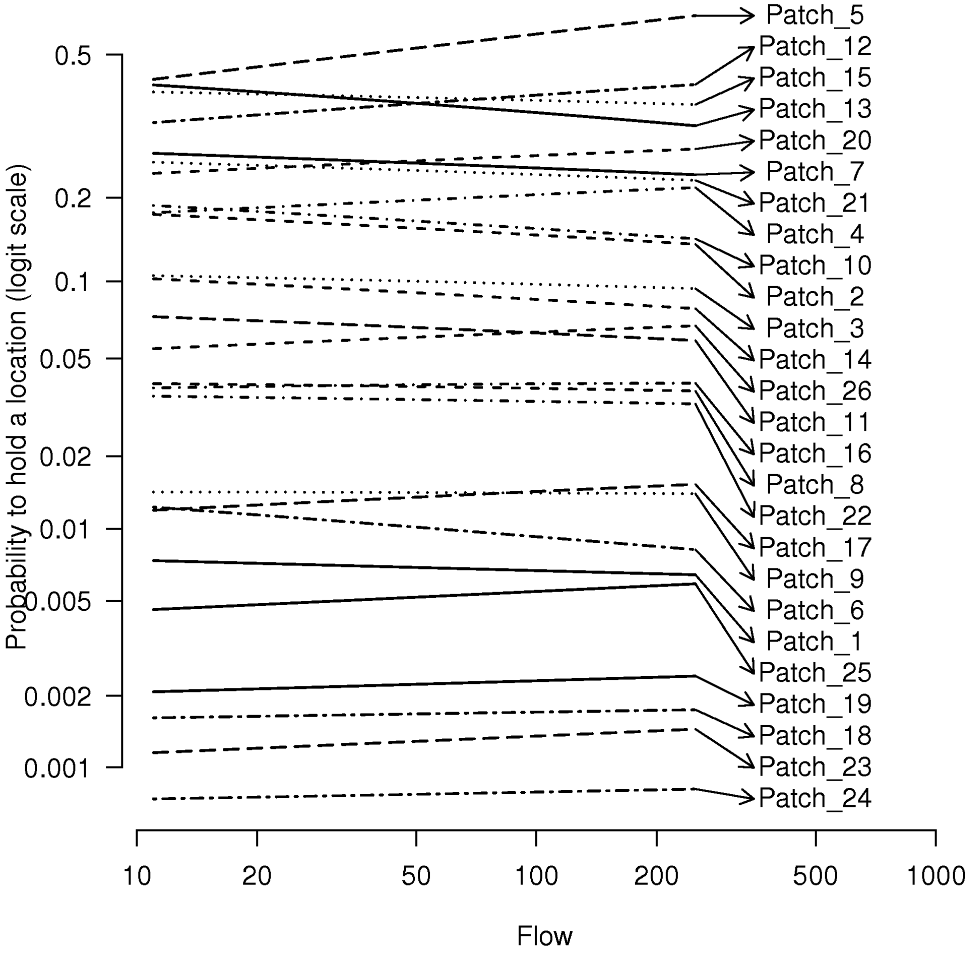

Figure 4 Probability from the ANN that a fish hold its location (retention model) in a specific habitat patch (logit scale) depending on the flow magnitude at which the habitat selection is performed.

4.4.3. Models of attraction and retention

Significance of the explanatory variables in both the attraction and retention models was assessed using the student's t-test on the basis of its empirical distribution under the null model as simulated using the random walk algorithm described previously. In the attraction model

(Table 3), results show that the patch attractiveness is higher for habitat patch where the water velocity increases rapidly with flow magnitude (velocity slope: estimate = 1165.71, p = 0.001), but this, only at the lowest range of flows. Incidentally, for higher flows, pike were rather attracted to habitat where water velocity increased more gently with the flow (interaction between flow magnitude and velocity slope: estimate = -113.39, p = 0.002). Similarly, as flow magnitude increased, pike were more attracted by habitats that have lower water velocities in average (interaction between flow magnitudes and the velocity intercept: estimate = -1.026, p = 0.031). In general, pike were more inclined towards habitat where the depth at base flow (11 $m^3 \cdot s$) was low (depth intercept: estimate = -0.767, p < 0.0001), but would rather move to a habitat with a depth that increases sharply with increasing flow magnitude than to locations with gentler depth-flow relationships (depth slope: estimate = 729.499, p = 0.007). The results also indicate that the attraction was a predictable function of the depth as the flow fluctuated; pike would rather move to habitats with linear depth-flow relationships than to habitats with non-linear depth-flow relationships (residual coefficient of variation of depth: estimate = -1.307, p = 0.035). Vegetation also has an effect on the probability that a pike be attracted to a habitat patch: we found that pikes had a propensity towards areas with abundant submerged vegetation (submerged vegetation height: estimate = 1.068, p = 0.012). However, as flow magnitude increase, pike preference for high cover habitat tended to attenuate (interaction between flow magnitude and vegetation: estimate = -0.069, p = 0.042). Similarly, patch attractiveness was higher for hard than for soft substrate (estimate = 1.084, p = 0.004), but that attractiveness weakened as the flow increased (interaction between flow magnitude and substrate: estimate = -0.0862, p = 0.004).

Table 3 Estimate, standard error (SE) and associated t value of the logit-MLR of the two bilinear models: attraction and retention models. t* is a value of the t statistic taken from the null model distribution and p is the probability that value of the t statistic be obtained from the null model. The intercept velocity/intercept depth, slope velocity/slope depth, coefficient of variation of the residuals of the velocity (coef. var. velocity)/ coefficient of variation of the residuals of the depth (coef. var. depth) represent the regression parameters between water velocity/water depth and flow magnitudes. Flow is the flow magnitude, vegetation is the submerged vegetation height and substrate is the substrate type. Variables separated by colon punctuation mark designed interaction.

Parameter	**Estimate**	**SE**	**t value**	**t*<-|t|**	**t*= -|t|**	**-|t|<t*<|t|**	**t*=|t|**	**t*>|t|**	**p**
Attraction model									
Intercept	-13.123	1.460	-8.988	17360	0	82639	1	0	0.174
Flow	0.205	0.821	0.249	387	0	99213	1	399	0.008
Habitat patch area	7.5E−05	1.5E−05	4.850	0	0	22912	1	77087	0.771
Flow : Habitat patch area	2.8E−06	8.6E−06	0.319	3573	0	93162	1	3264	0.068
Intercept velocity	-0.767	5.308	-0.144	51356	0	10535	1	38108	0.895
Flow : Intercept velocity	-1.026	2.983	-0.344	1429	0	96911	1	1659	0.031
Slope velocity	1165.710	335.836	3.471	107	0	99868	1	24	0.001
Flow : Slope velocity	-113.390	188.732	-0.601	76	0	99824	1	99	0.002
Coef. var. velocity	-1.370	0.747	-1.835	22244	0	75984	1	1771	0.240
Flow : Coef. var. velocity	0.059	0.420	0.141	8445	0	83374	1	8180	0.166
Intercept depth	-0.767	0.121	-6.324	4	0	99995	1	0	<0.0001
Flow : Intercept depth	-0.002	0.068	-0.035	40060	0	22910	1	37029	0.771
Slope depth	729.499	147.143	4.958	1	0	99320	1	678	0.007
Flow : Slope depth	0.594	82.691	0.007	47291	0	6718	1	45990	0.933
Coef. var. depth	-1.307	0.400	-3.271	1079	0	96465	1	2455	0.035
Flow : Coef.var. depth	0.025	0.225	0.109	13120	0	73658	1	13221	0.263
Vegetation	1.068	0.321	3.332	1133	0	98844	1	22	0.012
Flow : Vegetation	-0.069	0.180	-0.382	1910	0	95836	1	2253	0.042
Substrate	1.085	0.393	2.762	14	0	99560	1	425	0.004
Flow : Substrate	-0.086	0.221	-0.391	176	0	99631	1	192	0.004
Retention model									
Intercept	-17.606	2.433	-7.235	1855	0	98144	1	0	0.019

Flow	0.812	1.368	0.594	0	0	99996	1	3	<0.0001
Habitat patch area	0.0001	2.6E−05	4.025	0	0	62451	1	37548	0.375
Flow : Habitat patch area	3.8E−06	1.4E−05	0.264	521	0	99027	1	451	0.010
Intercept velocity	-4.085	8.847	-0.462	56110	0	27946	1	15943	0.721
Flow : Intercept velocity	-1.938	4.972	-0.390	4	0	99994	1	1	<0.0001
Slope velocity	1939.870	559.731	3.466	662	0	99334	1	3	0.007
Flow : Slope velocity	-227.210	314.555	-0.722	0	0	99999	1	0	<0.0001
Coef. var. velocity	-1.878	1.245	-1.508	21724	0	65953	1	12322	0.340
Flow : Coef. var. velocity	0.032	0.700	0.046	20771	0	58654	1	20574	0.413
Intercept depth	-1.326	0.202	-6.560	0	0	99999	1	0	<0.0001
Flow : Intercept depth	-0.006	0.114	-0.052	19442	0	63140	1	17417	0.369
Slope depth	1211.760	245.240	4.941	1	0	97739	1	2259	0.023
Flow : Slope depth	-22.522	137.819	-0.163	1357	0	97378	1	1264	0.026
Coef. var. depth	-2.015	0.666	-3.025	4627	0	91126	1	4246	0.089
Flow : Coef.var. depth	0.055	0.374	0.147	2471	0	95066	1	2462	0.050
Vegetation	1.643	0.534	3.075	1564	0	98420	1	15	0.016
Flow : Vegetation	-0.219	0.300	-0.729	0	0	99999	1	0	<0.0001
Substrate	1.262	0.655	1.928	1975	0	97137	1	887	0.029
Flow : Substrate	-0.179	0.368	-0.486	3	0	99995	1	1	<0.0001

Results of the retention model were similar to that obtained for the attraction model, with the notable exception of the residual coefficient of variation of the depth (i.e. how much linear was the depth-flow relationship) that was only marginally significant (estimate = -2.015, $p = 0.089$) in the retention model, but significant in the attraction model ($p = 0.035$). The explanatory variables also affect the retention probabilities of a habitat patch in the same direction as that of the attraction probabilities. Another exception involved two variables that explained only the retention probability but not the attractiveness. Firstly, pike seems to prefer to stay in patches with higher surface areas as the flow increased (estimate = 3.8E−06, $p = 0.01$). Secondly, the retention probability of habitat patches with a steep depth-flow relationship tended to decrease sharply with increasing flow magnitude (interaction between flow magnitude and depth slope: estimate = -22.522, $p = 0.026$).

4.5. Discussion

The present study describes an analytical framework for using presence-only data to build numerical habitat modelling (NHM). More specifically, we were able to integrate, in the same analysis, the effect of a contextual variable interacting with habitat descriptors. This approach allowed us to quantify the effects of the contextual variable and how it alters habitat selection by motile organisms.

The first step of the analytical framework consists in building a classification model (the ANN) providing probabilities of animals among a set of discrete habitat patches as a function of the contextual variable. Machine learning techniques (e.g. ANN) are becoming increasingly common in ecological informatics (Green et al. 2005), and are showing great potential in the field of numerical habitat modelling. Method such as ANN can model complex relationship, thus allowing for accurate prediction in forecasting the effect of environmental changes (Olden et al. 2008). Additionally, these methods can account for interactions between descriptors without prior specifications (Hastie et al. 2001). In addition to these advantages, we used ANN in the present study because using telemetry data to observe animal habitat selection in the wild do not provide us with animal occurrences in every discrete habitat over the complete range of the contextual values. In practice, researchers track a rather restricted number of animals, without actually knowing the density of the animals in the habitat for the whole range values of the contextual variable. For example, in the pike telemetry study, we did not have pike abundance data in the habitat patches. The use of a traditional modelling method such as logistic regression would have required us to either add absence data or simulate pseudo-absence. It is never entirely rigorous to simulate absences to a data set unless sampling can reasonably be assumed to be exhaustive. If sampling is not exhaustive, the habitat may well contain individuals of the species under study that were simply not detected. When that occurs, habitat that is worthwhile to a species may be considered unsuitable by the model. The approach chosen here to model transition probability (i.e. the ANN) did not require pseudo-absences. Rather than explaining animal occurrences (i.e. number of animals) in each of the discrete habitats using the contextual variable values, observations of fish movements across the different patches were sequentially added to train the ANN. In our opinion, and specifically in regard to the exemplary scenario presented here where our fishing effort was relatively small and limited to the number of radio-tracking tags we could afford, the addition of pseudo-absences could have resulted in poor model performance.

In the exemplary scenario, the correct classification rate of the ANN was estimated to 44% using cross-validation (100% corresponds to perfect classification of the observed animals in the patches where they were observed and 0 corresponds to an ANN that never predicted the observed destinations). Machine learning algorithms have been shown to produce accurate predictions in numerical habitat modelling. For example, Nohner and Diana (2015) developed a model of muskellunge (*Esox masquinongy*) spawning site selection using the maximum entropy method (Phillips et al. 2006). They found that the mean area-under-the-curve (AUC) was 0.647 for 28 lakes (AUC is an indicator of predictive power where a value of 0.5 indicates that the predictions are no better than random and 1.0 indicates a perfect assignment; Nohner and Diana 2015). Predictors of muskellunge spawning sites included a large set of variables such as bathymetric features (slope, curvature, aspect, and the size of nearby shallow areas), distances to outflow and inflow streams, effective fetch, emergent vegetation, to name but a few. Predictions from the ANN on habitat selection by northern pike in the present paper included only the flow magnitude at the initial and final tracking times, and the time elapsed between tracking. We did not include the habitat descriptors in the ANN as the whole idea behind the present analytical framework is to decouple the contextual variable from the habitat descriptors in order to assess their interaction. For example, the mean water velocity and depth in each habitat patch depends heavily on the flow magnitude. While it would have been marginally possible to include them in the ANN, their effect on habitat selection would have been hardly distinguishable from that of the flow magnitude. Instead, we used the ANN to apply a strict control on the effect of flow magnitude and a bilinear model to reveal the relationship between habitat patch suitability (attractiveness and retentiveness) and the habitat descriptors.

In the present study, the standard ANN outputs were probabilities that a northern pike be attracted or retained by a habitat patch after one hour at a constant flow magnitude. However, the framework allows for a wide range of relevant standard conditions to be investigated, for instance, one where flow magnitude varied from 11 to 250 $m^3 \cdot s^{-1}$ over four hours might have provided useful information in guiding decision-management initiatives in hydropeaking rivers.

The second step of the analytical framework, the bilinear models, allows one to detect which habitat descriptors, possibly interacting with the contextual variable, significantly explain habitat selection by the animals. We have exemplified our analytical framework using only one contextual variable (i.e. the flow magnitude) for the sake of simplicity, but the analytical framework allows for a broad range in the number of contextual variables to be used. For example, on the one hand, as bird habitat selection is a function of the tree species, the altitude of the habitat patch is thought to be an important contextual variable that affect the tree community. On the other hand, the habitat descriptor such as the percentage of canopy cover would also vary depending on the percentage of cloud cover. In this example, both the altitude and the percentage of cloud cover might also have been included as contextual variables in the ANN. Increasing the number of contextual variables in a bilinear model will also augment drastically the size of the bilinear regression problem. For that reason, care must be taken when planning the data collection to assure that the number of animal positions collected on the field is large enough for the number of contextual variables to be controlled by the ANN and then studied by the bilinear regression model.

Northern pike prefer to use habitat with slow water velocity and dense submerged vegetation cover, where they can ambush their prey and capture them using brief anaerobic bursts (Raat 1988, Savino and Stein 1989). This trait may suggest that northern pike are more sensitive to flow fluctuations than species that prefer faster water velocities. Pike would, therefore, have to trade-off some aspect of its most suitable habitat as the flow increases or decreases. Our analytical framework allowed us to evidence this hypothesis: the type of environmental conditions that northern pikes selected depended on the flow magnitude, which could indicate that as its preferred habitat shifted as a function of flow magnitude.

Fish habitat selection has been traditionally modelled using preference curves for water depth, water velocity and substrate type, all parameterized separately, and then combined into a habitat suitability index (HSI; Bovee 1982, Morantz et al. 1987). Species-specific suitable values in these habitat descriptors are usually assessed at low flow, or in a narrow range in flow magnitudes. The quality and quantity of available fish habitats across a large range of flows is then calculated from the habitat suitability indices using the method of weighted usable area (WUA; Katopodis 2003, Lamouroux and Capra 2002, Lee et al. 2010), thus producing predictions of the fish habitat suitability in the stream at any desired flow magnitudes. The HSI and WUA methods have been considerably criticized and it has been shown that other analytical frameworks perform better at predicting and interpreting fish distribution patterns (Guay et al.

2000, Mouton et al. 2012). A common premise for all of these methods in estimating habitat suitability is that the physical conditions selected by fish stay constant throughout all flow magnitudes, thus overlooking potential trade-offs for fish habitat descriptors in their habitat selection. Hence, the most suitable physical structures at a low flow are unlikely to be the same at a high flow in a hydropeaking river such as the Mississagi. The results presented herein therefore contradict traditional and contemporary methods that are based on the premise that selection of physical conditions by fish stays constant throughout all flow magnitudes. For this reason, we expect that our new analytical framework will have major repercussions on the way that aquatic ecologist will model fish habitat selection in the future. It has already been suggested that fish preferences vary among different systems where prevailing biotic and abiotic conditions differ (Rosenfeld 2003). In the present paper, we have shown that the way fish chose a habitat varies significantly with flow variations, advised that numerical habitat models include the interactions between flow magnitudes and every habitat descriptors, and provided a method to achieve this.

The analytical framework described in the present paper allows us to go one step further in the ultimate reaching goal of the wildlife ecologist, which consists in achieving the best model prediction and accuracy (Peters 1991, Wiens 2002). We hope that it will help other ecologists pinpoint the environmental conditions that must be maintained to ensure species conservation in a changing environment as well as unravel new relationships blurred by changing environmental context. As such, we expect the method to be of great interest for decision makers in the field of biodiversity conservation.

4.6. Acknowledgements

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Chapitre 5 Les variations des indicateurs physiologiques de base et maximaux suivant un stresseur aigu entre deux rivières qui présentent des régimes de débit contrastés

Between-river variation in baseline and stress-induced physiological indicators of a top predator in two rivers with contrasting flow regimes

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Abstract

Fish physiological indicators can help understand the mechanisms underlying the whole-animal (e.g. behaviour, fitness) responses to environmental changes. They can also provide insights on the effects of anthropogenic disturbance at the population and community levels (e.g. density, diversity). A relatively few studies have investigated the influence of habitat quality on fish physiology, in comparison to studies conducted on birds, mammals, amphibians and reptiles. Hydroelectric dams have the potential to severely impact fish habitat conditions in rivers. In particular, “hydropeaking” is an operational strategy that release water from the reservoir based on demand for electricity, thus resulting in short-term (i.e., mins to hours) and drastic (several fold increase or decrease) flow changes in rivers. This study compares the baseline and acute stress-induced responses in plasma cortisol, and blood glucose and lactate of northern pike in two rivers located in northeastern Ontario, Canada: the Mississagi River, hydropeaking, and the Aubinadong River, unregulated. We found that both the baseline and the acute stress-induced response in plasma cortisol were significantly lower in the hydropeaking river than in the unregulated river. No differences in the blood glucose and lactate were observed. Our results suggest that repeated mild stressors associated to the hydropeaking flow regime have led to a modulation of both the baseline and the acute-stress response in term of plasma cortisol in pike. This study provides novel mechanistic findings on the effects of flow regulation on fish populations and communities, and also reveals baseline and acute stress-induced responses of the northern pike physiology in rivers.

Key words: Fish, physiology, cortisol, glucose, lactate, altered habitat, hydropeaking, *Esox lucius* L., river, glucocorticoids

5.1. Introduction

Animal physiology is the study of organisms' functional systems, including metabolism, nutrition and thermal relationships (Ricklefs and Wikelski 2002). Especially for ectotherms such as fish, these functions are directly related to the surrounding environment (Huey 1991), comprised of abiotic and biotic conditions (Homyack 2010). Fish physiology can help understand the mechanisms underlying the whole-animal (e.g. behaviour, fitness) and the community (e.g. density, diversity) responses to environmental changes, in an integrative view of an ecosystem health (Austin 2007, Chown and Gaston 2008, Horodysky et al. 2015).

Flow regimes altered by anthropogenic activities have been recognized as a global threat to the biodiversity and ecosystem functions of rivers (Marks et al. 2010, Nilsson et al. 2005). Hydroelectric facilities are present in approximately 50 % of earth's freshwater ecosystem (Rosenberg et al., 2000), and although it is considered as a renewable energy production, some strategy in operating a hydroelectric facility may lead to severe impacts on fish habitat conditions in rivers (Scruton et al. 2005). The hydropeaking operational strategy is a widespread practice that consists in releasing water from the reservoir based on demand for electricity (Cushman 1985, Morrison and Smokorowski 2000), thus resulting in short-term (i.e., minutes to hours) and drastic (several fold increase or decrease) flow changes in rivers.

Researchers have identified the detrimental effects of hydropeaking on fish at scales ranging from the individual (e.g. growth; Kelly et al. 2015, Korman and Campana 2009, Puffer et al. 2015) to higher levels like the ecosystem (e.g. fish community; Gehrke et al. 1995, Macnaughton et al. 2015b, Schmutz et al. 2015). One of the drawbacks of these studies is that the effects of hydropeaking happen at the scale at which the habitat is selected by fish, i.e. at the scale of seconds, minutes or hours, whereas the changes in individual to population happen at the scale of days, months, years, decades or even centuries. These two processes thus happen at different temporal scale. By looking at the effect of hydropeaking using the changes observed at scale ranging from individual to population, researchers can only observe negative effects of such anthropogenic disturbance on fish when, for example, growth reduction and the associated loss in abundance/changes in population structure has already happened. The mechanisms that underlie such relationships are still obscured at the sub-individual physiological scale. Assessing the impacts of hydropeaking disturbances on fish using an integrative approach with physiology indicators could help predict, prevent and mitigate the negative impact of flow alteration at the population-level.

Fish stress response is directly related to fitness through the energetic demand associated to an environmental stressor. In this paper, the term "stressor" is reserved for stimulus that threatens fish homeostasis, which is the stability of organisms' physiological parameters, such as blood glucose concentrations (Cannon 1932, Koolhaas et al. 2011). Allostasis is the process of maintaining homeostasis through physiological adjustments in order to restore physiological parameters to acceptable life-sustaining ranges (McEwen and Wingfield 2003). In the presence of an acute stressor, the amount of energy needed to restore homeostasis is increased and the fish is said to be under an allostatic load. The way fish respond to the allostatic load is called the stress response. When the allostatic load becomes too elevated for an extended period of time, fish can enter the phase of allostatic overload, also called chronic stress. On the one side, the stress response is crucial in avoiding the detrimental effect of environmental or internal conditions that could affect animals' health, reproduction and survival, and is therefore highly conserved across all vertebrate (Sapolsky et al. 2000). On the other side, long-term chronic stress is also recognized as a mechanism causing harm and damage to the organism (Breuner et al.

2008). Intuitively, a fish that performs a high stress response following an acute stressor, herein referred to as the acute stress-induced response, would be better suited to face environmental stressor than a fish that respond to a lesser extent (Belanger et al. 2016, Breuner et al. 2008). However, this is only true if fish can restore homeostasis promptly when the organism as overcome the stressor, thus avoiding chronic stress, which can be assessed by looking at the wild fish baseline in physiology indicator.

Fish stress response is under the control of two major systems: the hypothalamic-sympathetic-chromaffin (HSC) cell and the hypothalamic–pituitary–interrenal (HPI) axes. In the presence of a stressor, the HSC axis leads to a release in plasma catecholamines (CA) by the chromaffin cells located in the head kidney: epinephrine and norepinephrine (Gesto et al. 2014). The increase of plasma CA results in the activation of hepatic β-adrenoceptors that leads to hyperglycemia through glycogenolysis (Fabbri et al. 1998). The response by the HPI axis starts with the release of corticotropin hormones (CRH) by the hypothalamus, which in turn acts as a signal for the pituitary gland in releasing the adrenocorticopropic hormones (ACTH). ACTH than mediate the liberation of glucocorticoids, cortisol in telostean fish, by the interrenal cell located in the head kidney (Wendelaar-Bonga 1997). An increase in cortisol can also promote gluconeogenesis and glycogenolysis metabolic pathways, thus resulting in an increase in fish blood glucose (Laiz-Carrión et al. 2003, Mommsen et al. 1999). Other metabolic consequences are associated to the stress response, such as a change in the fish activity, either hyper-activity (i.e. exercising through exhaustive swimming) leading to muscle fatigue, or hypo-activity (i.e. hiding behaviour). One of the main consequences, among many others, of exhaustive exercising on physiology is an increase in plasma lactate concentration, resulting in blood acidosis (Gladden 2004).

Northern pike (*Esox lucius* L.) is a top predator found in lakes, rivers, and brackish waters of the northern hemisphere (Craig 2008). The selection by northern pike of habitats characterized by low water velocities (Raat 1988, Savino and Stein 1989) could indicate to some extent that they could be under chronic stress while experiencing hydropeaking conditions. More, pike stress responses have been assessed in lake (Arlinghaus et al. 2009), but not much is known on the basal plasma cortisol and blood glucose and lactate of wild river pike. The objective of our study was to compare the baseline levels and the acute stress-induced responses of plasma cortisol, and blood glucose and lactate between a hydropeaking river and a free-flowing unregulated river. We hypothesized that 1) the pike baseline in plasma cortisol, and blood glucose and lactate are significantly higher in a hydropeaking river than in an unregulated river, and 2) the acute stress-induced response in these same three physiological indicators are lower in a hydropeaking river than in an unregulated river.

5.2. Methods

5.2.1. Study area

Our study was conducted in two rivers of northeastern Ontario, Canada (Figure 1: voir chapitre 3) having contrasting flow regimes: the Mississagi River, regulated, and the Aubinadong River, unregulated. Aubrey Falls Dam is a hydroelectric facility built in 1969 that regulates the Mississagi River flows (average daily flow = 38 $m^3 \cdot s^{-1}$). The hourly flow in the studied area on the Mississagi River can vary from 6 $m^3 \cdot s^{-1}$ (minimal flow) to 307 $m^3 \cdot s^{-1}$ (maximum flow) within 3-4 hours. Such important and sudden flow changes related to hydropower production are referred to as ‘hydropeaking”. Hourly flow data (from 2004 to 2014) provided by the hydroelectric company that operates Aubrey Falls dam (i.e Brookfield Renewable Power, Ontario) has shown that, for this period of time, the operation strategy has been consistently hydropeaking, with minor seasonal differences. The Aubinadong River is an unregulated river that flows into the Mississagi River 15 km downstream of Aubrey Falls Dam (Figure 1: see chapter 3). The flow of the Aubinadong River (average daily flow = 15 $m^3 \cdot s^{-1}$; Government of Canada 2014) can change at most by 26% (going from 97 to 126 $m^3 \cdot s^{-1}$ in 4 hours at the fall of 2013). Both study rivers are similar in terms of watershed area, altitude, fish densities and morphology (Harvey-Lavoie et al. 2016). They also share all but one of the 14 fish species present in the two rivers (blacknose dace [*Rhinichthys atratulus*] is present in the Aubinadong River but absent from the Mississagi River; Macnaughton et al. 2015a).

5.2.2. Fish collection

Fish were collected during summer months at the latitude of the study area: June (8th to 15th in 2012 and 7th to 9th in 2013), July (11th and 12th in 2012) and August (10th to 26th in 2011 and 5th to 21st in 2013). Fish from the Mississagi River were captured on an 8 km segment (80 m<river width<180 m) located from 5 km (46°53′57″N, 83°16′9″W) to 13 km (46° 51' 44"N, 83°20' 49"W) downstream Aubrey Falls Dam (Figure 1: voir chapitre 3). Fish from the Aubinadong River were collected over a 19.5 km segment (20 m<river width<115 m) located from 21.5 km (46° 57' 12"N, 83° 25' 14" W) to 2 km (46° 51' 48"N, 83° 22' 40" W) upstream from the junction of the Aubinadong and Mississagi rivers.

We assessed our objectives by collecting fish from both rivers and subjecting them to one of the two different treatments: 1) the baseline treatment and 2) the acute stress-induced response treatment. Fish for both treatments were captured by angling from a canoe or from the shore using a variety of barbless artificial lures and nylon monofilament line (4.5 kg test). Fish for baseline treatments were swiftly reeled near the canoe or the shore, taken using a rubber dip net, blood samples in less than three minutes following the moment that the pike bite on the hook, and placed in an insulated container (990 x 480 x 480 mm) filled with well-aerated river water. This procedure allowed us to obtain pre-capture levels in plasma cortisol, blood glucose and blood lactate, thus corresponding to the levels of those indicators for a fish in the river (Gamperl et al. 1994, Gesto et al. 2013, Romero and Reed 2005, Sumpter 1997). In the Mississagi River (hydropeaking), we tried to collect fish from a wide range of flow magnitudes (i.e. from 6 $m^3 \cdot s^{-1}$ to 307 $m^3 \cdot s^{-1}$) to avoid having fish baseline values in physiological indicators at a narrow range in flow magnitude. Fish for the acute stress-response treatment were played for a standardized 30 seconds upon hooking, then reeled near the canoe or the shore, taken using a rubber dip, transferred to an insulated container (990 x 480 x 480 mm) filled with well-aerated river water, and blood sampled following either a waiting time of 30 or 60 minutes. These two waiting times were chosen to correspond to the maximum values for plasma cortisol, blood glucose and blood lactate, following an acute stressor (Barton 2002, Belanger et al. 2016, Gesto et al. 2013). Blood samples (0.5-1.0 mL) were taken by puncture of the caudal vessel with a 21G Precision Glide BD Vacutainer® needle fitted to a 2 mL BD Vacutainer® tube coated with 37 USP lithium heparin (Ostrander 2000). Fish were subsequently placed in an insulated container (990 x 480 x 480 mm) filled with well-aerated river water. Fish total length (TL, in mm), mass (g) and sex (external examination; Casselman 1974), river water temperature (°C; Traceable thermometer, ThermoFisher Scientific, USA), and time of day were recorded. Ectoparasite load (number of trematode grubs on the skin taking the form of black dots probably corresponding to *Uvulifer ambloplitis*; Lemly and Esch 1984) was recorded for every fish because of its anticipated effect on fish stress (Tveiten et al. 2010). Fish were returned to their point of capture immediately after data collection. All work reported herein was conducted in accordance with the guidelines of the animal care committee of the Université de Montréal and was approved by Ontario Ministry of Natural Resources and Ontario Parks.

5.2.3. Blood sample analysis

Immediately after blood sampling, portable handheld meters were used to estimate the blood glucose ($mmol \cdot L^{-1}$; Accu-Check, Roche, Canada; detection limits: 0.6 - 33.3 $mmol \cdot L^{-1}$) and lactate ($mmol \cdot L^{-1}$; Lactate Pro, Arkray Inc., Japan: detection limits: 0.8 to 23.3 $mmol \cdot L^{-1}$). A small amount of whole blood (Accu-check: 0.001 mL; Lactate Pro: 0.001 mL) was transferred to a meter specific test strip, previously inserted in either the Accu-Check or Lactate Pro. Validation of these portable instruments to estimate blood glucose and lactate in the field was done, respectively, by Cooke et al. (2008) and by Brown et al. (2008). The remaining blood from any given fish was transferred with a pipette in a micro-centrifuge tube (1.5 mL with screw cap, Fisher Scientific, USA), and immediately centrifuged (3000 rpm, 5 min.) with a micro-centrifuge (model Lx100, Chang Bioscience, CA, USA). The supernatant was transferred to a second micro-centrifuge tube and stored in liquid nitrogen for further analyses. Plasma cortisol ($ng \cdot mL^{-1}$) analyses were conducted at Mount Allison University on October 29 2011 for samples collected in 2011, and at Université de Montréal on March 12 2013 for samples collected in 2012 and on October 22 2014 for samples collected in 2013. Duplicates of diethyl ether ($(C_2H_5)_2O$) extracted plasma samples were analyzed by enzyme-linked immuno-sorbent assay (ELISA) quantification (cat # 402710, Neogen corp, KY, USA), a method previously validated for measurement of total plasma cortisol in teleosts fish (Hosoya et al. 2007, Velasco-Santamaría and Cruz-Casallas 2007). Intra- and inter-assay coefficients of variation obtained using this method in a previous study were, respectively, 6% and 9%.

5.2.4. Statistical analyses

Mann-Whitney-Wilcoxon tests (MWW) were used to detect among-river differences in baseline values of plasma cortisol, and blood glucose and lactate, the dependent variables and to ensure that no among-river significant differences existed in the fish TL and mass, river water temperature, time of the day, and ectoparasite load. Analyses of variances (ANOVA) were used to assess the among-river differences, the effect of the waiting time (30 or 60 minutes) and the interaction of those two variables on the acute stress-induced response in plasma cortisol, and blood glucose and lactate. Among-river and among waiting time difference in fish TL and mass, river water temperature, time of the day, and ectoparasite load were also assessed by ANOVA. Among-river differences in the sex of pike caught for the baseline or for the acute stress-induced treatments were assessed by Fisher-exact tests. The assumptions of normality and homogeneity in variances for ANOVA were assessed by, respectively, the Shapiro-Wilk's test and the Bartlett's test. In the case of violation of one or both of these two assumptions, log and square root transformations were applied to obtain both normality and homogeneity of variance. All statistical analyses were conducted with R (R Development Core team, 2015).

5.3. Results

5.3.1. Baseline values

A total of 41 pike (Mississagi River = 25; Aubinadong River = 16) were caught for the baseline treatment (Table 1). Flow magnitude at which fish were caught was higher in the Mississagi River (mean: 95.9 $m^3 \cdot s^{-1}$; range: 6 - 270 $m^3 \cdot s^{-1}$) than in the Aubinadong River (mean: 10 $m^3 \cdot s^{-1}$; range: 4 – 19 $m^3 \cdot s^{-1}$). We found that the Mississagi River pike had, in average, a significantly lower concentration in plasma cortisol than the Aubinadong River pike ($W = 298$, $p = 0.009$;

Figure 2). No significant between-river differences were found in the blood glucose (*W* = 159, *p* = 0.283) and lactate (*W* = 245, *p* = 0.233) concentrations. We found no between-river difference in the length (*W* = 197, *p* = 0.947), the mass (*W* = 212, *p* = 0.748), the sex (Fisher's exact test; *p* = 0.195), the water temperature (*W* = 174, *p* = 0.503), the time of the day (*W* = 149, *p* = 0.181) or the ectoparasite load (*W* = 209, *p* = 0.797).

Table 1 The number of replicates (*n*), mean (range) fish total length, mean (range) fish mass, number of females/number of males, mean (range) water temperature, mean (range) time of the day, mean (range) ectoparasite load, and mean (range) plasma cortisol, blood glucose and blood lactate of fish, by treatment and river of origin.

Treatment			**Mississagi River fish**	**Aubinadong River fish**
Baseline		*n*	25	16
		Total lenght (mm)	544 (440-653)	541 (447-639)
		Fish mass (g)	929.5 (470-1600)	930.4 (427-1410)
		Sex (number of female/number of male)	13 F/ 12 M	12 F/ 4M
		Water temperature (°C)	19.4 (14-25)	19.1 (17-22)
		Time of the day (hours: minutes)	15:46 (9:29-21:02)	14:19 (8:00-19:17)
		Ectoparasite load (number of grubs)	3 (0-20)	2 (0-10)
		Plasma cortisol (ng·mL^{-1})	0.93 (0.01-4.87)	3.79 (0.13-14.72)
		Blood glucose (mmol·L^{-1})	2.61 (1.7-4.3)	2.29 (1.4-3.3)
		Blood lactate (mmol·L^{-1})	1.76 (0.8-3.4)	2.11 (1.0-4.7)
Acute stress-induced response	30 minutes waiting time	*n*	7	5
		Total lenght (mm)	511.6 (459-650)	558.6 (515-600)
		Fish mass (g)	815.0 (516-1595)	1078.6 (798-1289)
		Sex (number of female/number of male)	3 F/ 4 M	5 F/ 0M
		Water temperature (°C)	20.4 (16-23)	20.8 (20-21)
		Time of the day (hours: minutes)	13:52 (8:45-17.59)	10:24 (6:59-15:18)
		Ectoparasite load (number of grubs)	2 (0-8)	1 (0-2)
		Plasma cortisol (ng·mL^{-1})	92.67 (37.03-213.92)	261.83 (160.60-408.47)

	Blood glucose (mmol·L^{-1})	5.99 (2.3-9.8)	7.20 (4.9-8.9)
	Blood lactate (mmol·L^{-1})	11.04 (9.0-12.3)	11.74 (10.9-13.4)
60 minutes waiting time	*n*	7	5
	Total lenght (mm)	544.3 (450-646)	572.4 (495-610)
	Fish mass (g)	959.9 (519-1396)	1063.8 (661-1270)
	Sex (number of female/number of male)	3 F/ 4 M	4 F/ 1 M
	Water temperature (°C)	20.0 (18-22)	22.5 (21-24)
	Time of the day (hours: minutes)	12:35 (11:12-14:34)	13:31 (11:22-15:17)
	Ectoparasite load (number of grubs)	3 (0-6)	1 (0-2)
	Plasma cortisol (ng·mL^{-1})	104.20 (0.00-258.19)	204.20 (127.86-281.09)
	Blood glucose (mmol·L^{-1})	8.88 (5.0-11.5)	9.66 (5.8-11.2)
	Blood lactate (mmol·L^{-1})	10.96 (10.2-11.9)	10.96 (10.3-11.6)

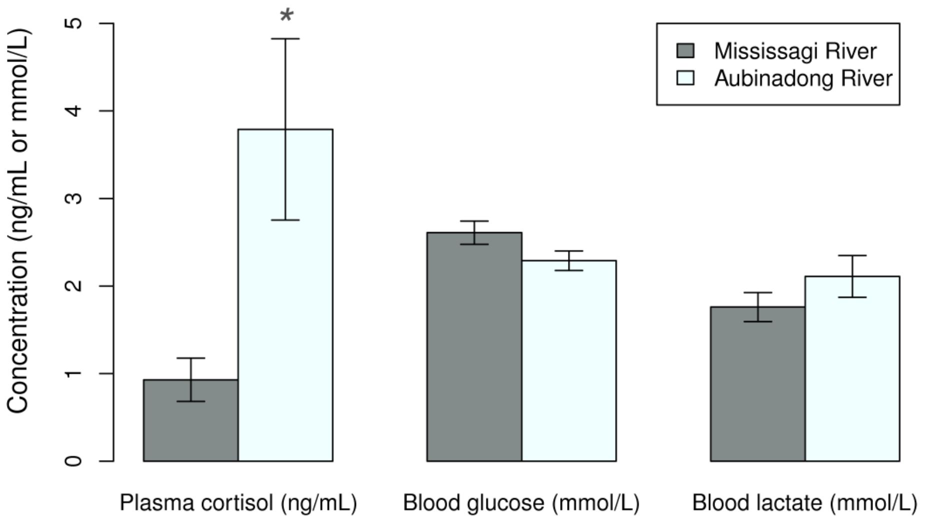

Figure 2 Mean ± SEM concentrations of baseline plasma cortisol, blood glucose, and blood lactate of northern pike capture from the Mississagi River (*n* = 7 fish) or the Aubinadong River (*n* = 5 fish). The asterisk designed significant between-river difference.

5.3.2. Acute stress-induced response

A total of 24 pike were caught in the Mississagi River (30 minutes waiting time = 7; 60 minutes waiting time = 7) and Aubinadong River (30 minutes waiting time = 5; 60 minutes waiting time = 5) for the acute stress-induced response (Table 1). We found a significant difference in the between-river plasma cortisol concentrations (F = 15.91, $p < 0.001$; Figure 3), but the waiting time and interaction had no effect on this indicator (waiting time: F = 0.27, p = 0.608; interaction: F = 1.05, p = 0.317). The waiting time had a significant effect on blood glucose (F = 9.97, p = 0.005), but not the river (F = 1.30, p = 0.268), nor the interaction of these two variables (F = 0.06, p = 0.803). Neither the river (F = 1.06, p = 0.314), nor the waiting time (F = 1.26, p = 0.275), nor the interaction of these two variables (F = 1.05, p = 0.318) had a significant effect on blood lactate. We found no difference between the river, the waiting time or the interaction of these two explanatory variables in the length (river: F = 1.83; p = 0.191, waiting time: F = 0.823, p = 0.375; interaction: F = 0.12, p = 0.737), the mass (river: F =1.75, p = 0.201; waiting time: F = 0.33, p = 0.574; interaction: F = 0.33, p = 0.572), the sex (Fisher's exact test; p = 0.076), the water temperature (river: F = 3.69, p = 0.069; resting time: F = 0.42, p = 0.522; interaction: F = 1.95, p = 0.177), the time of the day (river: F = 1.13, p = 0.299; waiting time: F = 0.23, p = 0.636; interaction: F = 3.42, p = 0.079) or the ectoparasite load (river: F = 3.15, p = 0.091; waiting time: F = 0.35, p = 0.559; interaction: F = 0.49, p = 0.490).

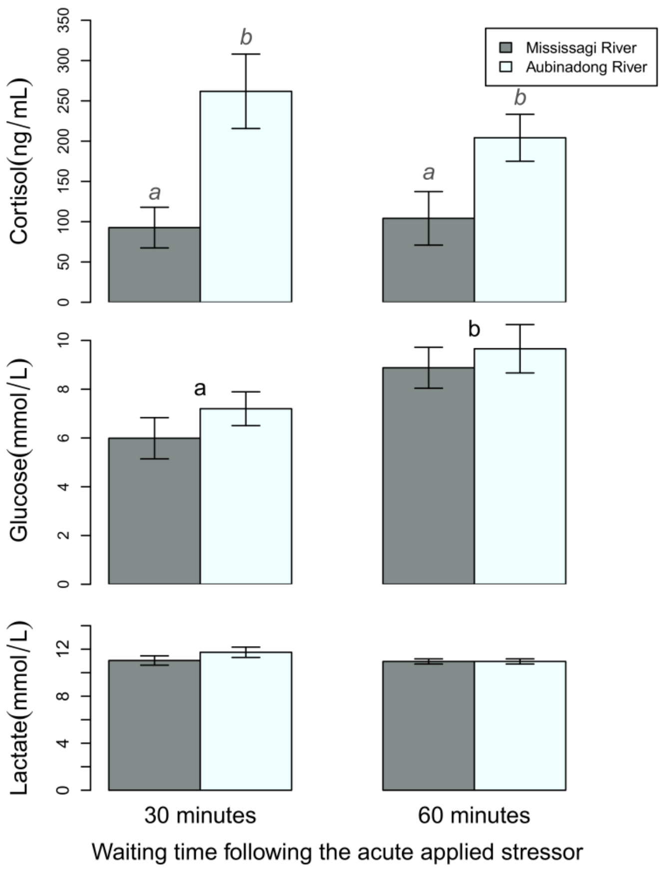

Figure 3 Mean ± SEM concentrations of plasma cortisol, blood glucose, and blood lactate of northern pike subjected to a waiting time of 30 minutes (Mississagi River = 7 fish, Aubinadong River = 5 fish) or 60 minutes waiting time (Mississagi River = 7 fish, Aubinadong River = 5 fish). The different grey italicized letters represent between-river significant difference tested within each waiting time, while the black letters represent significant differences tested between-waiting time. The absence of letters represent that no between-river or between-waiting time differences were found.

5.4 Discussion

The present study tested the hypothesis that the baseline and the acute stress-induced response in plasma cortisol, and blood glucose and lactate of northern pike differ between two rivers with contrasting flow regimes. Between-river differences were observed only for the pike plasma cortisol, whereas the blood glucose and lactate were comparable in both the baseline and the acute stress-induced response. Both the baseline and the acute stress-induced response in plasma cortisol concentrations were significantly diminished for pike inhabiting the regulated hydropeaking river than for pike living in the unregulated river.

The physiological status of wild individuals can give indications of the quality of the habitat in which they live; elevated baseline values in plasma cortisol testify of more stressful environment than animals that have lower baseline values (Wingfield and Romero 2011). The baseline plasma cortisol can therefore be used as an indicator of the animal health (Bonier et al. 2009). Flow changes lead to drastic modifications of the fish habitat (Scruton et al. 2005). In a hydropeaking river, such changes happen frequently; we hypothesized these unstable habitat conditions could be stressful for pike, in comparison to pike living in the unregulated river. Our results show that the between-river baseline in pike plasma cortisol was significantly lower in the hydropeaking Mississagi River than in the unregulated Aubinadong River. This result is contrary to our predictions. Results from a study on mountain whitefish (*Prosopium williamsoni*) also found that the fluctuating flows in a hydropeaking (mean flow: 621 $m^3 \cdot s^{-1}$; range = 0–1770 $m^3 \cdot s^{-1}$) is not a stressful event for these fish (Taylor et al. 2012). Although a significant positive relationship existed between the mountain whitefish baseline cortisol and the hourly mean flow, the mean cortisol concentration was overall low (mean ± SD = 1.60 ± 0.09 $ng \cdot ml^{-1}$) and comparable to baseline cortisol concentrations of other salmonids (e.g. 1.0 ± 0.3 $ng \cdot ml^{-1}$ for brown trout [*Salmo trutta*]; Barton 2002). Moreover, a study by Flodmark et al. (2002) found that mean plasma cortisol of brown trout in an artificial stream channel was significantly elevated (61.3 ± 26.8 $ng \cdot ml^{-1}$, mean ± SD) for fish subjected to daily cyclical flow fluctuations between

0.15 m^3 s^{-1} and 0.04 m^3 s^{-1}, in comparison to control (4.9 ± 3.7 ng·ml^{-1}, mean ± SD). They also found that the elevation in brown trout plasma cortisol only lasted for the first 3 days of the experiment. On the fourth day, cortisol concentrations were back to control levels, thereby suggesting a rapid habituation to the stressor. This same mechanism of habituation could explain why the plasma cortisol concentrations of fish in the Mississagi River was also at very low levels (i.e. mean = 0.93; range = 0.01-4.17 ng·ml^{-1}).

In addition to being at low levels, the mean baseline plasma cortisol of Mississagi River pike was significantly lower than that of Aubinadong River pike. Two different mechanisms can be evoked herein to explain such a result. First, the conditions could be more stressful in the unregulated Aubinadong River. Indeed, a number of physical conditions of pike habitat that differ between the two study rivers could have caused this difference in baseline cortisol. Identifying the sole variable or the combination of variables, responsible for this difference in plasma cortisol, was beyond the objectives of the present study. Among the long suite of physical conditions that can vary in-between rivers with contrasting flow regimes, we can mention the dissolved oxygen concentrations (Calles et al. 2007), the water depth and velocity (Zhong and Power 1996), the substrate composition and distribution due to different erosion and sedimentation patterns (Osmundson et al. 2002), and aquatic plant diversity and abundance (Aronsuu et al. 1999). It is also noticeable that, although statistically significant, the between-river difference in pike baseline plasma cortisol was 2.86 ng·ml^{-1} in average, which is rather small when compared to the acute stress-induced cortisol concentrations of ~ 100 ng·ml^{-1} for Mississagi River pike and ~ 200 ng·ml^{-1} for the Aubinadong River pike. Biological implications on fish fitness for such a small difference (i.e. 2.86 ng·ml^{-1}) are unknown at this point in time.

Data on growth and conditions of pike from these rivers are currently being assessed and should give interesting results.

Second, it has been previously shown that the repetition of mild psychological stressors over 18 days in European Starlings (*Sturnus vulgaris*) has resulted in a significant decrease in plasma cortisol baseline concentrations (Cyr et al. 2007). These findings suggested that birds can dampen their baseline cortisol to avoid pathology associated to a prolonged activation of the hypothalamic-pituitary-adrenocortical axis, the equivalent of the HPI axis in fish. Pike in the Mississagi River could have modulated their cortisol secretion by negative feedback of the HPI axis and the ACTH release (Mommsen et al. 1999).

Baseline plasma cortisol concentrations alone do not enable us to determine which one of the two mechanisms mentioned previously was causing the differences observed in this physiological indicator. Assessing the baseline values along with the acute stress-induced response in plasma cortisol can give further insights on this matter. The acute stress response is seen as beneficial because it prevents the animals from health-threatening situations (Breuner et al. 2008). Following this line of thoughts, a robust (i.e. of great magnitude) response to an acute stressor is often considered to lead the organisms to high fitness endpoints, such as growth and reproductive capacity. This, in turn, also indicates that the animal live in a habitat of good quality (Belanger et al. 2016). In accordance with this, we found that the acute stress-induced response in plasma cortisol of pike living in a river with unstable flow conditions (the hydropeaking Mississagi River) was significantly diminished by approximately half in comparison to that of pike living in the unregulated Aubinadong River. Several studies have found that animals living in low habitat quality have diminished acute stress-induced responses. Most studies on the effect of the habitat quality on the acute stress-induced cortisol response have been conducted in birds, mammals or herpetofauna (Belanger et al. 2016). For these taxa, the diminished acute stress-induced response in plasma cortisol has been suggested to be caused by a number of environmental variables, ranging from food availability (Bauer et al. 2013, Buck et al. 2007) to urban habitat (French et al. 2008). Field fish studies on the habitat quality and the acute-stress response have been conducted mainly on pollutants. For examples, Hontela et al. (1992) and Norris et al. (1999) found that an increased concentration in water pollutants decreased the cortisol response of northern pike in the St-Lawrence river (Canada) system and of brown trout in the Eagle River (Colorado, USA), respectively. No water pollutant concentrations were found outside of the Canadian guidelines for stream water quality and pollutant (Government of Canada, 2011) by the Government of Canada [http://www.yourenvironment.ca/ontario-rivers.php]) in the Mississagi River and thus we excluded this explanation in the present study. Data on water pollutants in the Aubinadong River are not available, but to our knowledge, it has never been shown that water pollutants could increase the cortisol response in fish.

A study on spotted salamanders (*Ambystoma maculatum*) also found that the individuals breeding in a disturbed habitat with housing development (i.e. the disturbed habitat) had a lack of acute stress-induced cortisol response (Homan et al. 2003). In comparison, the individuals breeding in an intact habitat, also assessed in this study by Homan et al. (2003), had a significant increase in cortisol following a standardized capture. The most probable explanation formulated by the authors for this lack in cortisol stress response for the salamander living in the disturbed habitat is that they were under chronic stress. Although Mississagi River pike had a reduced acute stress-induced response, chronic stress can be excluded as being the cause of such a reduced stress response because 1) the plasma cortisol concentrations of pike living in the Mississagi River were very low, and 2) a 100-fold cortisol response was observed between the baseline (0.93 ng·ml^{-1}) and the acute stress-induced response (mean between the 30 and 60 min waiting time= 98.44 ng·ml^{-1}). As said previously, a robust stress-induced response in cortisol serves the organism in a positive manner, but only if the values can go back to baseline rapidly. In an environment where flow fluctuations happen several times during a day, a reduced acute stress-induced response in plasma cortisol might serve the organism better than having a highly sensitive and robust cortisol stress response. We are, therefore, tempted to speculate that mechanisms related to phenotypic plasticity or genetic changes can maintain cortisol concentration of Mississagi River pike at low levels, as a result of repeated and frequent exposure to stressors (Rich and Romero 2005, Schulte 2014).

The present study provides baseline and maximum stress-induced values in plasma cortisol, and blood glucose and lactate for wild northern pike living in rivers. To our knowledge, our study is the first to report baseline plasma cortisol of wild northern pike. Plasma cortisol for pike originating from the Mississagi and Aubinadong rivers were perhaps lower than previously reported basal values for other wild teleost (< 10 ng·mL^{-1}; Pankhurst 2011). Pike blood glucose resting values for wild fish kept in laboratory have been previously reported to be in average 3.9 (converted from an average plasma concentration of 5.5 mmol·L^{-1}; Arlinghaus et al. 2009), 3.1 (converted from an average plasma concentration of 4.4 mmol·L^{-1}; Schwalme and Mackay 1985) and 5.9 mmol·L^{-1} (whole blood concentration; Soivio and Oikari 1976) after an acute handling stressor and a recuperation phase of 2, 6 or 7 days, respectively. These concentrations have been suspected of being higher than the resting values for wild fish due to the captivity stress. From the baseline blood glucose found in the present study, it does seem that the previous blood glucose values from laboratory fish were above the wild river pike average values (Mississagi River: 2.61 mmol·L^{-1}, Aubinadong River: 2.29 mmol·L^{-1}), especially when compared to results from Soivio and Oikari (1976; blood glucose concentration = 5.9 mmol·L^{-1}). In contrast, baseline blood lactate concentrations were comparable to pike resting values previously found in laboratory conditions (0.8-1.4 mmol·L^{-1}; Schwalme and Mackay, 1985; Soivio and Oikari 1976).

Recent concepts in animal stress responses have identified that the term “stressor” *per se* should be restricted to environmental challenges that happen outside of the daily routine or seasonal cyclical of an animal, thus characterized as unpredictable and uncontrollable (Koolhaas et al. 2011, McEwen and Wingfield 2003). As flow fluctuations happen daily in the Mississagi River, this environmental challenge should not be seen as a “stressor” *per se* by northern pike. Our results are in accordance with these concepts, where the baseline plasma cortisol levels show that pike are not stressed from living in a habitat with unstable flow conditions (i.e. in the Mississagi River, hydropeaking), and that they are able to respond to the acute stress of capture. Our results, therefore, suggest that pike inhabiting the Mississagi River are not chronically stressed by the conditions that prevail in their environment, even though the flow fluctuations cause drastic habitat changes.

Fish plasma cortisol concentrations can be under the influence of daily rhythms such as feeding behaviour or activity patterns (López-Olmeda and Sánchez-Vázquez 2010) or under the circadian (endogenous) rhythm (Olivera et al. 2013). Studies conducted in laboratory conditions can control for this confounding factor while comparing cortisol concentrations between groups of fish. In the present study, we tried to minimize as much as possible the potential effect of these rhythms on the plasma cortisol concentrations by sampling fish during daylight (i.e. between 7:00 and 19:00), because the alternation between light and darkness is the most important environmental factor synchronizing daily rhythms (Carr et al. 2006). Although no significant among-group differences were observed in the time of the day, we cannot completely exclude the potential bias of the time of the day at which blood samples were taken.

Results suggest that pike in the Mississagi River have a diminished acute-stress induced plasma cortisol response that is likely caused by an HPI axis adjustment, due to repeated challenges in their environment. To date, the exact variable, or combination of variables, that is responsible for such a diminished response for pike in the Mississagi River have not been identified, due to the many differences in between-river environmental variables. However, the present study reveals an important finding on the fish sub-lethal effect of flow regulation; flow fluctuations in the range 6-307 $m^3 \cdot s^{-1}$ appear to be mild stressors to which the stress responses of predatory fish can be physiologically modulated. Although we showed that the flow fluctuations in the regulated river do not seem to cause physiological disruption in the stress response of pike, the energetic implications (e.g. growth, fish conditions) of the observed physiological mechanisms to cope with fluctuating flows have not been assessed herein. The existence of relationship between such energetic implications and the physiological status should be assessed in future studies on regulated river. This is especially urgent in the actual context where the energy consumption worldwide is expected to increase drastically in the next decades, along with the number of hydroelectric facilities (Almeida Prado Jr et al. 2016).

5.5. Acknowledgements

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Chapitre 6 Conclusions

6.1. L'écophysiologie: la physiologie et l'écologie dans une approche intégrée

Cette thèse présente une approche intégrative des concepts physiologiques et écologiques dans le but de conserver les communautés de poissons en rivières. La réponse au stress est un concept qui est étudié chez les poissons en laboratoire depuis maintenant plusieurs décennies pour permettre une croissance optimale chez les poissons d'aquaculture. En transposant et appliquant les connaissances acquises dans ce domaine, il est possible d'accroître nos connaissances de l'écologie, plus particulièrement des mécanismes qui régissent la façon dont les poissons sélectionnent et se distribuent à travers leurs habitats. Cette approche, appelée communément écophysiologie, est utilisée depuis quelques décennies et s'avère être une avenue prometteuse dans la conservation de la biodiversité des écosystèmes d'eau douce (Cooke et al. 2013a).

6.2. Les poissons sont-ils stressés par les changements de débit?

Le but principal de cette thèse était de répondre à la question: les poissons sont-ils stressés par les changements de débit en rivière? Quatre approches différentes ont été utilisées pour tenter de répondre à cette question. La première approche (chapitre 2) a évalué les différences comportementales inter-rivières des brochets sur le plan des distances parcourues ($m \cdot h^{-1}$), de la portée de leur déplacement, de leur type de mouvement préféré (longitudinal ou latéral) ainsi que de leur taux de déplacement latéral. La deuxième approche, axée sur des (chapitre 3) a été de sélectionner une variable physique de l'habitat des poissons qui est directement affectée par les changements de débit, et d'évaluer la réponse au stress à un changement dans cette variable. Pour ce faire, la vitesse de l'eau a été sélectionnée puisqu'il s'agit d'une variable importante dans la sélection des poissons de leur habitat (Jackson et al. 2001). La troisième approche (chapitre 4) a constitué la conception d'un nouveau cadre analytique qui permette d'évaluer l'effet du débit sur la façon avec laquelle les poissons choisissent leur habitat. La quatrième approche (chapitre 5) a été de quantifier l'effet d'un régime de débit par éclusées sur les valeurs de base et maximales de trois indicateurs de la réponse au stress chez des poissons dans les deux rivières à l'étude.

6.2.1. Première approche : le comportement des brochets

Nous avons évalué le comportement de brochets qui habitent les deux rivières à l'étude. Cela nous a informés sur la façon dont ces poissons réagissent en fonction du débit. Cette approche constituait la première étape dans l'atteinte de l'objectif principal de cette thèse qui était de réponse à la question : les poissons sont-ils stressés par les changements de débit en rivière? Nous avons attaqué la question de cet angle puisque le comportement est le lien entre la physiologie et l'écologie des populations de poissons (Horodysky et al. 2015). Ainsi, nous avons utilisé le comportement comme un indicateur de l'effet du débit sur la réponse au stress chez les poissons. Les résultats de ce chapitre démontrent que le comportement des brochets diffère entre les deux rivières et que l'effet du débit sur le taux de déplacement ($m\ h^{-1}$) des brochets dépend de la gamme de débit dans laquelle ces poissons vivent. Les différences comportementales observées entre les deux rivières ont témoigné d'une certaine réponse au stress qui a conduit à des modifications dans la sélection de leur habitat. Ainsi, les chapitres suivants ont servi à aider à comprendre le mécanisme qui sous-tend ces modifications comportementales.

De plus, les résultats de ce chapitre ont permis d'évaluer les conséquences écologiques potentielles des fluctuations de débit rapides et répetées dans une rivière avec un régime d'éclusées. La première conséquence est située au niveau de l'énergie supplémentaire dépensée par les brochets lorsque le débit est élevé. De par la relation positive entre le taux de déplacement des brochets et le débit de la rivière, nous avons calculé que les dépenses en énergie sont considérables (16% de perte énergétique en comparaison avec les brochets de la rivière avec débit naturel) pour les brochets qui habitent la rivière avec régime d'éclusées. Dans une optique de conservation des populations de brochet, la gestion des débits pourrait être améliorée en diminuant le débit maximal de la rivière. Puisque les brochets augmentent leur taux de déplacement plus le débit augmente, une interdiction d'élever le débit du barrage à des valeurs extrêmes, telles que > 150 $m^3 s^{-1}$ dans la rivière Mississagi particulièrement, serait bénéfique pour la conservation des populations. De plus, les résultats démontrent que cette espèce utilise de façon augmentée les zones inondables et les habitats situés près de la berge, lorsque comparée avec les mouvements des poissons dans la rivière non régulée. Nous croyons que la conservation des populations de brochets en rivière est intimement liée à la protection des berges et particulièrement des herbiers en zone peu profonde près des berges. Des études faites chez les brochets en lacs ont déjà démontré l'importance de la protection des berges, mais l'étude présentée ici met l'emphase sur cette recommandation pour les brochets de rivières. Ceux-ci trouvent refuge dans ces endroits, qui ont normalement des vitesses d'eau plus faibles, et la conservation des berges naturelles semble donc être de première importance dans un écosystème lotique avec régime de débit par éclusées.

6.2.2. Deuxième approche : la vitesse de l'eau en tant que stresseur

6.2.2.1. La cognition chez les poissons

Les résultats de la première approche ont permis de mieux comprendre les différences dans la réponse au stress entre des poissons qui sont soumis à de fréquentes fluctuations de débit (rivière avec éclusées) et des poissons qui vivent dans des conditions plus stables (rivière non régulée). Il a été proposé récemment que la notion de stress doit être abordée principalement avec considération du caractère incontrôlable et imprévisible du stresseur à l'étude (Koolhaas et al. 2011). Le caractère incontrôlable relève de la cognition de l'animal. La cognition désigne les processus mentaux par lequel les animaux intériorisent les signaux externes par apprentissage ou par mémorisation (Shettleworth 2009). Le type de connaissance qu'un animal a d'un stimulus en particulier représente donc l'aspect cognitif de la réponse au stress. Certains auteurs ont signalé que le cortisol plasmatique pourrait ne pas être idéal pour témoigner de la nature de la connaissance et donc du caractère stressant d'un stimulus. En fait, le cortisol plasmatique est parfois libéré dans des conditions qui ne menacent pas l'homéostasie, par exemple lors de la reproduction (Bronson et Desjardins 1982). Le glucose sanguin, qui est relâché *via* majoritairement une augmentation de l'adrénaline (Van Raaij et al. 1995), pourrait donc être une bonne alternative dans le but de déceler les stresseurs chez les animaux (Scheurink et al. 1989). Lorsque nous avons soumis des poissons à une augmentation rapide de la vitesse d'eau dans les tunnels de nage, nous avons observé que les concentrations sanguines en glucose des brochets qui provenaient de la rivière Mississagi, régulée selon la gestion par éclusées, n'étaient pas augmentées. Par contre, les concentrations sanguines pour ce même indicateur chez les brochets de la rivière Aubinadong étaient significativement augmentées. Ceci indique que les brochets de la rivière Mississagi perçoivent un changement rapide dans la vitesse d'eau comme non dangereux pour leur homéostasie, tandis que, pour ceux de la rivière Aubinadong, ce stimulus semble être un stresseur. Il est important de mentionner ici que ces conclusions sont seulement vraies s'il n'y a pas de possibilités que des variations génétiques puissent expliquer les différences observées pour le glucose sanguin. Ceci a été démontré par les résultats du chapitre 5; les brochets de la rivière Mississagi ont une capacité de réponse, en termes de glucose sanguin, aussi forte que les brochets de la rivière Aubinadong à un stresseur aigu. Nous avons donc été en mesure d'exclure la possibilité que les poissons aient des différences génétiques qui causent des réponses divergentes en termes de glucose. Il est aussi peu probable que les différences en lactate sanguin soient causées par les différences en glucose sanguin puisqu'il a été démontré qu'une augmentation du premier ne provoque pas de changements dans le deuxième chez des truites arc-en-ciel (Omlin et al. 2014).

Ainsi, les résultats sur le glucose sanguin de brochet soumis à une augmentation de vitesse d'eau suggèrent que les brochets ont une certaine capacité de mémorisation de leur acquis pour au moins 24 heures. En effet, les brochets devaient attendre 24 heures dans les tunnels de nage avant les expérimentations, ce qui indique que les brochets de la rivière Mississagi ont su garder leur acquis de différenciation de la réponse au stress à une augmentation de la vitesse d'eau pour au moins cette période. À ce jour, les connaissances sur la mémoire des poissons en sont à leur début, mais de plus en plus d'études s'intéressent à ces questions (Brown et al. 2011). Ainsi, il est très difficile de prédire pendant combien d'heures, de jours, ou encore de semaines, les brochets pourraient conserver ce qu'ils ont acquis en termes de connaissance de leur milieu naturel.

Il semble que le type d'expérience que nous avons effectué, c'est-à-dire d'installer directement les tunnels de nage en rivière, plutôt que d'amener les poissons dans une station de recherche, nous a permis d'observer les caractéristiques cognitives chez des poissons sauvages. Très peu d'études semblent avoir utilisé ce même type d'installation. Si nous avions amené les poissons en laboratoire et les avions laissés s'acclimater pendant quelques jours à leur nouvel environnement, ils auraient potentiellement perdu leur apprentissage. Dans les faits, les expériences effectuées dans le but d'examiner la réponse au stress des poissons soumis à une augmentation de la vitesse d'eau ont été faites majoritairement en laboratoire (Hernández et al. 2002, Palstra et Planas 2011, Woodward et Smith 1985, Young et Cech Jr 1993). La mémorisation de 24 heures chez les brochets est plutôt surprenante puisque les poissons sont reconnus pour avoir une mémoire de très courte durée. Cela provient assurément des rares études de cognition effectuées sur le poisson rouge, qui ont conclu que les poissons analysaient l'information de façon moins rationnelle que les mammifères, ce qui indiquerait un potentiel cognitif moindre (Allen 2013, Bitterman 1975). Malgré ces résultats préliminaires sur le poisson rouge, quelques études effectuées sur des poissons sauvages (et d'autres espèces) suggèrent que ceux-ci pourraient, au contraire, avoir développé une approche cognitive avancée de leur environnement (Patton et Braithwaite 2015). De plus, il semble que les poissons de rivière soient particulièrement sujets à développer des fonctions cognitives puisqu'ils sont sujets à des environnements plus variables (Patton et Braithwaite 2015). Par exemple, une étude a comparé la façon dont l'environnement peut moduler la mémoire et l'apprentissage de populations d'épinoches à trois épines (*Gasterosteus aculeatus*) qui provenaient soit de rivière, ou soit d'étang (Girvan et Braithwaite 1998). Les habitats de rivière sont plus instables, considérant les changements potentiels et fréquents de débit ou de turbidité, par exemple; il n'est donc pas adaptatif de se fier à des signaux visuels tels que des morceaux de bois pour se repérer spatialement. En comparaison, ce genre de signaux visuels est plus fiable dans des environnements plus stables tels que des étangs. Girvan et Braithwaite (1998) ont trouvé que les épinoches de rivière se fiaient moins à des signaux visuels, tels que des plantes, pour trouver de la nourriture, que les épinoches d'étang. Une expérience supplémentaire leur a permis de déterminer que ces différences cognitives entre les épinoches provenant de rivière et d'étang n'étaient pas causées par des différences génétiques. Les résultats de cette thèse ouvrent donc la porte sur une multitude d'études originales et potentielles sur le sujet de l'apprentissage chez les poissons qui vivent dans des conditions changeantes de débit.

Notre conclusion est donc que les poissons de la rivière Mississagi ne sont pas stressés par une augmentation de la vitesse d'eau, mais que les poissons de la rivière Aubinadong le sont.

6.2.2.2. La capacité de nage des brochets

Des différences dans les concentrations de lactate ont été observées entre les brochets de la rivière Mississagi et ceux de la rivière Aubinadong. Il semble que les poissons de la rivière régulée aient des mécanismes qui permettent la diminution de l'accumulation du lactate dans le sang lorsqu'ils sont soumis à une augmentation de la vitesse d'eau. Tel que discuté dans le chapitre 3, le mécanisme de conditionnement par exercice pourrait être la cause d'une telle différence. La morphologie des poissons a aussi le potentiel d'améliorer la capacité de nage et donc de diminuer la quantité de lactate qui s'accumule dans le sang des poissons (Chapman et al. 2015, Gladden 2004). Nous avons évalué la morphologie des brochets des rivières Mississagi et Aubinadong dans le but d'explorer la possibilité que les régimes de débits aient un effet sur la forme du corps (Annexe 1, article intitulé: «Différentiation morphologique chez le grand brochet : l'influence des conditions environnementales et du sexe sur la forme du corps»). Les résultats démontrent que les brochets de la rivière Mississagi et Aubinadong ont des morphologies différentes. Les poissons qui habitent la rivière Mississagi ont une tête significativement plus allongée, un corps et un pédoncule caudal plus haut, ainsi qu'une insertion de dorsale plus longue que les poissons de la rivière Aubinadong. Ces résultats suggèrent un certain compromis chez les poissons de la rivière Mississagi pour avoir une meilleure capacité de nage, due à une forme plus allongée de la tête, tout en gardant une bonne accélération rapide pour chasser par embuscade, due à un corps et un pédoncule caudal plus haut. De plus, l'insertion de nageoire plus longue indique une amélioration de la stabilité et de la manœuvrabilité chez les poissons de la rivière Mississagi, ce qui pourrait s'avérer bénéfique dans des conditions instables en termes de débit (Standen et Lauder 2005). La forme de tête, plus allongée chez les poissons de la Mississagi, concorde avec les résultats obtenus lors de l'étude des mouvements des brochets et de l'étude en tunnels de nages. En effet, une tête plus allongée permettrait aux poissons de la Mississagi de nager à de plus grandes vitesses sans s'épuiser, ce qui a été observé.

6.2.3. Troisième approche : l'effet du débit sur la sélection des habitats par les poissons

Nous avons développé une nouvelle approche qui a permis de confirmer notre hypothèse selon laquelle le débit modifie la sélection des variables physiques de l'habitat par les brochets. Cette découverte a une implication considérable pour les biologistes de poissons qui travaillent sur les modèles numériques d'habitat. Nos résultats contredisent les concepts généralement acceptés et encore utilisés de nos jours en écologie des poissons, selon lesquels la sélection des poissons de leur habitat se fait selon des indices d'habitat favorable (*habitat suitability index* en anglais) calculés à partir d'observations faites à un ou une gamme étroite de débits (Bovee 1982, Li et al. 2015). La quantité et qualité d'habitat disponible pour les poissons à travers une large gamme de débits est par la suite calculée à l'aide de la méthode des aires utilisables pondérées (weighted usable area en anglais; WUA; Katopodis 2003, Lamouroux et Capra 2002, Lee et al. 2010). Une prémisse importante pour l'application de ces modèles est que les conditions physiques favorables de l'habitat ne varient pas en fonction du débit, ce que nos résultats contredisent. Les résultats présentés ici suggèrent qu'il pourrait être profitable, dans une optique de conservation des communautés de poissons de rivière, d'évaluer les indices d'habitat favorable en intégrant l'effet de larges gammes de débits dans les modèles numériques d'habitat.

De plus, les résultats du chapitre 4 renseignent sur la façon dont les brochets font des compromis dans la sélection des conditions physiques de leur habitat à travers une large gamme de débits. Ceci a une implication importante pour la conservation des populations de brochets puisque notre cadre analytique permet d'évaluer, pour chaque valeur de débit, la valeur de chaque habitat (par des mesures d'attraction et rétention) pour des brochets adultes (longueur totale = 440-635 mm). Ainsi, dans le but d'assurer la pérennité des populations de brochets en rivières, nos résultats suggèrent qu'à bas débit, les habitats à préserver seraient ceux où la vitesse de l'eau est plus grande lorsque comparée avec la vitesse d'eau des habitats où sont attirés les brochets à des débits élevés. Autrement dit, ceci implique donc que les vitesses d'eau des habitats protégés à bas débit devraient être plus élevées que celles des habitats protégés à haut débit. De plus, lorsque les brochets font face à des débits élevés, ils semblent qu'ils soient plus attirés vers des habitats où les vitesses d'eau et les profondeurs sont bien corrélées. Nous suggérons donc de prioriser aussi la conservation de ce type d'habitat. Pour ce qui est du pourcentage de couverture des habitats, contrairement à ce que les études précédentes semblent indiquer, nos résultats suggèrent que les habitats où la couverture en plantes aquatiques est faible sont importants pour les brochets lors de débits élevés. Les habitats où la couverture en plantes aquatiques est élevée attirent aussi les brochets, mais de façon plus importante à bas débit. Notre cadre analytique à permis de mettre en évidence ce type de compromis, qui semble être primordiale dans la sélection de l'habitat par les brochets.

6.2.4. Quatrième approche : la rivière régulée par éclusées en tant que stresseur

Les résultats de la deuxième approche ont permis d'évaluer les valeurs de base et maximales des indicateurs de la réponse au stress chez des poissons qui vivent dans les deux rivières à l'étude (chapitre 5). Selon les données obtenues, les brochets de la rivière Mississagi semblent être capables de modulation de l'axe HHI, permettant ainsi de maintenir les valeurs de cortisol plasmatique à de bas niveaux. Une activation à long-terme de l'axe HHI mène à des surcharges allostatiques, phénomène appelé stress chronique, et cause la défaillance de l'organisme par des maladies et pathologies reliées à la stimulation accrue et prolongée du cortisol plasmatique (Breuner et al. 2008). Les boucles de rétroaction négative constituent le caractère adaptatif de la réponse au stress: la sécrétion du cortisol est régie par l'hypothalamus, la glande pituitaire et la production d'ACTH, qui eux même sont sous l'influence négative de la quantité de cortisol sanguin (Mommsen et al. 1999). Les résultats présentés dans cette thèse suggèrent que les poissons de la rivière Mississagi contrent les effets pervers du stress engendré par les variations de débit par une diminution de l'activation de l'axe HHI.

L'ajout des données de cortisol plasmatique de base et maximum (chapitre 5) aux connaissances acquises préalablement par les tunnels de nage (chapitre 3) a permis de déterminer que les brochets de la rivière Mississagi ont non seulement une réponse de l'axe HHI diminuée lorsqu'ils sont soumis à une augmentation en vitesse d'eau, mais que cette réponse diminuée n'est pas spécifique à un seul stresseur. En effet, même lorsqu'un stresseur aigu était appliqué, tel qu'une capture, les brochets de la rivière Mississagi avaient une réponse plus petite en cortisol plasmatique. Nos résultats démontrent que l'utilisation conjointe de plusieurs approches permet ainsi d'évaluer avec une plus grande précision l'état physiologique des poissons sauvages. Cela procure, par la même occasion, une meilleure compréhension des effets potentiels à court et long termes sur le fitness des poissons de rivière.

Pour ce qui est de répondre à la question : « les poissons sont-ils stressés par les changements de débit? », nous pouvons ainsi conclure qu'il semble que les poissons ont le potentiel de mettre en place des mécanismes (comportement, morphologie, cognition, modulation de l'axe HHI) qui leur permettent de ne pas être stressés par les conditions changeantes de débit qui prévalent dans leur habitat.

6.3. Les effets des changements climatiques sur la modification des débits naturels

Les changements climatiques sont reconnus pour avoir un effet sur la température globale de l'eau et de l'air, mais d'importants changements qui sont aussi à prévoir dans le régime des débits des rivières (Millenium Ecosystem Assessment, 2005). En effet, les modifications dans la quantité, la fréquence, ainsi que le moment de l'année où les précipitations surviennent auront un impact majeur sur les débits et donc sur la quantité et la qualité des habitats disponibles pour les poissons (Kundzewicz et al. 2007). Par exemple, une étude a évalué les effets des modifications de débit causées par les changements climatiques sur les sédiments en suspension dans des rivières alpines (Scheurer et al. 2009). Ils ont trouvé qu'une croissance dans la quantité de sédiments dans les alpes aura potentiellement un effet non-négligeable et négatif sur la reproduction des truites brunes. Une autre étude s'est concentrée sur la comparaison entre les effets des barrages et les effets des changements climatiques projetés jusqu'en 2050 sur les régimes de débits naturels mondialement (Döll et Zhang 2010). Leurs modèles prédisent que les modifications de débit induites par les changements climatiques lorsque nous arriverons en 2050 seront de plus grandes amplitudes que ceux induits par les barrages et les prélèvements d'eau observés jusqu'à maintenant. Cela met encore plus d'emphase sur la nécessité d'évaluer les effets des modifications de débit sur les poissons. Ainsi, une meilleure compréhension des mécanismes par lesquels les poissons font face à de tels changements dans leur environnement permettra de prédire, avec une plus grande précision, quels seront les effets les plus dommageables des changements climatiques pour les communautés. De plus, cette connaissance permettra de mettre en place des mesures d'atténuation des effets des changements de débits sur les poissons.

6.4. Perspectives d'avenir

6.4.1. Intégrer un nombre plus élevé de rivières dans l'étude de la réponse au stress en fonction des fluctuations de débit

Dans un premier temps, le mouvement des brochets a été étudié en fonction du débit dans deux rivières avec des régimes de débit contrastés. Cette étude amène de nouvelles connaissances sur la façon dont le régime de débit affecte les déplacements de poissons et constituait une étape obligatoire dans l'identification des effets des fluctuations rapides de débit sur les poissons. Par contre, cette étude ne nous a pas permis d'identifier avec certitude la variable, ou l'agencement de variables, qui sont responsables des différences de mouvement entre les deux rivières. Maintenant que nous savons que d'importantes variations existent dans le comportement des poissons entre une rivière régulée par éclusées et une rivière non régulée, la prochaine étape serait d'étudier chaque patron de mouvement dans un nombre plus élevé de rivières (> 10 rivières) qui varient par leur régime de débit. Aucune étude de ce type n'a été effectuée encore, selon notre connaissance actuelle de la littérature sur le sujet. Ceci est certainement dû aux coûts très élevés d'un tel cadre d'analyse, vu le coût élevé de chaque émetteur radio, ainsi que de la main d’œuvre nécessaire pour effectuer des relevés détaillés des caractéristiques physiques de l’habitat des poissons et du suivi des positions spatiales des poissons.

Il en va de même avec l’étude sur les niveaux de base et maximaux de cortisol plasmatique des poissons. Puisque les études présentées dans cette thèse ne permettent pas d’identifier avec précision la variable, ou l’association de variable environnementale, qui a causé la diminution de la réactivité de l’axe HHI chez les brochets de la rivière Mississagi (chapitre 5), il serait intéressant de monter une étude sur les niveaux de base et maximaux de cortisol plasmatique dans un grand nombre de rivières (> 10 rivières) qui varient de par leur régime de débit. Selon les résultats présentés dans le chapitre 5 sur les niveaux de base et maximaux de cortisol plasmatique, il semble probable que la façon dont les barrages sont gérés pourrait mener à différentes modulation de l’axe HHI. Ainsi, en échantillonnant un grand nombre de rivières régulées, il serait probablement possible d’identifier les caractéristiques des régimes de débit qui causent la modulation de l’axe HHI. Ces caractéristiques sont déjà étudiées dans le domaine de l’écologie par des indices de débits (Macnaughton et al. 2015b, Olden et Poff 2003, Poff et Zimmerman 2010). Ces indices permettent de décrire les différences entre les rivières dans leur débit, et ce à l’aide des 5 composantes du débit: la magnitude, la fréquence, la durée, la prévisibilité, et le taux de changement (Poff et al. 1997). Ces concepts pourraient aussi être appliqués en écophysiologie.

6.4.2. Utiliser le cadre analytique développé au chapitre 4 pour évaluer l’effet du débit sur la sélection des habitats par les poissons

La réponse au stress chez les animaux dépend des conditions environnementales auxquelles ils ont été soumis dans leur habitat au courant de leur vie. Une des grandes difficultés d’étudier la réponse au stress chez des poissons sauvages est qu'il est ardu d'établir des relations entre la physiologie ou le comportement et les conditions que les poissons sélectionnent dans leur habitat. Le nouveau cadre analytique que nous avons développé (chapitre 4) afin d'analyser l'effet du débit sur la sélection des conditions physiques de l'habitat des poissons, nommé descripteurs de l'habitat, est un premier pas dans l'atteinte de ce but. Ce nouveau cadre analytique a permis de démontrer que les poissons sélectionnent des valeurs différentes de descripteurs de l'habitat dépendamment du débit de la rivière. Nous avons présenté cette étude dans le cadre de cette thèse car nous voulions évaluer les vitesses d'eau auxquelles les poissons sont soumis. Les études présentées dans les chapitres 2 et 3 suggèrent que les poissons sont soumis à des vitesses d'eau plus élevées dans la rivière régulée, ce qui pouvait indiquer que le débit a un effet sur la façon dont les poissons sélectionnent leur habitat. Ce nouvel outil a permis de confirmer qu'une interaction existe entre le débit et la vitesse d'eau dans la sélection d'un habitat par les brochets. Des analyses supplémentaires, à partir des modèles de régressions bilinéaires, seront nécessaires dans le futur pour définir exactement les vitesses d'eau auxquelles les brochets de la Mississagi sont soumis. Éventuellement, ce même cadre analytique pourra être utilisé pour modéliser la sélection des habitats par les brochets de la rivière Aubinadong. Nous avons toutes les données nécessaires pour ainsi comparer l'effet du débit sur la sélection des habitats chez les brochets qui vivent dans la rivière Mississagi et Aubinadong.

Cette thèse avait comme objectif de présenter une approche intégrative des concepts de physiologie et d'écologie. En évaluant les mouvements des poissons, leur réponse à une augmentation de la vitesse d'eau, la sélection de leur habitat, leur stress de base et maximum, ainsi que leur morphologie, nous croyons être arrivés à remplir notre objectif. Cette thèse a aussi permis d'identifier de nombreux sujets potentiels d'études sur l'effet des fluctuations de débit sur la réponse au stress des poissons. Tel que mentionné tout au long de ce document, les changements de débits ont un effet sur une multitude de variables physiques des habitats de poissons. Nous avons évalué la réponse au stress des brochets soumis à seulement quelques une de ces variables. Il existe d'innombrables autres questions de recherche à répondre sur l'effet des fluctuations de débit sur la réponse au stress des poissons, situées particulièrement à l'intersection entre la physiologie et l'écologie. Les études présentées à travers le présent document révèlent qu'il est aussi indispensable d'intégrer des systèmes non-altérées dans l'identification des effets de l'altération anthropologiques des conditions de débits sur les écosystèmes d'eau douce.

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Annexe 1 : Morphological differentiation in northern pike (*Esox lucius L.*): The influence of environmental conditions and sex on body shape

Morphological differentiation in northern pike (*Esox lucius L.*): The influence of environmental conditions and sex on body shape

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Morphological differentiation in northern pike (*Esox lucius* L.): The influence of environmental conditions and sex on body shape

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Abstract

Intra-specific morphological differentiation may allow individuals possessing particular traits to better cope with prevailing environmental conditions. For instance, different fish body shape and fin size may affect swimming modes and be adaptive in specific conditions. The few instances when morphological differentiation was compared across species suggested that genetically or behaviourally distinctive species may respond differently to similar environmental conditions. Morphological differentiation in fish characterized by sagittiform body shape and lie-in-wait behaviour, such as northern pike (*Esox lucius* L.), has rarely been addressed. Therefore, our objectives were to: 1) compare the morphology of northern pike between two rivers, and 2) assess if morphological differentiation was consistent between sexes. Northern pike were angled in the Mississagi, a hydropeaking river, and the Aubinadong, an unregulated river. Fish morphology significantly diverged between rivers and sexes. Individuals from the Mississagi River had more elongated heads, deeper bodies and caudal peduncles, and longer dorsal fin insertions than individuals from the Aubinadong River. Caudal fin differences between rivers were not consistent between sexes. Morphological differentiation in northern pike suggested a potential trade-off between morphological adaptations for sustained swimming, burst swimming, and manoeuvrability to cope with larger and more variable discharge in a hydropeaking river.

Key-words**:** *Esox lucius* L., evolutionary ecology, flow regime, habitat use, hydroelectricity, northern pike, phenotypic plasticity

Introduction

Environmental conditions are inherently heterogeneous in space and dynamic in time, and act as a guide for ecological strategies and species traits (Southwood 1977; Townsend et al. 1997; Mérigoux et al. 2001). Consequently, no single phenotype is expected to be optimal under the complete range of environmental conditions that a species may encounter. Phenotypic differentiation is often observed in individuals of a species across different environmental conditions (Ford 1964; Levins 1968; Hassell 1978). Intra-specific phenotypic differentiation of life-history, behavioural, physiological, and/or morphological traits (Smith and Skúlason 1996) has been examined in fish, reptiles, birds, and mammals (Wimberger 1994). Phenotypic traits may be affected by abiotic (e.g. water velocity, water temperature, oxygen concentration; Pakkasmaa and Piironen 2000; Schaack and Chapman 2003; Senay et al. 2015) and biotic conditions (e.g. prey type, presence of competitors or predators; Rüber and Adam 2001; Bourdeau and Johansson 2012; Brodersen et al. 2015), and may also vary between sexes (Ritchie et al. 2007; Colborne et al. 2011). Intra-specific phenotypic differentiation may result from two mechanisms: genetic divergence or phenotypic plasticity (West-Eberhard 1989; Robinson and Wilson 1996). Genetic divergence is a measurement of genetic change between individuals, populations or species lineages (Taylor 1991; Collin and Fumagalli 2011), while phenotypic plasticity is a condition where a variety of phenotypes may develop from a common genetic background (Scheiner 1993; Pfennig et al. 2010). The mechanisms underlying the maintenance of phenotypic differentiation are attracting considerable interest because of its role in the evolution of new traits, or even new species (Schluter 1996; Draghi and Whitlock 2012).

Intra-specific morphological differentiation may affect predator avoidance, foraging, locomotion, or reproductive success, and may allow individuals possessing particular traits to better grow, reproduce, and survive under prevailing environmental conditions (Uller 2008; Burton and Metcalfe 2014). Intra-specific morphological differentiation has been reported between fish using the littoral and the pelagic zones of lakes (Dynes et al. 1999), inhabiting lakes and rivers (Sharpe et al. 2008; Hass et al. 2010; Collin and Fumagalli 2011), and found in a series of rivers (McLaughlin and Grant 1994; Drinan et al. 2012; Senay et al. 2015). Intra-specific morphological differentiation, such as differences observed in the general body shape, and the size and placement of fins, is often related to different swimming modes (Drucker and Lauder 2002; Imre et al. 2002; Peres-Neto and Magnan 2004). Hydrodynamic theory suggests that elongated and shallow body shapes, along with smaller fins, reduce drag and swimming costs at a given speed, thereby enhancing sustained swimming capacity (i.e. prolonged swimming; Webb 1982, 1984a; Drucker and Lauder 2002; Robinson and Parsons 2002; Chapman et al. 2015). Conversely, deeper body shapes and longer fins increase burst swimming (i.e. rapid acceleration) and maneuverability (i.e. precise control of direction; Webb 1982, 1984a; Drucker and Lauder 2002; Robinson and Parsons 2002; Chapman et al. 2015). The environmental conditions that define the minimal swimming capacity required to use a particular habitat or adopt a particular behaviour, are expected to affect fish morphology. Hence, fish living in high water velocities or travelling long distances should exhibit elongated and shallow body shapes with smaller fins (Webb 1982, 1984a; Robinson and Parsons 2002; Chapman et al. 2015).

Sexual dimorphism is widespread across the animal kingdom (Vollrath and Parker 1992; Bonnet et al. 1998; Williams and Carroll 2009), with males and females often differing, not only in reproductive organs, but also in external structures not directly related to reproduction (Andersson 1994; Williams and Carroll 2009). Between-sex differences in behaviour, physiological requirements, intra-sexual competition, and sexual selection can drive sexual dimorphism of external structures (Parker 1992; Andersson 1994). In fish, sexual dimorphism affects both the size and the shape of individuals of different sexes (Quinn and Foote 1994; Ritchie et al. 2007), and reproductive tactics (e.g. parental and cuckholders; Colborne et al. 2011). For instance, males with large fins have been known to be more successful at mate acquisition due to increased burst swimming capacity and maneuverability, providing a greater access to females (Fleming and Gross 1994; Kokita and Mizota 2002).

The few instances when the morphology of more than one species or families were compared suggest that inter-specific morphological differences to similar changes in environmental conditions may be related to species-specific interactions between genetics, behaviour, and environmental conditions (Pakkasmaa and Piironen 2000; Langerhans 2008; Binning and Roche 2015; Senay et al. 2015). Several studies investigated intra-specific morphological differentiation in salmonids (Taylor and McPhail 1985; McLaughlin and Grant 1994; Pakkasmaa and Piironen 2001; Drinan et al. 2012). Typically, salmonids have a fusiform shape with the dorsal fin located at the middle of their body (Scott and Crossman 1973; Webb 1978). They prefer areas free of macrophytes for drift feeding, and predominantly use sustained swimming to capture their prey (McLaughlin and Grant 1994; Blake 2004; Quinn 2011). In many cases, fast water velocity was associated with more elongated shapes and smaller fins in salmonids (McLaughlin and Grant 1994; Imre et al. 2002; Peres-Neto and Magnan 2004), mainly supporting hydrodynamic theory towards improved sustained swimming capacity (Webb 1982, 1984a; Robinson and Parsons 2002). However, it is unclear that conclusions obtained for salmonids may be applicable to fish species possessing different forms, behaviours, and swimming capacities. Northern pike (*Esox lucius* L.) have a long, laterally compressed, sagittiform body shape (arrow-like), with dorsal and anal fins positioned posteriorly (Scott and Crossman 1973; Webb 1978). They are ambush predators, using the cover of macrophytes for stalking prey and burst swimming to capture them (Webb 1984b; Raat 1988; Bry 1996; Craig 2008). Compared to salmonids, northern pike possess a better capacity for burst swimming and an inferior ability for sustained swimming (Blake 2004). Morphological differentiation in response to environmental conditions for fish characterized by such a combination of shape, behaviour, and swimming capacity has rarely been investigated. Therefore, our objectives were to: 1) compare the morphology of northern pike between two rivers having contrasting environmental conditions, and 2) assess if the patterns of morphological differentiation were consistent between sexes.

Material and Methods

Study area

The study was conducted in the Mississagi and the Aubinadong rivers, both located in Ontario, Canada (Figure 1). These rivers were selected because they are similar in a number of environmental conditions (Table 1), and share all but one of the 14 fish species present (blacknose dace, *Rhinichthys atratulus* present only in the Aubinadong River*;* Macnaughton et al. 2015). However, these rivers have contrasted flow regimes (Government of Canada 2014; Brookfield Renewable Energy Partners; Senay et al. 2016). The Mississagi River is regulated by a hydropeaking facility, the Aubrey Falls Dam, built in 1969. The annual median discharge of the Mississagi River is 30 cms (cubic meter second), and the flow regime is characterized by large and frequent fluctuations.Water released from the hydropeaking facility can typically increase from 0 to 138 cms, reaching peak flows of 330 cms within the span of an hour (Figure 2). The Aubinadong River flows into the Mississagi River 13 km downstream from the Aubrey Falls

Dam (Figure 1). The Aubinadong River is an unregulated river that has a median annual discharge of 8 cms (Table 1 and Figure 2).

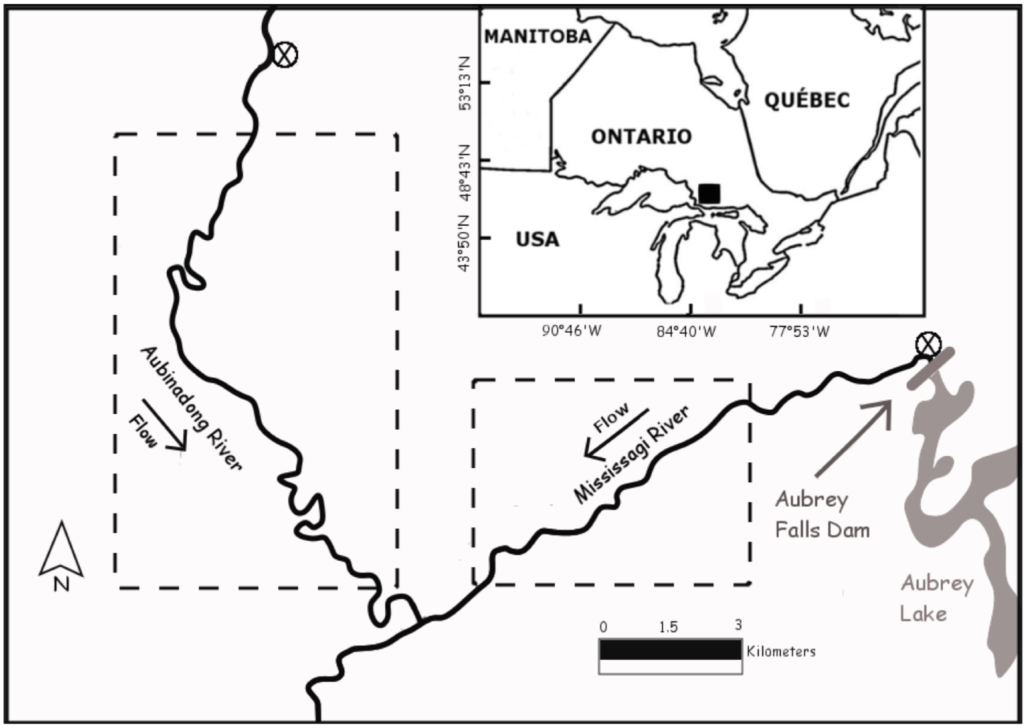

Figure 1 Map of the study area showing the Mississagi River, regulated as hydropeaking by the Aubrey Falls Dam, and the Aubinadong River, having an unregulated flow regime. Both rivers are located in Ontario, Canada, identified by the black square. The studied river segments are surrounded by dotted lines, the direction of the flow indicated by arrows, and flow gauges by circles with ``X``.

Table 1 Location and characteristics of the study rivers.

Characteristics	Mississagi River	Aubinadong River
GPS coordinates	46°54′N, 83°16′W	46° 55′N, 83° 26′W
Regulation type	Hydropeaking	Unregulated

Watershed drainage area (km^2)	4152.2	1580.5
Watershed drainage density (km/km^2)	0.1088	0.1317
Median watershed elevation (m above sea level)	455	484
Maximum watershed elevation (m above sea level)	590	607
Watershed slope (mean; %)	5.7	8.9
Watershed slope (standard deviation, %)	4.2	5.8
Total precipitation (1961-1990; mm/year)	906	973
River slope (m/m)	0.0007	0.0009
River wetted width (m)	80-180	20-115
Median annual discharge (cms=cubic meter second)	30	8
Discharge coefficient of diel variation (%)	209.16	2.18

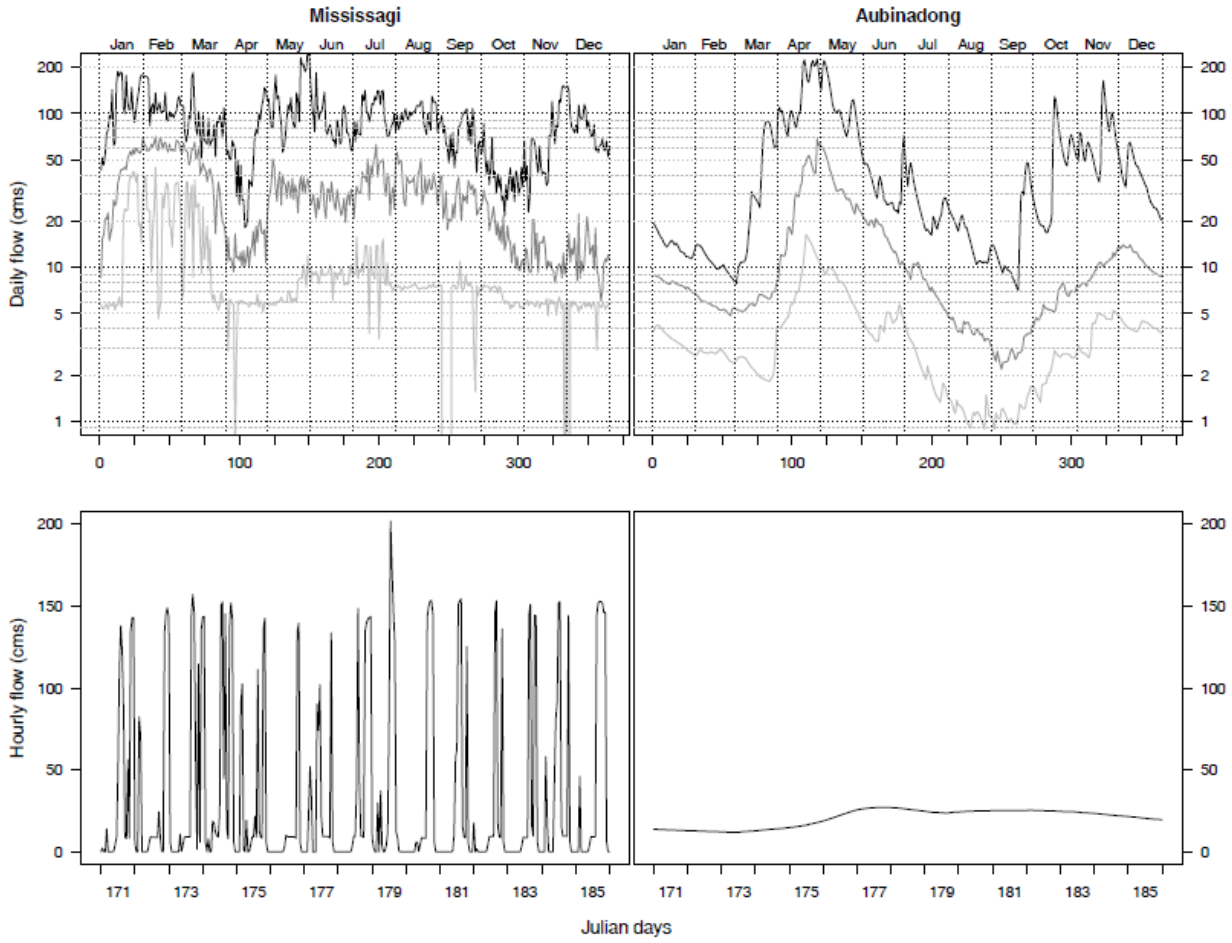

Figure 2 Hydrographs contrasting the flow regime of the Mississagi River (water released from the hydropeaking facility, left panels) and the Aubinadong River (unregulated, right panels). In the upper panels, annual flow regimes are described by maximum (dark gray), median (medium gray) and minimum (light gray) daily discharge (cms = cubic meter second). In the lower panels, typical summer intra-daily flow fluctuations in response to a rain event are illustrated. Daily discharges are represented on a logarithmic scale for enhanced clarity.

Morphological analyses

In the Mississagi River, northern pike were captured over an 8 km river segment located between 5 and 13 km downstream of the Aubrey Falls Dam. In the Aubinadong River, northern pike were captured over a 19.5 km river segment located 2 km upstream from the junction with the Mississagi River (Figure 1). This strategy was adopted to minimize the probability of capturing fish that travelled between the two rivers. Northern pike were captured by angling between 08-08-2011 and 26-08-2011. In each river, 16 adult northern pike ranging from 44.3 to 65.3 (total length, ±0.1 cm) were captured. Fish were aligned on their right side, fins were pinned to ensure consistency in body position across individuals, and their complete body was photographed using a camera mounted on a leveled tripod. Sex was determined by dissection, after fish were euthanatized by cutting their spinal cord, as per our animal care certificate approved by the Université de Montréal. On each picture, 25 homologous landmarks were recorded (Figure 3). Geomorphometric analyses were conducted based on a two-dimensional landmark system positioned on digitized pictures using the software tpsDig2 (Hjelm et al. 2001; Zelditch et al. 2004; Rohlf 2005a). A generalized orthogonal least-squares Procrustes superimposition was used to compare landmarks across individuals using CoodGen6 software (Sheets 2004a). This analysis standardized and rotated the coordinate system (landmarks) to control for body length differences and minimized the sums of squared distances between homologous landmarks, respectively. A total of 46 partial warps describing individual fish morphology were produced based on the Procrustes superimposition using PCAGen6 software (Sheets 2004b; Zelditch et al. 2004). A principal component analysis and a broken stick procedure were conducted to quantify the variance of the warps explained by principal component axis (PCs) and determine the number of PCs to keep for statistical analysis, respectively (Legendre and Legendre 2012; Oksanen et al. 2013; R Core Team 2014).

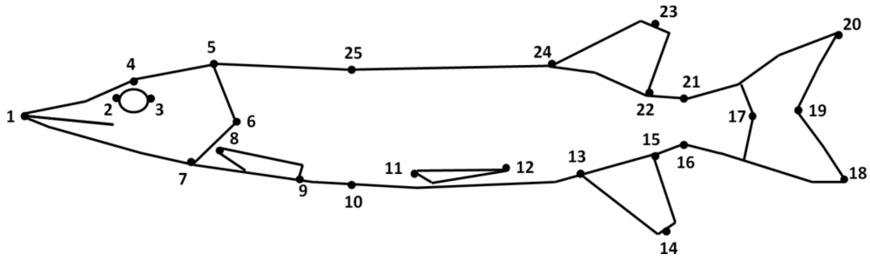

Figure 3 Positioning of the 25 homologous landmarks used to describe northern pike morphology.

Statistical analyses

Differences in fish body length between rivers and sexes were quantified with a two-way analysis of variance (ANOVA) tested by 999 permutations. Fish morphology represented by PCs was contrasted between rivers and sexes with a discriminant function analyses (DFA), using a forward selection (StatSoft Inc. 2002). The correct classification rate of the discriminant functions was assessed by cross-validation (i.e. jackknife, leave-one-out procedure). In other words, an individual was removed from the dataset at a time, classified into a particular group (Mississagi or Aubinadong; female or male) according to the discriminant function developed using the remaining individuals, and correct classification rates were computed. Deformation grids were developed using thin-plate splines generated on the basis of the partial warps using the tpsRegr software (Rohlf 2005b). Deformation grids were produced for significantly different groups (river and/or sex) based on the DFA, which allowed for the visualization of differing pairs of landmarks among groups. Meaningful morphological traits and distances between pairs of landmarks were also quantified (McLaughlin and Grant 1994; Imre et al. 2002; Robinson and Parsons 2002; Peres-Neto and Magnan 2004). Similar to Imre et al. (2002), percent differences between the distances derived for individuals from the Mississagi (D_M) and the Aubinadong (D_A) rivers were computed using:

1) $100 * (D_M - D_A) / D_A$

To assess whether morphological differentiation was associated with individual length, the relationship between morphology and length was assessed using a multivariate linear regression (Oksanen et al. 2013; R Core Team 2014).

Results

In the Mississagi River, 8 females and 8 males were captured, whereas 9 females and 7 males were captured in the Aubinadong River. Fish total length did not vary significantly between rivers (Mississagi: average 52.9, range 44.3-65.3 cm; Aubinadong: average 53.3, range 47.3-64.9 cm), or sexes (female: average 54.9, range 47.2-65.3 cm; male: average 51.1, range 44.3-62 cm; river: $p = 0.7371$, sex: $p = 0.0574$, interaction: $p = 0.8532$). The 46 partial warps representing overall morphology resulted in 6 PCs that explained 79% of the partial warps variation. These 6 PCs were used to represent individual fish morphology in statistical analyses. When analyzing all fish simultaneously, the morphology of northern pike differed significantly between rivers (Wilks' Lambda: 0.66, $F(4,27) = 3.26$, $p = 0.0262$, average classification rate = 72%) and sexes (Wilks' Lambda: 0.67, $F(5,26) = 2.64$, $p = 0.0468$, average classification rate = 65%). On the one hand, morphological differentiation was significant between rivers for females (Wilks' Lambda: 0.41, $F(3,13) = 6.27$, $p = 0.0073$) and males (Wilks' Lambda: 0.67, $F(1,13) = 6.39$, $p = 0.0252$). On the other hand, morphological differentiation was significant between sexes in the Mississagi River (Wilks' Lambda: 0.37, $F(4,11) = 4.7257$, $p = 0.0183$), but not in the Aubinadong River (Wilks' Lambda: 0.85, $F(1,14) = 2.56$, $p = 0.1316$). Therefore, each sex was treated separately to avoid any bias resulting in correct river classification rates for females and males of 82% and 80%, respectively.

Individuals from the Mississagi River, irrespective of their sex, had more elongated heads (distance between landmarks 1-6), deeper bodies (distance between landmarks 10-25) and caudal peduncles (distance between landmarks 16-21), and longer dorsal fin insertions (distance between landmarks 22-24) than individuals from the Aubinadong River (Figures 3 and 4). Differences between rivers for these morphological traits ranged from 1.4% to 9.2% (Table 2). In contrast, the shape of the caudal fin was not consistently different between sexes (Table 2 and Figure 4). In the Missssissagi River, females had 5.1% shorter and 20.2% deeper caudal fins (distances between landmarks 17-19, and 18-20, respectively), whereas males had 10.9% longer and 7.6% narrower caudal fins than individuals of the same sex in the Aubinadong River (Table 2 and Figure 4). Significant relationships between morphology and length within the range of fish lengths covered by this study were not observed ($p = 0.0914$, $R^2_{Adj} = 0.02$).

Table 2 Morphological differentiation between rivers and sexes, illustrated by percent differences (%) between the distances derived for northern pike from the Mississagi (D_M) and the Aubinadong (D_A), calculated as $100*(D_M-D_A)*D_A^{-1}$ (see Figure 3 for landmarks positioning).

Morphological trait	Landmark pairs	Female % difference	Male % difference
Head length	1-6	2.8	3.6
Body height	10-25	2.5	9.2
Caudal peduncle height	16-21	3.5	3.3
Dorsal insertion	22-24	1.4	2.2
Caudal length	17-19	-5.1	10.9
Caudal height	18-20	20.2	-7.6

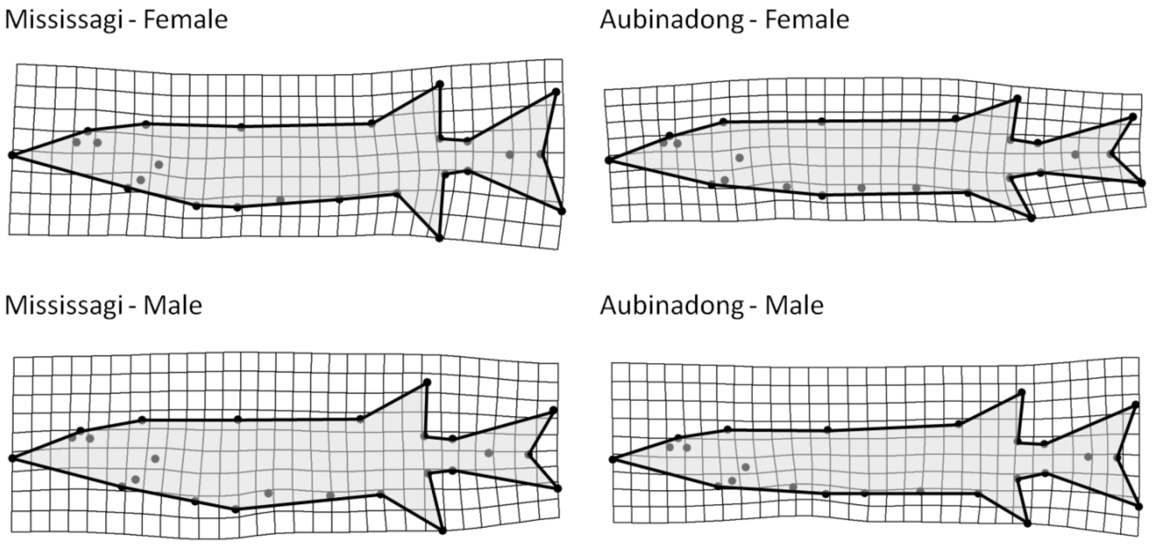

Figure 4 Deformation grids comparing morphological differentiation within females and males northern pike from the Mississagi and Aubinadong rivers. Deviations in deformation grids are magnified by a factor of 3.

Discussion

Morphological differentiation was detected for adult northern pike between rivers and sexes, which may be explained by a number of environmental conditions that vary between the rivers. First, the Mississagi River is regulated by a hydropeaking facility, and has a greater annual discharge and more important daily flow variability than the Aubinadong River. As such, fish from the Mississagi River would have to cope with larger and more variable discharge than their Aubinadong River counterparts. Second, the wetted widths of the rivers differed, potentially forcing fish from the Mississagi River to travel greater distances, crossing from one shore to the other to gain access to suitable habitats such as macrophytes beds. Based on the existing knowledge of hydrodynamic theory in other species (salmonids; Webb 1982, 1984a), we had hypothesized that northern pike in the Mississagi River would exhibit more elongated shapes and smaller fins to improve their sustained swimming capacity. These morphological adaptations were thought to aid with coping with greater discharge variability (magnitude and frequency of flow peaks) and/or to travel longer distances. For example, arctic charr (*Salvelinus alpinus*) that were experimentally raised in high velocities exhibited more elongated heads compared to their counterparts raised in low velocities (Peres-Neto and Magnan 2004). Our results partially supported this hypothesis.

Irrespective of sex, individuals in the Mississagi River had a more elongated head compared to those in the Aubinadong River, suggesting that elongated and shallow shapes may reduce drag and the energy expended while swimming at a given speed, thus enhancing overall sustained swimming capacity (Webb 1982; 1984a). However, individuals in the Mississagi River had deeper bodies and caudal peduncles than individuals in the Aubinadong River, thus contradicting our hypothesis. Deeper bodied fish tend to have slower sustained swimming capacities, but greater burst swimming and maneuverability (Webb 1984a), potentially benefiting fish that consume cryptic prey by increasing capture probability (Svanbäck and Eklöv 2002, 2003)., Individuals from the Mississagi River also had longer dorsal fin insertions, which may reduce sustained swimming, but increase stability and manoeuvrability (Standen and Lauder 2005). Greater stability and manoeuvrability, in this scenario, may allow for the maintenance of stationary swimming in greater and variable discharge, preventing possible downstream displacement of fishes.

Altogether, these results suggest that environmental conditions, such as increased discharge magnitudes and variability by hydroelectric facilities may modify this species' morphology, behaviour, and swimming capacity (Webb 1984b; Bry 1996; Craig 2008). Our results suggest a potential trade-off between elongated and shallow shapes for sustained swimming capacity, deep shapes for burst swimming, and longer fin insertion for improved manoeuvrability to cope with large and variable discharge. This finding is consistent with Blake (2004) who suggested that fish that had to perform more than one type of swimming tended to exhibit compromised morphologies. In fact, the differences in morphology observed in the present study may be linked to contrasted swimming capacities and movement behaviours. Using manual tracking by radio-telemetry, Harvey-Lavoie et al. (2016) found that northern pike in the Mississagi River significantly moved at a higher rate compared to the Aubinadong River.

Apart from body size (adult females are usually larger) and the urogenital region (Brederc and Rosen 1966; Casselman 1974), morphological differences between sexes has not been reported in the literature for northern pike. In the Mississagi River, females had shorter and deeper caudal fins, while males had longer and shallower caudal fins, whereas significant differences were not observed between sexes in the Aubinadong River. Generally speaking, caudal fins are used as a swimming propeller (Webb 1982) and may not be sexual dimorphic. During reproduction, however, the male northern pike aligns with the female genital pore, flips his caudal fin under the female's body and mixes the eggs and the sperm as they are extruded (Fabricius and Gustafson 1958). In other studies, longer caudal fins were observed in individuals exposed to higher velocities (McLaughlin and Grant 1994; Imre et al. 2002). When comparing caudal fin length in two species of salmonids reared at different velocities (0.0, 0.5, 1.0, and 1.5 times fish body length s^{-1}), Peres-Neto and Magnan (2004) obtained complex patterns (polynomial relationships) where caudal fins were most similar in the still (0 time fish body length s^{-1}) and fast (1.5 time fish body length s^{-1}) treatments. Caudal fin morphology may be highly flexible or associated to environmental conditions and sex-related behaviours that were not accounted for in our study.

Varying degrees of morphological differentiation have been observed across fish taxa. For instance, differences between the benthic and limnetic forms of arctic charr are conspicuous (Skúlason et al. 1989; Jonsson and Jonsson 2001; Andersson 2003), whereas they are subtle for brook charr (*Salvelinus fontinalis*; Bourke et al. 1997; Dynes et al. 1999). In our case, northern pike showed up to a 20.2 % difference between specific landmarks representing morphological differentiation, which is comparable in magnitude to the variation found by Carl and Healey (1984; chinook salmon, *Oncorhynchus tshawytscha*, 1-13%), McLaughlin and Grant (1994; brook charr*, Salvelinus fontinalis,* 5-9%), Imre et al. (2002; brook charr, 0-8%), Meyer (1987; jaguar guapote, *Cichlasoma managuense*, 1-19%), and Wimberger (1992; pearl cichlid and redhump eartheater, *Geophagus brasiliensis* and *Geophagus steindachneri*, 2-4%). Unfortunately, percent differences of specific traits are not always reported in the literature and general trends are difficult to draw for explaining the degree of morphological differentiation in regards to particular species or environmental conditions. Nevertheless, the magnitude of morphological differentiation we observed in northern pike is comparable to that observed in other species possessing different shapes, behaviours, and swimming capacities; irrespective of the specific relationships between traits and the environmental conditions that may drive these differences.

Many studies have outlined the need to quantify the relative contribution of genetic divergences and phenotypic plasticity in generating phenotypic differentiation (Wimberger 1994; Burton and Metcalfe 2014), however, directly assessing their effects in driving morphological differentiation is challenging when little is known about the genes controlling specific morphological traits. To better elucidate whether the morphological differentiation we observed had a genetic component, common garden experiments similar to those conducted by Pakkasmaa and Piironen (2001), and

McGinnity et al. (2003) would be needed. In North America, however, northern pike are known to have low levels of genetic divergence, indicative of a recent common ancestral population and a single refuge during the last glaciation (Miller and Senanan 2003). Given the close geographical proximity of the Mississagi and Aubinadong rivers, it is also likely that if genetic divergences existed between these rivers, it may have played a relatively small role in promoting morphological differentiation versus phenotypic plasticity.

Despite the difficulty in capturing a large number of adult (relatively small sample size by river and sex), significant morphological differentiation between rivers and sexes was observed, indicating important differences in morphology for this species. As sample size is directly related to detectable effect size, it is understood that increasing our sample size would have enabled us to detect smaller morphological differences. However, the significant morphological differences observed in the current study are expected to remain significant should sample size increase (Peterman 1990; Scherrer 2007; Legendre and Legendre 2012). Therefore, we are confident that morphological differentiation in northern pike may be a trade-off between morphological adaptations for sustained and burst swimming, and manoeuvrability; phenotypic adaptations that may allow northern pike populations to exploit a larger range of spatially and temporally variable environmental conditions, such as those stemming from river regulation.

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