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Environnement physique et environnement social – conséquences physiologiques de la sélection des habitats

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Résumé

La sélection des habitats est un comportement important reliant des individus aux conditions environnementales de leur habitat. Elle est généralement étudiée pour faire des inférences sur les patrons de distribution des populations. Or, la sélection des habitats peut varier entre individus d'une même population et cette variation peut excéder la variation observée entre les populations. D'une part, si la sélection des habitats est adaptative, on peut supposer que les individus sélectionneront des habitats leur permettant de maximiser leur performance. D'autre part, les conditions environnementales dans les habitats peuvent affecter les performances individuelles, impliquant ainsi que la sélection des habitats peut avoir des conséquences physiologiques. Par ailleurs, l'environnement social peut influencer la performance physiologique des individus. L'objectif général de la thèse est l'étude des déterminants et des conséquences physiologiques de la sélection des habitats chez les poissons.

Dans un premier temps, nous avons créé et comparé la capacité prédictive de modèles de sélection des habitats pour l'achigan à petite bouche *Micropterus dolomieu* intégrant la variabilité individuelle. Nos résultats ont démontré que l'intégration de la variabilité individuelle permettait d'identifier les variables influençant la sélection des habitats au niveau individuel, des groupes et de la population. Les modèles incluant les variables représentant la présence de refuges dans les habitats avaient un meilleur pouvoir prédictif que ceux qui ne les incluaient pas. Par ailleurs, des groupements d'individus présentant des similitudes dans leur sélection d'habitats ont été identifiés. Malgré tout, la variabilité dans la sélection des habitats entre les individus était nettement plus grande que la variabilité entre les groupes.

Nous avons démontré que la présence de refuge était la variable la plus importante à considérer dans les modèles de sélection d'habitats pour les achigans à petite bouche. Nous avons ensuite investigué si la présence de refuge pouvait influencer différents traits métaboliques des achigans à petite bouche grâce à des expériences de respirométrie en laboratoire. La présence de refuge a diminué les taux métaboliques au repos (RMR) des achigans provenant d'un lac alors qu'il n'y a pas eu d'effet sur les achigans provenant d'une rivière. En considérant la position hiérarchique des individus, nous avons noté que les individus dominants avaient un temps de récupération plus court en présence de refuge alors que la présence de refuge n'a rien changé pour les individus soumis.

Finalement, nous avons étudié si l'environnement social, en particulier la taille du groupe social, pouvait influencer l'estimation des taux métaboliques des poissons en présence ou en absence de refuge. Nous avons cette fois mené des expériences sur des vairons *Phoxinus phoxinus*, des poissons très sociaux. Les vairons gardés en petits groupes avaient des taux métaboliques plus élevés que ceux gardés en grands groupes. La présence de refuge a diminué les taux métaboliques indépendamment de la taille des groupes. Nos résultats ont démontré que la taille des groupes peut influencer les dépenses énergétiques des individus, ce qui souligne l'importance de comprendre le rôle des dynamiques sociales sur les variations dans les traits métaboliques.

Les résultats de la thèse démontrent l'importance de tenir compte de l'environnement physique et de l'environnement social pour mieux comprendre les conséquences physiologiques de la sélection des habitats.

Mots clés : sélection des habitats, fonctions de sélection des ressources, variabilité individuelle, refuge, achigan à petite bouche, capacité aérobique, taux métaboliques, temps de récupération, environnement social, densité

Abstract

Habitat selection is an important behaviour that relates individuals to the environmental conditions in their habitat, and is generally studied to infer population-level patterns of distributions. Habitat selection varies among individuals and there is growing evidence that individual differences often exceed population differences in habitat selection. On the one hand, if habitat selection is adaptive, it could be hypothesized that individuals would select habitats that would maximize their fitness. On the other hand, environmental conditions in habitats can have physiological consequences, which can be amplified or masked by the social environment. Therefore, the general objective of this thesis was to better understand the determinants and physiological consequences of habitat selection.

We created and compared the predictive capacity of habitat selection models for smallmouth bass *Micropterus dolomieu* integrating individual variability. Our results show that by integrating individual variability, we could identify variables influencing individual-, group-, and population-level habitat selection. Models that included variables referring to presence of shelter had the best predictive capacity. Further, we identified groups of individuals defined by their habitat selection. Nevertheless, variation in habitat selection among individuals was higher than that among groups.

Presence of shelter was the main correlate of habitat selection for smallmouth bass. We then we tested whether presence of shelter could influence smallmouth bass metabolic traits estimated during respirometry trials. In presence of shelter, resting metabolic rates (RMR) were lower than in absence of shelter for smallmouth bass from a lake population. There was no difference in RMR for smallmouth bass from a river population. Further, dominant individuals showed reduced recovery time (RT) in presence of shelter, while no difference was observed in subordinate individuals.

We investigated how social group size and availability of shelter could influence metabolic rate. This project was conducted on Eurasian minnow *Phoxinus phoxinus*, a highly social fish. Fish held in smaller groups had higher standard metabolic rate as compared to that of fish held in larger groups. Presence of shelter during respirometry trials was associated with reduced metabolic rates, regardless of group size fish were held in. Our results suggest that social group size may directly influence energy demands of individuals, highlighting the importance of understanding the role of group size on variations in physiological traits associated with energy expenditure. Our results highlight the importance of considering the physical and social environment to better understand the physiological consequences of habitat selection.

Keywords : habitat selection, resource selection functions, individual variation, shelter, smallmouth bass, aerobic scope, metabolic rates, recovery time, social environment, density

Table des matières

Liste des tableaux

Chapitre 1 :

Chapitre 2 :

Chapitre 3 :

Table 2: Results of linear mixed model relating metabolic rates of Eurasian minnows to the moment of the respirometry trials, group size, and shelter availability. Fish ID and batch number were included in the SMR model as random effects. Only fish ID was included as a random effect for MMR and AS models. R^2_m is the marginal R^2 (% of variance explained by the fixed effects) and R^2_c is the conditional R^2 (% of variance explained by the fixed and the random effects).

Table S1: Results of linear model relating specific growth rate (SGR) of Eurasian minnows to the social treatment (group size and shelter availability).

Table S2: Results of linear model relating final standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) of Eurasian minnows to the specific growth rate (SGR), the social treatment (group size and shelter availability), and their interaction.

Table S3: Results of linear mixed model relating maximum metabolic rate (MMR) and aerobic scope (AS) of Eurasian minnows to the moment of the respirometry trials and the social treatment (group size and shelter availability). Fish ID and batch number were included in the models as a random effect in a nested structure (batch number/Fish ID). R^2_m is the marginal R^2 (percentage of variance explained by the fixed effects) and R^2_c is the conditional R^2 (percentage of variance explained by the fixed and the random effects).

Liste des figures

Introduction :

Figure 1 : Schématisation des différents traits métaboliques pouvant être estimés sur un poisson. La figure présente la diminution des taux métaboliques $\dot{M}O_2$ d'un poisson en fonction du temps après une activité d'intensité maximale. Le métabolisme sera maximal (MMR) lors de l'activité et il diminuera graduellement vers le niveau minimal (SMR). Le délai entre le moment où MMR est mesuré et où l'animal atteint SMR représente le temps de récupération (RT). La différence entre MMR et SMR représente la capacité aérobique (AS). Finalement, l'aire sous la courbe de diminution de $\dot{M}O_2$ avec le temps représente la consommation d'oxygène excédentaire post-activité (EPOC).

Figure 2 : Schématisation de l'utilisation d'une perspective écophysiologique dans l'étude des associations poissons-habitats. Au niveau individuel, les conditions environnementales sont perçues comme des stimuli. Le stimulus perçu par l'individu induira une réponse physiologique qui influera sur la réponse comportementale. L'itération des réponses comportementales de chaque individu en réponse à ce stimulus génèrera un patron observé au niveau de la population. Des rétroactions (représentées par les flèches pointillées) sont possibles. Par exemple, les interactions biotiques liées à l'environnement social peuvent influencer le comportement individuel et induire de nouvelles réponses physiologiques. Figure adaptée de Horodysky et al. (2015).

Chapitre 1 :

Chapitre 2 :

Chapitre 3 :

back into the chamber to obtain MMR (black points). Blue and yellow rectangles represent the range of data used for estimation of night-time and day-time minimum $\dot{M}O_2$, respectively, with or without plant shelter. Top and bottom horizontal dotted lines show estimates of MMR and SMR.

Figure 2: Observed night-time (A, B) and day-time (C, D) metabolic rates in initial (clear) and final (shaded) respirometry trials. Grey and green dots represent estimates in absence or in presence of plant shelter, respectively. Middle thick line of the boxplots corresponds to the median, lower and upper limits correspond to the first and third quartiles of the data, and whiskers extend to the range of the data.

Figure 3: Observed SMR (A-B), MMR (C-D), and AS (E-F) of Eurasian minnow. Light blue and dark blue boxes and points represent estimates for fish held in groups of four and eight, respectively. Clear and shaded boxes represent initial and final respirometry trials, respectively. A-C-E panels refer to experimental tanks without plant shelter, and B-D-F refer to experimental tanks containing plant shelter. Middle thick line of the boxplots corresponds to the median, lower and upper limits correspond to the first and third quartiles of the data, and whiskers extend to the range of the data.

Figure S1: Boxplot of specific growth rate (SGR; in % day^{-1}) of fish in each social treatment consisting in a combination of group size (left: four fish; right: eight fish) and shelter availability (no plant shelter in blue; with plant shelter in turquoise). Middle thick line of the boxplots corresponds to the median, lower and upper hinges correspond to the first and third quartiles of the data, and whiskers extend to the range of the data. Each fish SGR is overlayed on the boxplot (black dots).

Figure S2: Observed SMR, MMR, and AS of Eurasian minnow (in mg O_2 kg^{-1} hr^{-1}) during the initial (top row) and final (bottom row) respirometry trial in relation to specific growth rate (SGR; in % day^{-1}).

Figure S3: Maximum metabolic rates (MMR) per batch of fish captured together from the stock tank. Left panel shows rates measured in the initial respirometry trial, right panel shows rates measured at the final respirometry trial. Middle thick line of the boxplots corresponds to the median, lower and upper hinges correspond to the first and third quartiles of the data, and whiskers extend to the range of the data. Each fish MMR is overlayed on the boxplot (black dots).

Conclusion

Figure 1 : Schématisation des contributions de la thèse dans la perspective écophysiologique de l'étude des associations poissons-habitats, telle que présentée en introduction.

Liste des abréviations

(Les caractères italiques indiquent les termes en anglais)

AIC : *Akaike information criterion*

AS : capacité aérobique | *aerobic scope*

BO_2 : taux de consommation d'oxygène résiduelle | *background oxygen consumption*

CDEA : Comité de déontologie de l'expérimentation sur les animaux

EPOC : consommation d'oxygène excédentaire post-activité | *excess post-exercise oxygen consumption*

GLMM : *generalized linear mixed model*

LMM : modèle linéaire mixte | *linear mixed model*

MDE : modèle de distribution des espèces

MMR : taux métabolique maximal | *maximum metabolic rate*

$\dot{M}O_2$: taux de consommation d'oxygène | *oxygen consumption rate*

$\dot{M}O_{2min}$: taux métabolique minimum | *minimum metabolic rate*

RMR : taux métabolique au repos | *resting metabolic rate*

RSF : fonction de sélection des ressources | *resource selection function*

RT : temps de récupération | *recovery time*

SBL : Station de biologie des Laurentides

SGR : taux de croissance spécifique | *specific growth rate*

SMR : taux métabolique standard | *standard metabolic rate*

À ma tante Monique,
partie trop tôt

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Rivière Kiamika, Québec (Photo : E. Chrétien)

Introduction

Les milieux d'eau douce : disproportionnellement diversifiés et menacés

Les milieux d'eau douce représentent environ 0.01% de l'eau disponible sur la planète mais abritent un nombre disproportionné d'espèces, incluant environ 40% de la diversité des poissons (Dudgeon et al. 2006). Ils font à la fois partie des écosystèmes les plus diversifiés mais aussi des plus menacés par l'activité humaine (Vörösmarty et al. 2010). Les écosystèmes fluviaux (e.g. rivières) en particulier fournissent un grand nombre de bénéfices aux sociétés humaines telles l'eau potable, la nourriture, l'irrigation des terres agricoles et la production d'électricité (Wilson and Carpenter 1999, Hanna et al. 2018). La demande pour ces bénéfices, qu'on nomme services écosystémiques, est en croissance et menace la résilience des écosystèmes (Millenium Ecosystem Assessment 2005). En particulier, environ 65% des rivières sont considérées modérément à très menacées, la plus grande menace pour la biodiversité étant la dégradation des habitats résultant des barrages et des diminutions de débits naturels (Vörösmarty et al. 2010). Les changements climatiques devraient exacerber la pression sur les écosystèmes d'eau douce par l'altération des régimes d'écoulement des rivières et l'augmentation de la température de l'eau (Millenium Ecosystem Assessment, 2005, Ficke *et al.*, 2007). Or, afin de prédire les effets des perturbations actuelles et futures sur les écosystèmes d'eau douce et la résilience des espèces qu'ils abritent, dont les poissons, il est nécessaire de mieux comprendre les liens entre les espèces et leur environnement (Guisan and Thuiller 2005).

Modéliser les associations espèces – environnement

Des approches de modélisation sont généralement utilisées afin de comprendre et de prédire les patrons de distribution des espèces et d'identifier les habitats critiques pour la conservation (Guisan and Thuiller 2005, Aarts et al. 2013). L'habitat est ici défini comme étant la combinaison des ressources et conditions biotiques et abiotiques retrouvées à un endroit occupé par un organisme durant son cycle de vie (Hall et al. 1997). L'utilisation d'un habitat réfère à la manière dont un organisme fait usage d'une ou de plusieurs de ces composantes biotiques ou abiotiques. La sélection d'un habitat se manifeste par l'utilisation en plus grande proportion d'un certain type d'habitat (caractérisé par ses composantes biotiques et/ou abiotiques) par rapport à sa disponibilité dans un territoire (Northrup et al. 2021). La qualité de l'habitat réfère à la capacité du milieu de fournir des conditions appropriées pour la résilience et la survie d'individus ou de populations (Hall et al. 1997).

La majorité des approches de modélisation développées pour prédire la distribution des espèces sont basées sur la quantification des relations entre les espèces et l'environnement (Guisan and Thuiller 2005). Par exemple, les modèles d'utilisation des habitats tentent d'associer des données d'abondance d'espèces (biomasse, abondance, présence/absence, etc.) à des sites aux conditions environnementales retrouvées dans ces sites. Ces modèles peuvent prendre la forme, entre autres, de régressions multiples, d'ordinations, d'arbres de régression, de réseaux neuronaux artificiels ou d'analyses bayésiennes (Guisan and Thuiller 2005). Ils peuvent être spatialement explicites ou non. La terminologie utilisée pour caractériser ces modèles varie selon le type de données dont ils sont composés, l'échelle spatiale ou temporelle pour laquelle ils ont été développés et le niveau d'organisation (ex. individu, population, communauté) qu'ils concernent. Les associations espèces-habitat peuvent être modélisées à plusieurs échelles spatiales : les modèles de distribution des espèces concernent les grandes échelles (ex. entre différents bassins versants), les modèles de capacité s'appliquent au mésohabitat (ex. un segment de rivière) alors que les modèles de microhabitat concernent une échelle encore plus petite (Rosenfeld 2003). Il n'existe pas d'échelle universelle de modélisation puisque des patrons peuvent émerger à plusieurs échelles au niveau du paysage (Guisan and Thuiller 2005). L'échelle spatiale appropriée pour la modélisation dépend du phénomène étudié. L'extrapolation entre échelles spatiales n'est donc pas toujours possible, par exemple lorsque la relation entre une variable et l'habitat à différentes échelles est non-linéaire ou caractérisée par des seuils critiques (Turner and Gardner 2015).

Le développement des systèmes d'information géographiques et l'avancement des méthodes statistiques ont mené au développement de modèles de distribution des espèces (MDE) spatialement explicites (Guisan and Zimmermann 2000). Guisan et Thuiller (2005) distinguent trois phases ayant marqué le développement des MDE : les modèles statistiques non spatialement explicites basés sur des données empiriques, la modélisation spatiale de la distribution des espèces (non statistique et non empirique) et les modèles statistiques empiriques spatialement explicites. Par ces derniers, la distribution potentielle d'une espèce donnée dans un espace défini est prédite par des modèles statistiques associant la distribution observée de cette espèce (en termes de positions obtenues par télémétrie, présence/absence, abondance, etc.) et les conditions environnementales mesurées dans cet espace (Teal et al. 2015). Les fonctions de sélection de ressources (RSF; sensu *resource selection functions*) en sont un exemple. Ces modèles comparent les ressources disponibles (e.g. conditions environnementales) aux endroits utilisés par les individus de ceux disponibles pour ces individus dans un espace donné, et sont généralement formés à partir de positions d'individus obtenues par télémétrie (Manly et al. 2002, Morris et al. 2016). Une carte des valeurs de RSF pour un espace donné peut ainsi être générée, présentant de manière spatialement explicite les prédictions de sélection selon les ressources disponibles. De manière plus générale, les cartes de RSF et les MDE sont des outils beaucoup plus concrets et accessibles que l'équation d'un modèle pour les utilisateurs dans le domaine de la conservation ou de la gestion des ressources naturelles (Johnson et al. 2006, Morris et al. 2016). Les MDE sont couramment utilisés pour prédire les changements dans les aires de répartition des espèces ou encore pour évaluer la menace de propagation d'espèces envahissantes (Guisan and Thuiller 2005, Teal et al. 2015).

Les données de télémétrie : des individus aux populations

Grâce au développement et au raffinement des émetteurs électroniques, les données de télémétrie ont graduellement remplacé les données d'abondance obtenues par différentes techniques d'échantillonnage pour créer des MDE ou des RSF (Brownscombe et al. 2021). De nombreuses études sur l'écologie spatiale des poissons ont été publiées et des chercheurs prônent l'utilisation des données probantes obtenues par les technologies de télémétrie pour améliorer les modèles d'habitats et les efforts de conservation (Cooke et al., 2016; Cooke et al., 2013). L'étude des mouvements des poissons dans leur habitat naturel peut nous informer, entre autres, sur leur sélection d'habitat et sur l'étendue de leur domaine vital. Les mouvements sont tous les changements de position (d'individus, de populations ou de parties de populations) dans l'espace, quelle que soit l'échelle temporelle et spatiale (Hansson and Akesson 2014). Ces mouvements incluent les déplacements d'individus entre des habitats de repos, les mouvements liés à la protection contre les prédateurs ou à l'alimentation. La télémétrie est une technique intéressante pour étudier les animaux mobiles (comme les poissons) dans des habitats difficiles à échantillonner, comme les rivières profondes (Cooke et al. 2013b). Les positions de poissons portant un émetteur obtenues par télémétrie permettent d'étudier la variabilité interindividuelle dans les comportements et stratégies de sélection des habitats (Leclerc et al. 2016, Muff et al. 2020, Brownscombe et al. 2021).

Les données de télémétries impliquent par ailleurs plusieurs défis pour la modélisation. Premièrement, la télémétrie fournit des données de présence fiables (i.e. des positions d'individus) pour un espace donné mais pas d'absences. Ce défi peut toutefois être contourné en utilisant des « pseudo-absences », c'est-à-dire des positions aléatoires placées dans l'espace, permettant ainsi l'analyse des données de télémétrie par des modèles linéaires généralisés avec réponse binaire (ou régressions logistiques ; Johnson et al. 2006). C'est la stratégie utilisée dans les RSF, qui comparent les conditions environnementales aux endroits utilisés par les individus (présences) de ceux disponibles (pseudo-absences) pour ces individus dans un espace donné. Cependant, puisque les pseudo-absences ne sont pas équivalentes à des absences, leur nombre doit être très élevé et leur poids dans le modèle doit être plus important que celui des présences (Northrup et al. 2013, Muff et al. 2020). Deuxièmement, les données de télémétrie sont composées de plusieurs positions prises sur un nombre limité d'individus. Il faut alors utiliser des approches de modélisation permettant l'inclusion d'effets aléatoires afin de tenir compte du fait que les données sont structurées par individu, tels les modèles linéaires mixtes généralisés (GLMM; Bolker et al. 2009). L'inclusion de l'ordonnée à l'origine et de pentes aléatoires variant entre individu permet de tenir compte de la dépendance entre les données et de mieux estimer l'erreur standard des paramètres des modèles (Schielzeth and Forstmeier 2009). Puisque les GLMMs peuvent faire appel à une distribution binomiale pour l'analyse de données binaires, ils sont généralement utilisés pour modéliser les RSFs. L'utilisation des GLMMs permet d'ailleurs d'explorer la variabilité interindividuelle dans la sélection des habitats (Gillies et al. 2006, Dingemanse and Dochtermann 2013).

Des études utilisant la télémétrie ont mis en évidence que la variabilité entre les individus d'une même population dans les taux de mouvements (Harrison et al. 2019) ou la sélection des habitats (Capra et al. 2017) était plus importante que la variabilité entre les espèces. La variabilité interindividuelle est très étudiée en écologie comportementale (Réale et al. 2007, Dingemanse et al. 2010) et peut être liée, entre autres, au sexe, à la condition corporelle, à la personnalité ou à l'environnement social des individus (Burton et al. 2011, Killen et al. 2013). Les différences dans les comportements individuels ont d'importantes répercussions sur l'écologie des espèces. Le comportement de dispersion peut être lié à l'agressivité ou à la témérité des individus, influençant ainsi le potentiel pour une population de coloniser de nouveaux habitats (Duckworth 2008). Le statut hiérarchique peut restreindre l'accès aux habitats de qualité (Hertel et al. 2020). Évidemment, les données de positions d'individus obtenues par télémétrie ne permettent pas en elles-mêmes d'élucider le mécanisme expliquant les différences observées dans la sélection des habitats. Cela dit, considérer la variabilité entre les individus dans la sélection des habitats peut permettre de mieux identifier l'étendue des habitats utilisés ou révéler l'utilisation de niches spécialisées au sein d'une population.

Les traits métaboliques comme indicateurs de performance

L'étude des réponses physiologiques des poissons aux conditions environnementales peut permettre de mieux comprendre les mécanismes sous-jacents la distribution des espèces (Cooke et al., 2013). Les conditions environnementales agissent comme des stimuli affectant les processus physiologiques auxquels les individus répondent de manière comportementale (Horodysky et al. 2015). De ce fait, la sélection des habitats peut à la fois être définie par les limites physiologiques des individus mais également avoir des conséquences physiologiques (Huey 1991).

Un cadre conceptuel important pour l'étude de l'écophysiologie des poissons a été proposé par Fry (1947). Le paradigme de Fry suggère que les facteurs environnementaux affectent l'activité des organismes par leur effet sur le métabolisme. Il a introduit le concept de capacité aérobique pour l'activité (AS ; sensu *aerobic scope for activity* ou *aerobic scope*) qui représente une estimation de l'énergie métabolique disponible pour l'activité dans un contexte environnemental et physiologique donné (Fry, 1971; Pörtner, 2010; Steinhausen, Sandblom, Eliason, Verhille, & Farrell, 2008). On obtient AS par la différence entre le métabolisme maximal et le métabolisme standard. Le métabolisme maximal (MMR ; sensu *maximum metabolic rate*) correspond au taux maximal de consommation d'oxygène et est mesuré au niveau d'activité maximal de l'organisme, par exemple à sa vitesse de nage maximale (Clark et al. 2013). Le métabolisme standard (SMR ; sensu *standard metabolic rate*) est une approximation de la demande minimale d'oxygène pour une température donnée (Brett 1971, Gillooly et al. 2001). Fry a également développé une classification des facteurs environnementaux selon leurs conséquences sur le métabolisme. Il distingue ainsi les facteurs de contrôle, limitants, masquants, directifs ou létaux sur le métabolisme (Claireaux & Lefrançois, 2007; Fry, 1971). Par exemple, la température de l'eau serait un facteur de contrôle puisqu'elle détermine le SMR (Claireaux & Chabot, 2016) alors que la concentration en oxygène dissous serait un facteur limitant puisque celle-ci contraint le MMR, et donc la capacité aérobique (Horodysky et al. 2015). La capacité aérobique (AS) est donc un indicateur de performance important pour les ectothermes, comme les poissons, et pourrait avoir des conséquences à long terme sur la croissance et la reproduction des individus (Claireaux & Lefrançois, 2007; Mckenzie et al., 2016).

Outre SMR, MMR et AS, d'autres traits métaboliques peuvent être estimés pour déterminer la performance des organismes en fonction des conditions environnementales (Figure 1) comme le temps de récupération (RT ; sensu *recovery time*) et la consommation d'oxygène excédentaire post-activité (EPOC ; sensu *excess post-exercise oxygen consumption*). Ils représentent respectivement la durée et la quantité d'oxygène requises pour se remettre de l'épuisement complet dû à l'exercice, ou en d'autres mots, pour passer du MMR au SMR (Hancock et al. 2001). Ces traits peuvent influencer la capacité d'un organisme à reprendre ses activités après un effort intense et peuvent donc avoir des conséquence sur la performance (Zeng et al. 2010). D'autres coûts métaboliques liés aux différentes activités (e.g. locomotion, digestion, excrétion) sont variables et peuvent représenter une portion importante de AS, surtout les coûts de nage (Boisclair & Leggett, 1989).

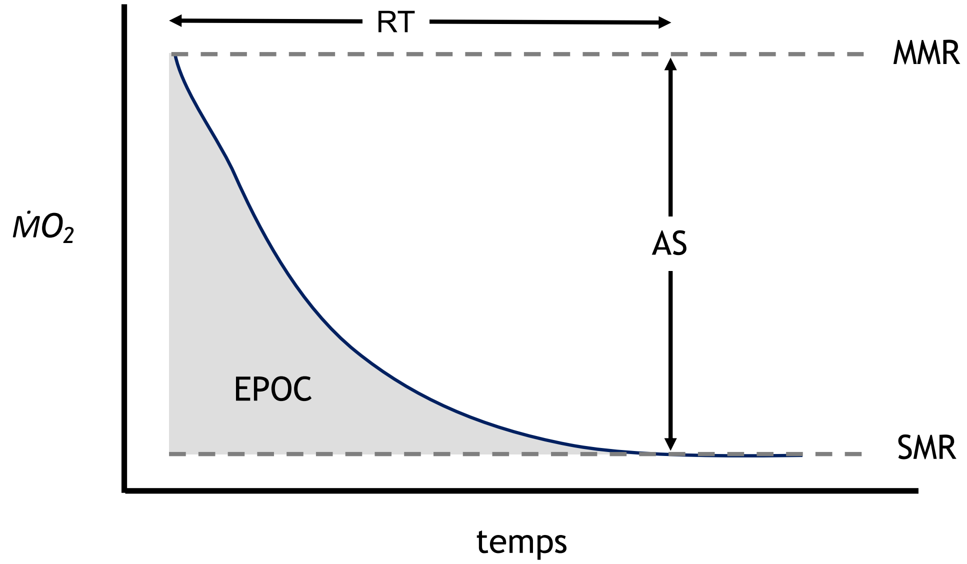


Figure 1 : Schématisation des différents traits métaboliques pouvant être estimés sur un poisson. La figure présente la diminution des taux métaboliques $\dot{M}O_2$ d'un poisson en fonction du temps après une activité d'intensité maximale. Le métabolisme sera maximal (MMR) lors de l'activité et il diminuera graduellement vers le niveau minimal (SMR). Le délai entre le moment où MMR est mesuré et où l'animal atteint SMR représente le temps de récupération (RT). La différence entre MMR et SMR représente la capacité aérobique (AS). Finalement, l'aire sous la courbe de diminution de $\dot{M}O_2$ avec le temps représente la consommation d'oxygène excédentaire post-activité (EPOC).

Bien que la température soit un facteur de contrôle dominant du métabolisme, d'autres conditions environnementales peuvent affecter les dépenses énergétiques des individus pour une température donnée. Ainsi, l'énergie pouvant être allouée à la croissance et la reproduction dépendra des dépenses énergétiques liées à la sélection des habitats. Les conditions environnementales affectant la locomotion, comme la vitesse du courant, sont susceptibles d'affecter la performance individuelle (Roche et al. 2014). L'utilisation de refuge peut permettre par ailleurs de limiter les dépenses énergétiques (Lind and Cresswell 2005) liées à la locomotion (Fausch 1984, Hafs et al. 2014) ou à la thermorégulation (Seebacher and Alford 2002, Beck and Jennings 2003). L'utilisation de refuge pourrait également remplacer la vigilance et de ce fait diminuer les taux métaboliques et RT (Hailey et al. 1987, Lind and Cresswell 2005, Millidine et al. 2006). L'étude des traits métaboliques des poissons en réponse à différentes conditions environnementales peut permettre de mieux comprendre les conséquences physiologiques de la sélection des habitats.

L'environnement social peut moduler les réponses individuelles

Plusieurs espèces de poissons vivent en groupes sociaux. Un groupe social est un ensemble stable (dans l'espace et dans le temps) d'individus interagissant entre eux (Krause and Ruxton 2002). Vivre en groupe est très répandu dans le règne animal et apporte plusieurs bénéfices incluant la réduction des risques de prédation et des coûts énergétiques liés à la vigilance, au mouvement et à la thermorégulation (Krause and Ruxton 2002, Evans et al. 2016, Jolles et al. 2020). La vie en groupe peut par ailleurs occasionner plusieurs coûts, comme la diminution de la croissance individuelle dû au partage des ressources alimentaires et l'augmentation des risques de parasitisme et de maladies (Altizer et al. 2003, Hoare et al. 2004, Guénard et al. 2012). La taille des groupes sociaux, les interactions et la variabilité des comportements individuels font émerger des structures sociales qui forment l'environnement social d'un individu (Jolles et al. 2020). L'environnement social peut grandement influencer l'expression des comportements individuels par des processus comme la conformité ou la facilitation (Ward 2012, Jolles et al. 2016, Ward and Webster 2016). Conséquemment, les individus peuvent avoir un comportement différent lorsqu'observés en groupe ou en isolation et ils peuvent moduler leurs comportement en fonction des comportements des congénères (Webster and Ward 2011, Jolles et al. 2020). Des travaux récents suggèrent également que l'environnement social auquel un individu a été exposé précédemment peut influencer les réponses comportementales dans d'autres contextes, par exemple lorsqu'un individu se retrouve seul (Jolles et al. 2016).

On considère généralement les processus physiologiques comme étant le mécanisme sous-jacent des comportements individuels. Or, l'environnement social pourrait non seulement moduler les comportements individuels mais également les réponses physiologiques (Gilmour et al. 2005). L'environnement social peut affecter les dépenses énergétiques et les niveaux de stress individuels (Webster and Ward 2011). Les individus téméraires ou agressifs, des comportements pouvant être associés au statut de dominance dans un groupe, ont généralement un SMR plus élevé que les individus soumis (Biro and Stamps 2010, Redpath et al. 2010, Arnold et al. 2021). Cela dit, dans des groupes ayant une hiérarchie de dominance forte, les individus soumis subissent un stress chronique qui peut mener à une augmentation du SMR (Sloman et al. 2000, Metcalfe et al. 2016). La dominance peut donc agir comme un stresseur modulant les dépenses énergétiques individuelles (Killen et al. 2013). La taille des groupes pourrait aussi influencer les dépenses énergétiques. D'un côté, le stress social lié à une compétition plus intense dans des grands groupes pourrait augmenter les dépenses énergétiques. D'un autre côté, les dépenses énergétiques liées à la vigilance individuelle diminuent avec la taille des groupes (Roberts 1996). Chez les poissons sociaux, il a d'ailleurs été démontré que la présence de congénères a un effet « calmant » et réduit le SMR (Nadler et al. 2016). Ces exemples démontrent l'importance d'investiguer comment l'environnement social peut influencer les interactions entre la physiologie et le comportement (Huang et al. 2020).

L'environnement social pourrait aussi affecter les réponses physiologiques et comportementales à des gradients environnementaux. Des études ont montré que les individus vivant du stress social avaient une tolérance thermique moins élevée (LeBlanc et al. 2011) et qu'ils étaient plus sensibles à l'hypoxie (Thomas and Gilmour 2012) que les individus moins stressés. Le niveau de cortisol sanguin élevé lié au stress chronique pourrait expliquer les différences observées (Sloman and Armstrong 2002). Les travaux de Culbert et al. (2019) supportent cette hypothèse. Des poissons qui se remettaient d'un stresseur externe au sein de leur groupe social ont vu leur cortisol sanguin baisser davantage et diminuer plus vite que les poissons qui ont dû récupérer en présence d'un nouveau groupe social (Culbert et al. 2019). Ces exemples soulignent l'importance de considérer l'environnement social dans l'étude des réponses physiologiques et comportementales à des gradients environnementaux (Munson et al. 2021). Ces exemples suggèrent également que l'environnement social pourrait influencer les conséquences physiologiques de la sélection des habitats.

Contexte de la thèse

Complémentarité des approches corrélatives et mécanistes

Les conditions environnementales affectent les mouvements des animaux et leur distribution dans l'espace (Cooke et al., 2016). Si les variations observées dans les patrons de distribution peuvent être corrélées aux conditions environnementales, l'étude des réponses physiologiques les contextualise (Horodysky et al. 2015). L'écophysiologie, c'est-à-dire l'étude des réponses physiologiques aux gradients environnementaux, permet de mieux comprendre les mécanismes sous-jacents la distribution des espèces (Figure 2). Les conditions environnementales sont perçues par les poissons comme des stimuli affectant les processus physiologiques auxquels ils répondent individuellement de manière comportementale. L'environnement social peut influencer les niveaux de stress individuels et moduler les réponses physiologiques et comportementales. Les réponses populationnelles observées reflètent l'itération de ces comportements individuels face aux conditions environnementales (Horodysky et al. 2015).

La combinaison des approches corrélatives et mécanistes est de plus en plus conseillée afin de mieux informer les efforts de conservation et de gestion des populations (Horodysky et al. 2015, Mckenzie et al. 2016). Les études observationnelles sur le terrain permettent d'identifier les conditions environnementales déterminant la sélection des habitats pour l'espèce d'intérêt. Des expériences en laboratoire permettent ensuite d'investiguer l'effet de ces conditions environnementales sur la performance des poissons. Dans ce contexte, l'objectif général de la présente thèse est l'étude des déterminants et des conséquences physiologiques de la sélection des habitats chez les poissons.

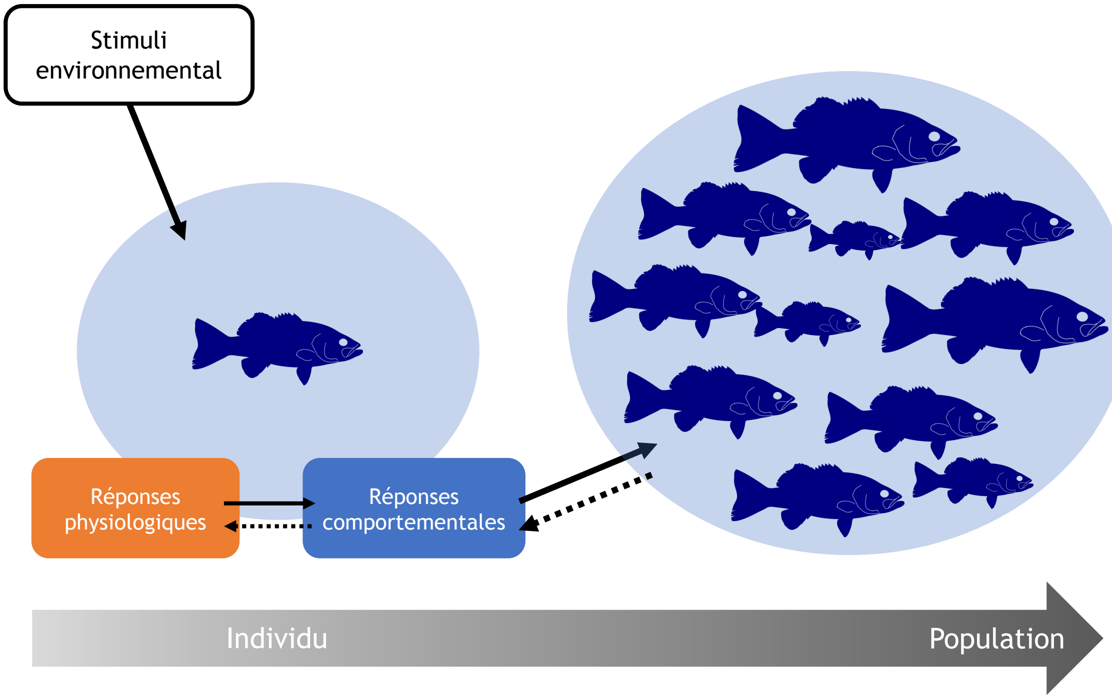


Figure 2 : Schématisation de l'utilisation d'une perspective écophysiologique dans l'étude des associations poissons-habitats. Au niveau individuel, les conditions environnementales sont perçues comme des stimuli. Le stimulus perçu par l'individu induira une réponse physiologique qui influera sur la réponse comportementale. L'itération des réponses comportementales de chaque individu en réponse à ce stimulus génèrera un patron observé au niveau de la population. Des rétroactions (représentées par les flèches pointillées) sont possibles. Par exemple, les interactions biotiques liées à l'environnement social peuvent influencer le comportement individuel et induire de nouvelles réponses physiologiques. Figure adaptée de Horodysky et al. (2015).

Les travaux de cette thèse se déclinent en trois chapitres. Le **Chapitre 1** implique le suivi de poissons par télémétrie dans une rivière afin d'identifier les conditions environnementales déterminant leur sélection d'habitats. Le **Chapitre 2** implique des expériences de respirométrie en laboratoire afin d'estimer différents traits métaboliques de poissons en fonction des conditions environnementales clés identifiées au **Chapitre 1** pour l'espèce d'intérêt. Le **Chapitre 3** vise à tester l'effet combiné de conditions environnementales et de l'environnement social sur les traits métaboliques.

Espèces modèles

L'espèce modèle utilisée pour le **Chapitre 1** et le **Chapitre 2** est l'achigan à petite bouche *Micropterus dolomieu*. C'est un poisson piscivore très prisé par la pêche sportive qu'on peut retrouver en grande abondance dans des milieux d'eau douce variés (e.g. rivière ou lac; Warren 2009). Il ne s'agit pas d'une espèce d'intérêt pour la conservation mais elle a été choisie car elle présentait les caractéristiques recherchées pour les travaux du **Chapitre 1** : l'achigan à petite bouche est une espèce abondante et facile à capturer dont la gamme de tailles permettait l'implantation d'émetteurs radios pour le suivi par radio-télémétrie. Puisque l'achigan à petite bouche est très associé à la présence de couvert submergé (e.g. troncs, chablis, crevasses, blocs métriques) dans les lacs et les rivières (Edwards et al. 1983, Todd and Rabeni 1989), la variable « refuge » occupe une place centrale dans la thèse.

Pour quantifier l'influence de l'environnement social sur les taux métaboliques pour le **Chapitre 3**, le vairon *Phoxinus phoxinus* a été utilisé. Il s'agit d'un petit poisson d'eau douce très social qui peut être retrouvé dans des groupes de quelques individus à quelques centaines d'individus dans les milieux d'eau douce en Europe (Magurran and Pitcher 1983). Cette espèce a été choisie car quelques centaines de vairons étaient déjà gardés en captivité dans le laboratoire de Prof. Shaun Killen à University of Glasgow, où les expériences pour ce projet devaient se dérouler.

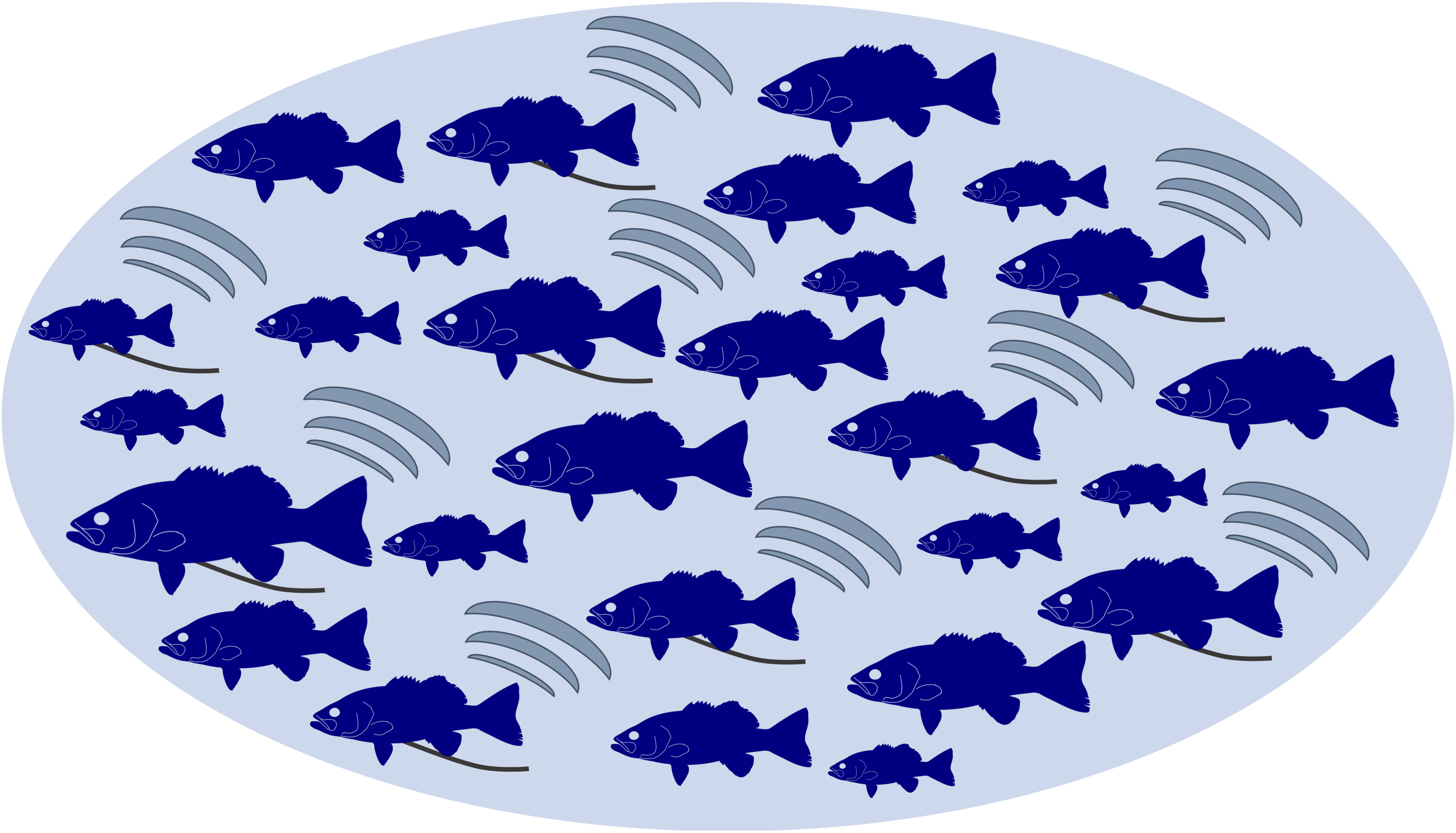
Structure générale et objectifs de la thèse

Le **Chapitre 1** est une étude sur la sélection des habitats des achigans à petite bouche en rivière. Nous avons effectué le suivi de 24 achigans à petite bouche portant des émetteurs radio par télémétrie sur une période de 37 jours dans un segment de la rivière Kiamika dans les Laurentides (Québec, Canada). Nous avons combiné ces données aux conditions environnementales observées dans le même segment de rivière afin d'identifier les conditions environnementales déterminant la sélection des habitats chez ces poissons. Le premier objectif était de créer et de comparer la capacité prédictive de modèles de sélection des habitats intégrant la variabilité individuelle. Le deuxième objectif était de tester l'existence de groupes de poissons présentant des similitudes dans leur sélection d'habitats. Le troisième objectif visait à identifier les conditions environnementales influençant la sélection des habitats au niveau individuel, des groupes et de la population. Les résultats ont montré que la présence de couvert submergé (ci-après : refuge) était la variable la plus importante à considérer pour ces poissons, tel que déjà démontré par des travaux précédents (Edwards et al. 1983, Todd and Rabeni 1989). Effectivement, les modèles incluant les variables représentant la présence de refuge dans les habitats avaient un meilleur pouvoir prédictif que ceux qui ne les incluaient pas. Par ailleurs, des groupements d'individus présentant des similitudes dans leur sélection d'habitats ont été identifiés. Malgré tout, la variabilité dans la sélection des habitats entre les individus était nettement plus grande que la variabilité entre les groupes. De manière générale, nos travaux ont souligné l'importance de considérer la variabilité individuelle dans la modélisation de la sélection des habitats, de la calibration à la validation des modèles.

Les travaux du **Chapitre 1** ont montré que la présence de refuge était la variable influençant le plus la sélection des habitats chez les achigans à petite bouche. De manière générale, l'accès à un refuge est une composante importante de la sélection des habitats (Fukui 2001, Michaels and Preziosi 2015) qui peut influencer l'acquisition de ressources et les dépenses énergétiques des animaux en plus d'augmenter leur chance de survie (Hughes and Ward 1993, Tufto et al. 1996, Moreno et al. 1996, Pollard 2006). Certaines études ont par ailleurs démontré que des poissons ayant accès à un refuge avaient des taux métaboliques plus bas que d'autres qui n'y avaient pas accès, probablement dû aux dépenses énergétiques liées à la vigilance en absence de refuge (Fischer 2000, Finstad et al. 2004, Millidine et al. 2006). Dans cette étude, nous avons posé l'hypothèse que les achigans à petite bouche pourraient également avoir des taux métaboliques plus bas en présence de refuge. Nous avons également posé l'hypothèse que si la présence de refuge pouvait limiter les dépenses énergétiques liées à la vigilance et influencer SMR, nous pourrions nous attendre à un effet de la présence de refuge sur AS, RT et EPOC. Ainsi, l'objectif du **Chapitre 2** était de quantifier l'effet de la présence de refuge sur plusieurs traits métaboliques des achigans à petite bouche. Pour ce faire, nous avons fait des expériences de respirométrie sur des achigans à petite bouche provenant de deux populations (Lac Long et Rivière Kiamika) afin d'estimer leurs traits métaboliques en présence et en absence de refuge. Les résultats ont montré que la présence de refuge n'affectait pas la majorité des traits métaboliques mais qu'il y avait un effet important de la population d'origine et une grande variabilité de réponses entre les individus. Chez les individus plus gros, SMR était plus bas en présence de refuge alors qu'il n'y avait pas de différence entre les taux métaboliques mesurés en présence ou en absence de refuge chez les plus petits individus. En tenant compte de la hiérarchie sociale des achigans (i.e. dominance), nous avons observé que le RT des individus dominants était plus court s'ils étaient en présence de refuge que lorsqu'ils n'y avaient pas accès. Cette étude n'a pas démontré d'effet constant de la présence de refuge sur les dépenses énergétiques, ce qui suggère que les bénéfices les plus importants de l'utilisation des refuges pourraient être liés aux interactions biotiques.

Pour le **Chapitre 3**, nous nous sommes intéressés au potentiel de l'environnement social de moduler les liens entre la sélection des habitats et les réponses physiologiques. En continuité avec les travaux du **Chapitre 2**, nous avons investigué si la taille des groupes sociaux pouvait influencer l'effet de la présence de refuge sur les taux métaboliques des poissons. L'objectif était de quantifier et de comparer les effets de la taille des groupes sociaux et de la présence de refuge sur le métabolisme de vairons *Phoxinus phoxinus*. Notre design expérimental consistait en une expérience sociale de 3 semaines précédée et suivie par des expériences de respirométrie. Durant l'expérience sociale, les poissons étaient gardés en groupes de 4 ou 8 poissons dans des aquariums qui contenaient un refuge (plante aquatique) ou non. Durant la respirométrie, les taux métaboliques étaient estimés en présence et en absence de refuge. La répétition des expériences de respirométrie permettait 1) de mesurer si l'effet de la présence de refuge sur les taux métaboliques serait similaire avant et après l'expérience sociale et 2) de mesurer le changement dans les taux métaboliques individuels dû à l'expérience sociale. La présence de refuge lors de la respirométrie a diminué les taux métaboliques des vairons indépendamment de la taille des groupes. En présence de refuge, les taux métaboliques étaient moins élevés avant et après l'expérience sociale. Nous avons également observé une augmentation des taux métaboliques après l'expérience sociale. Cette augmentation était d'ailleurs deux fois plus élevée pour les poissons gardés en groupes de 4 que pour les poissons gardés en groupes de 8. La présence de refuge dans les aquariums durant l'expérience sociale n'a pas eu d'effet sur les taux métaboliques. Nos résultats ont démontré que la taille des groupes peut influencer les dépenses énergétiques des individus, ce qui souligne l'importance de comprendre le rôle des dynamiques sociales sur les variations dans les traits métaboliques.

Les résultats associés aux **Chapitres 1, 2** et **3** sont présentés sous forme d'articles. Une conclusion générale suit les articles, afin de mettre en lumière les contributions à l'avancement de la recherche scientifique découlant de chacun des chapitres et de fournir des pistes de recherches futures. L'**Annexe I** présente une bande-dessinée inspirée des **Chapitres 1** et **2** réalisée en collaboration avec l'illustrateur Martin PM pour un concours de vulgarisation scientifique.



Chapitre 1 :

Intégrer la variabilité interindividuelle aux modèles d'habitats de poissons pour en augmenter la capacité prédictive

Integrating individual variability to increase the predictive capacity of fish habitat models

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In prep for: Ecography

Abstract

Habitat selection is an important behaviour that relates individuals to the environmental conditions in their habitat, and can be modelled using resource selection functions (RSF). There is increased use of locations of individual animals tracked by telemetry techniques to fit habitat selection models, which enables the study of variation in individual behaviours and habitat selection strategies. In fact, previous studies demonstrated that individual differences often exceeded species differences in habitat selection. Yet, individual differences are generally lost when mapping RSF and inferring population-level habitat associations. Exploring individual variation further could help identify individual to population level correlates of habitat selection, and even reveal the existence of groups within the population defined by their habitat selection. In this study, we used smallmouth bass (*Micropterus dolomieu*) telemetry data and a hydroacoustic survey of aquatic habitat in a river reach to investigate what can be gained by integrating individual variability into fish habitat selection modelling, from the calibration of models to their validation. First, we created and compared the predictive capacity of candidate models integrating individual variability in habitat selection. Second, we assessed the existence of statistically significant groups of fish defined by habitat selection. Finally, we identified which habitat variables influenced individual-, group- or population-level habitat selection. Candidate models including variables associated to submerged cover (i.e. macrophyte cover and woody debris) had a higher predictive capacity than those that did not include them. Groups defined by their habitat selection were also identified, but individual variation in habitat selection exceeded that of these groups. Considering individuals in the modelling process allowed identification of variables influencing individual-, group-, and population-level habitat selection.

Keywords: resource selection functions; habitat selection; smallmouth bass; submerged cover; cross-validation

Introduction

Understanding how animals relate to their environment is key for effective resource management and conservation efforts (Loiselle et al. 2003, Brownscombe et al. 2021). Habitat selection is an important behaviour that relates individuals to the environmental conditions in their habitat and is generally studied to infer population-level habitat associations and patterns of distribution (Matthiopoulos et al. 2015; Northrup et al. 2021). Habitat selection occurs when an animal uses a certain habitat in greater proportion than its availability in the landscape, and can be assessed using resource selection functions (RSF) in a use-availability design (Gerber and Northrup 2020, Muff et al. 2020, Northrup et al. 2021). This is done by comparing environmental conditions at locations used by an animal to environmental conditions at locations available to that animal (Muff et al. 2020). For computational convenience, logistic regression is typically used to analyze such data, where used and available locations are given the value of 1 and 0, respectively (Aarts et al. 2012, Northrup et al. 2013, 2021, Capra et al. 2017). The exponential of the linear predictor of the logistic regression is a RSF (Muff et al. 2020) and is used to map the predicted selection of habitats based on environmental conditions (Boyce et al. 2016). Maps of RSF are useful and informative tools for natural resource managers and conservation practitioners, provided that the predictive capacity of models used to generate them has been validated.

With advances in telemetry technologies, there is increased use of locations of individual animals tagged with electronic devices tracked by telemetry techniques to fit habitat selection models (Jepsen et al. 2014, Brownscombe et al. 2021, Northrup et al. 2021). Aside from being suitable for the detection of locations of mobile animals in habitats that are difficult to sample (e.g. deep rivers, dense forests), telemetry techniques provide a more continuous measure of habitat use and enable the study of variation in individual behaviours and habitat selection strategies (Leclerc et al. 2016, Muff et al. 2020, Brownscombe et al. 2021). Such studies demonstrated that individual differences often exceed species differences in explaining variation in movement rates (Harrison et al. 2019) and habitat selection (Capra et al. 2017). Moreover, such studies have also revealed that individual differences in habitat selection may be masked at the population level. For instance, brown bears (*Ursus arctos*) tracked by telemetry in south-central Sweden showed avoidance of bogs at the population-level but with varying intensity at the individual level (Leclerc et al. 2016). Barbel (*Barbus barbus*) and wells catfish (*Silurus glanis*) tracked by telemetry in Rhône River, France, showed positive selection at the population level to high coefficient of variation and maximum flow velocity over a 15 day period, but positive or negative selection at the individual level (Capra et al. 2017). These individual differences can be consistent over time, suggesting the existence of behavioural phenotypes or personalities (Stamps 2007, Leclerc et al. 2016). Understanding the determinants of individual differences in habitat selection can inform on the extent to which individuals develop specialized niches and improve our ability to predict resilience and adaptability of populations to changing environments (Ward et al. 2016).

Integrating individual variation into habitat selection models has been facilitated by approaches like generalized linear mixed effects models (GLMM; Gillies et al. 2006, Dingemanse and Dochtermann 2013). These models include fixed and random effects and handle non normal data such as binary data (0 or 1) by using link functions (Bolker et al. 2009a). GLMMs are suited to deal with non-independent data, such as telemetry data, which comprise multiple locations on the same individuals. In GLMMs, it is possible to include random intercepts and slopes, which vary among individuals, and inclusion of both is recommended to account for non-independence of data and to obtain appropriate standard errors around fixed coefficient values (Schielzeth and Forstmeier 2009). In other words, integration of random slopes that vary among individuals is thought to reduce bias in the estimation of mean (fixed) coefficient values for each habitat variable for the population, and improve model fit (Muff et al. 2020). However, integration of individual variation may lead to overfitted model that would perform poorly with new data (Roberts et al. 2017). This can be verified by testing the predictive capacity of models by cross-validation, which requires splitting data into calibration and validation subsets, the former being used to fit the model, the latter being used to assess model accuracy. Data can be split randomly or based on blocking criteria, such as time, space, or individuals. Roberts et al. (2017) showed that, in the case where repeated measures were done on individuals, random cross-validation overestimated predictive capacity of models, while blocked cross-validation by individuals did not. Taken together, both model calibration and validation would benefit from consideration of individuals, yet that aspect is lost when mapping RSFs and inferring population-level habitat associations.

Exploring individual variation further could reveal groups within the population defined by their habitat selection. Groups of individuals within a population associated to a specific habitat can show habitat-based polymorphism (Senay et al. 2015). This is common in fish, where differences in body morphology can stem from selective pressures in response to local environmental conditions (Peres-Neto and Magnan 2004). For example, benthic and limnetic morphs of Arctic charr (*Salvelinus alpinus*) can coexist in the same lake (Jonsson and Jonsson 2001). Moreover, stream fish show polymorphism related to their habitat selection. In other words, the same species of fish encountered in a riffle, run or pool may show morphological differences (Senay et al. 2015). Some of the similarities among individuals within population may be attributable to behavioural phenotypes or personality. Shy individuals may select habitats based on availability of cover while bold individuals may not (Found and St. Clair 2016). Density-dependent processes could also influence habitat selection, where more competitive individuals would have access to high quality habitats and less competitive ones would have to use alternate habitats (Hertel et al. 2020). Whatever the basis of the differences in habitat selection among groups within the population, which can rarely be assessed in a field setting, investigating the extent to which this variation compares to individual- and population-level variation in habitat selection could have implications for conservation. If distinct groups defined by habitat selection are identified, further research could be conducted to assess the temporal stability of such group and if they are associated to different reproductive success or survival. In any case, group-level RSF could be generated for practitioners so that alternate habitat selection be considered in conservation efforts.

In this study, we used smallmouth bass (*Micropterus dolomieu*) telemetry data and hydroacoustics survey of aquatic habitat in a river reach to investigate what can be gained by integrating individual variability into fish habitat selection modelling spanning both the calibration and validation phases. First, we created and compared the predictive capacity of candidate models integrating individual variability in habitat selection. Second, we assessed the existence of statistically significant groups of fish defined by habitat selection. Finally, we identified which habitat variables influenced individual-, group- or population-level habitat selection.

Methods

Study species

Smallmouth bass (*Micropterus dolomieu*) is a freshwater fish dwelling in lakes and rivers of North America highly valued by recreational anglers, and generally considered a top predator (Warren 2009). In rivers and streams, smallmouth bass are associated with presence of submerged cover (e.g. large woody debris), depth, rocky substrate, macrophytes, and also steep drop-offs (e.g. steep outer banks, high slopes; Coble, 1975; Edwards et al., 1983; Todd and Rabeni, 1989; Warren, 2009). Smallmouth bass are mainly visual predators and thus exhibit diurnal activity pattern (Demers et al. 1996), although they are opportunistic in their feeding over a 24-h period (Savitz et al. 1993).

Study site

The study was conducted in a 5.5 km reach of Kiamika River (Quebec, Canada; Fig.1), located downstream of a hydroelectric dam (Kiamika Dam) in summer 2017. The Kiamika River is part of the Outaouais River watershed and located in the Laurentian region of the Canadian Shield. The mean annual discharge of Kiamika River estimated at a gauging station located 2.6 km downstream of the study reach (Chute St-Philippe; 46.65°N, 75.24°W) is 15 m^3 s^{-1}. During tracking, daily discharge remained stable and was on average 55.3% higher than mean annual value (June-August 2017 mean ± sd discharge:

23.3 ± 1.6 m^{3}s^{-1}). Kiamika riverbanks are mostly natural, except for the occasional docks close to cabins.

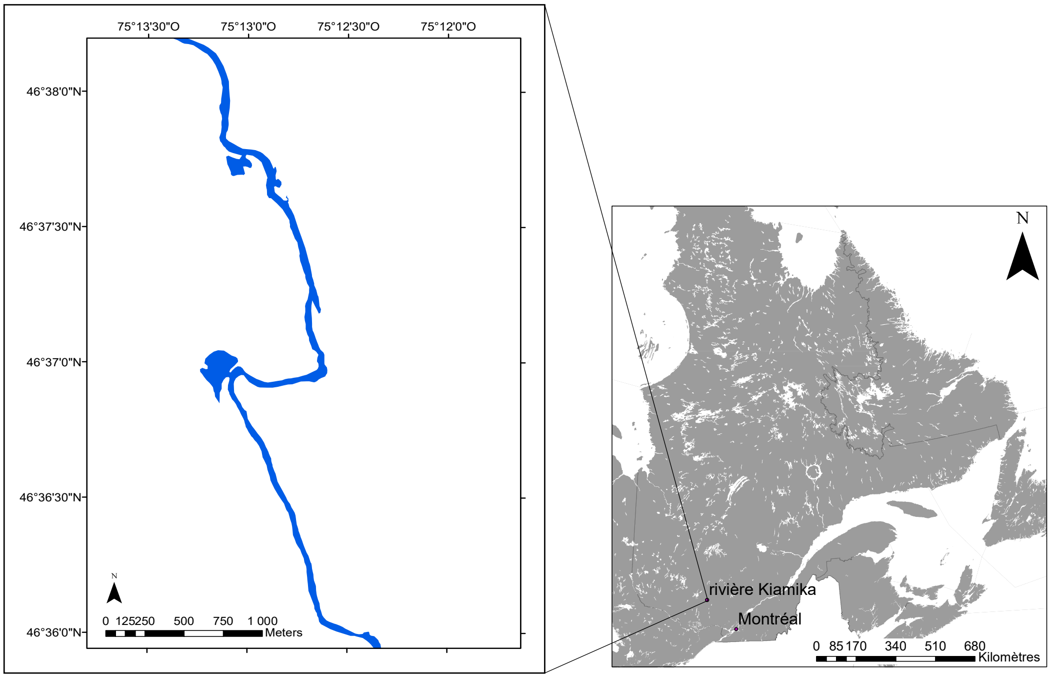


Figure 1: Map for the segment of Kiamika River sampled for this project (left) and its location (right) in Québec (Canada).

Fish tagging and tracking

Twenty-nine smallmouth bass of similar sizes (16.8 to 26.0 cm in total length) were captured between July 6 and July 17, 2017 by angling from shore using barbless circle hooks to minimize injuries (Cooke and Suski 2004). Within one hour after capture, fish were measured and underwent surgery for implantation of a radio transmitter (Lotek nano NTC-4 radio-telemeter, Lotek, Ontario, Canada; 1g in water, 3s pulse interval, battery life 74 days) in the peritoneal cavity, with the antenna extruding through the body wall. During the surgery, fish were electrosedated using electric fish handling gloves, a safe alternative to chemical sedation for fish released in the wild (Prystay et al. 2017). The incision was closed using three to four single independent sutures. Each surgery was completed within 2.5 - 5 minutes. After the surgery, fish were placed in an insulated container filled with aerated freshwater taken from Kiamika River for recovery. Fish started swimming and resumed gill ventilation and equilibrium once they were placed in the insulated container and were released near their capture site within 15 to 30 minutes post-surgery.

Fish tracking on the river reach was done between July 18 and August 23, 2017. During that period, the river reach was surveyed from upstream to downstream 33 times. These 33 tracking events lasted 3 to 4 h and were conducted every other day, sometimes twice a day, at different times, to cover habitat use over a diel cycle. Fish were tracked using a portable radio-receiver equipped with a three element Yagi antenna (Lotek SRX 800 Telemetry Receiver, Lotek, Ontario, Canada) using a successive gain reduction technique (Taylor et al. 2014). At each fish position, geographic coordinates were recorded using a portable GPS instrument (Garmin eTrex Venture HC, Garmin, Kansas, USA) with a precision of < 5m. Water temperature (°C), canopy cover (% of the celestial vault hidden by vegetation) and presence/absence of woody debris (*e.g.* sunken logs, or dead trees) were also noted at each fish position. Final dataset included a total of 588 fish positions for 24 fish (4 tagged fish were never found; one tagged fish was found dead and showed signs of infection, and was therefore excluded from the dataset).

Mapping of aquatic habitat

Mapping of depth (m), flow velocity (m s^{-1}), distance from shore (m), slope (º), macrophyte cover (%) and woody debris (presence/absence) on the reach was done using a combination of hydroacoustic and observational data as well as ArcGIS 10.6 (ESRI, Redlands, CA, USA) tools. The reach was surveyed on July 29 and 30, 2017 with a scientific echo-sounder (BioSonics DTX; BioSonics Inc. Seattle, Washington, USA; 420 kHz transducer) to collect data on river bathymetry (depth; m) and macrophyte cover (%). This hydroacoustic survey gathered >400 000 georeferenced data points (Garmin 17x HVS; Garmin International, Olathe, Kansas, USA) which were edited and analyzed in Visual Habitat software (BioSonics Inc., Seattle, Washington, USA). Using water depth measurements from the bathymetry data and hourly discharges recorded at Chute Saint-Philippe gauging station, a hydrodynamic model was developed with integrated software packages CCHE_MESH and CCHE_GUI (NNCHE, University of Mississippi, USA) to simulate flow velocities (m s^{-1}) along the reach. Depth, flow velocities, macrophyte cover, and woody debris data were then interpolated using ArcGIS 10.6 (ESRI, Redlands, CA, USA). Distance from shore (m) and slope (°) were calculated using ArcGIS tools. A raster layer was outputted for each of the habitat variables, each pixel (2 x 2 m) containing a unique value of depth, flow velocity, distance from shore, slope, macrophyte cover, or woody debris (Figures S1 and S2).

Groups defined by their habitat selection

We assessed similarities among individual fish habitat selection by computation of the Gower similarity coefficient. This metric is suitable to represent the association between objects (here, individual fish) and can handle a mix of binary, quantitative, and semi-quantitative variables (Legendre and Legendre 2012). However, objects could not be repeated multiple times. Consequently, the arithmetic mean habitat variable values assigned to each fish, as well as the mode for woody debris, were used to compute Gower similarity coefficients. We then used Ward's minimum variance clustering to partition fish into groups, based on the association matrix of Gower coefficients. This method of clustering defines groups based on the criterion of least squares, thus minimizing the within-group variance (Borcard et al. 2011). Validation of the number of groups as well as fish allocation to each group was done by calculation and visualization of silhouette widths. A negative silhouette width value would indicate that a fish was probably allocated in the wrong group (Borcard et al. 2011). Finally, we used linear models to assess if fish size, namely total length (L; in cm), mass (M; in grams), and condition (Fulton condition factor; $K = M * L^{-3} *100$), could explain differences among groups.

Modeling fish habitat selection

A common approach to quantify habitat selection as a function of habitat variables is resource selection functions (RSF) based on a use-availability design (Boyce et al. 2002, Aarts et al. 2013, Muff et al. 2020, Northrup et al. 2021). These RSF compare habitat variables of locations where organisms occur ("*used locations*") to those of "*available locations*" surrounding them (Aarts et al. 2013, Capra et al. 2017). Used locations are scored 1 whereas available locations are scored 0. For this reason, generalized linear modeling with a binomial distribution (i.e. logistic regression) is commonly used to fit RSF (Northrup et al. 2021). As available locations are not equivalent to absences, their number has to be very large (Northrup et al. 2013). For each used location, ten available location points were included in the model. The ratio of 10 available locations per used location was determined by assessing the sensibility of model parameters and significance levels to an increasing number of absences per presence (2 to 20) while ensuring a minimal 5-meter distance between each location. Available locations were picked randomly within a 100-m radius surrounding each fish position (used location), which represents the average distance that could be travelled by a fish during a day.

Before creating models, we explored the data by creating histograms of the range of habitat variables at used and available locations (Figure S3). We also generated plots of presence and available locations of fish to the range of each habitat variable (except the binary variable woody debris), and by adding a smoothed line for each individual using ggplot2 (Wickham 2016) in R v. 3.6.0 (R Foundation for Statistical Computing 2018). Visual exploration of data revealed that some individuals had non-linear or bell-shaped response to depth (m), flow velocity (m s^{-1}), distance from shore (m), and slope (°), but linear response to macrophyte cover (%). Therefore, we decided to include quadratic terms for depth, flow velocity, distance from shore, and slope as fixed and random effects in models to enable individual functional responses in habitat use.

Since our goal was to test the predictive capacity of models, we developed and compared a small number of candidate models instead of using stepwise regression. Model selection using stepwise regression would identify the best combination of habitat variables for the data available, but a different combination of variables could be identified for new data (Fieberg and Johnson 2015). Six candidate models were developed based on previously reported smallmouth bass habitat associations, hydrological variables, or both (Table 1).

Table 1: Candidate models describing habitat selection by smallmouth bass in Kiamika river in July-August 2017.

MODEL NAME	EQUATION
bass full	slope + slope^2 + distance + distance^2 + macro + woody debris
bass cover	macro + woody debris
hydro full	flow + flow^2 + slope + slope^2 + distance + distance^2 + depth + depth^2
hydro	flow + flow^2 + depth + depth^2
all quadratic	flow + flow^2 + slope + slope^2 + distance + distance^2 + depth + depth^2 + macro + woody debris
all linear	flow + slope + distance + depth + macro + woody debris

The “bass full” model included variables known to influence smallmouth bass habitat selection. For instance, smallmouth bass has been associated with steep outer banks and shade, such as that provided by canopy cover (Coble 1975, Warren 2009). As such, distance from shore and slope were included in the “bass full” model. Macrophyte cover and woody debris (presence/absence) were also included due to the frequently reported association between smallmouth bass and any type of submerged cover (Edwards et al. 1983, Todd and Rabeni 1989). Relatedly, the “bass cover” model included only macrophyte cover and woody debris. The “hydro full” and “hydro”, included morphological and hydrological habitat variables only (distance from shore, slope, depth, and flow velocity), the latter including only depth and flow velocity. The “all quadratic” and “all linear” models included all habitat variables, the most complex one, “all quadratic", also including their quadratic term (except for macrophyte cover and woody debris). All candidate models included random intercept and slopes among individuals for each variable and were fit using glmmTMB (Brooks et al. 2017). Given that available locations are not real absences, a weight (W=1000) was given to available locations (y=0) while the used points (y=1) had a weight of 1. Additionally, a large fixed prior variance was given to the individual-specific intercepts, as recommended by Muff et al. (2020), as random intercepts are otherwise mainly influenced by the ratio of used and available points for each individual, and thus have minimal variance. Candidate models were compared using Akaike's information criteria (AIC).

Continuous variables were standardized for fitting the models, which allows direct comparison of model coefficients. For mapping the predictions of the models, unstandardized model coefficients were used. Candidate model predictions were projected on the river reach using the exponential component of the model equation without the intercept (Morris et al. 2016, Northrup et al. 2021), and spatial analyses tools from the packages raster (Hijmans 2019) and rgdal (Bivand et al. 2019) in R (R Foundation for Statistical Computing 2018):

$$w(x) = exp(\beta_1 X_1 + \ldots + \beta_i X_i)$$

where $w(x)$ is the RSF score for each pixel on the map, β_1 is the coefficient estimated for variable X_1. For each candidate model, the raster layer generated represented the RSF surface across the study reach, which was then reclassed into 10 bins using quantiles, bin ranks 1 and 10 corresponding to the lowest and highest RSF score based on the model, respectively.

Model validation and analyses

A 5-fold, cross-validation by blocked individuals was used to validate candidate models and assess their predictive capacity (Roberts et al. 2017). Our dataset was divided into 5 folds of 80% calibration and 20% validation data, separated by individuals (19 individuals to be used to calibrate candidate models and the remaining 5 individuals to be used to validate them), meaning that each candidate model was calibrated and mapped 5 times (one for each fold). For each fold, each candidate model was validated by overlaying the locations of the individuals in the validation set to the mapped RSF scores, and the proportion of locations falling in each bin was calculated, and adjusted for the area occupied by each bin.

The predictive capacity of candidate models was assessed by calculation of Spearman rank correlations between area adjusted proportion of locations and binned RSF scores for each fold of the data in turn. A model with high predictive capacity should have a strong positive correlation (Boyce et al. 2002, Roberts et al. 2017). Individual, group, and population level correlates of habitat selection were identified by comparison of model coefficients generated by each of the 5-fold calibration data. Linear mixed effects models (LMM) were used to assess if individual coefficient values for each term included in the full model varied among groups identified by the cluster analysis, with fish ID as a random factor. Marginal R^2 (R^2_m: proportion of variance explained by fixed effects) and conditional R^2 (R^2_c: proportion of variance explained by fixed and random effects) were calculated from the models. As such, R^2_m represent variability in coefficient value among group and the difference between R^2_c and R^2_m represent variability among individual fish (Nakagawa and Schielzeth 2013).

Results

Habitat selection models

Based on the AIC computed for each candidate model , the "all quadratic" model was the best one (Figure 2). All candidate models were nonetheless mapped and overlayed with fish positions (Figure 3; see all maps on Figures S4 to S21). Visual inspection of maps revealed that the "all quadratic" and the two bass models ("bass full" and "bass cover") better predicted the selection of habitat variables, given that they included more fish positions in bins with high RSF scores. Compared to the other mapped candidate models, the "all linear" and "hydro full" models contained very few pixels (or none) with binned RSF scores higher than 5 despite the high number of observed fish positions in this area during tracking. They were therefore not included for further comparisons of candidate models.

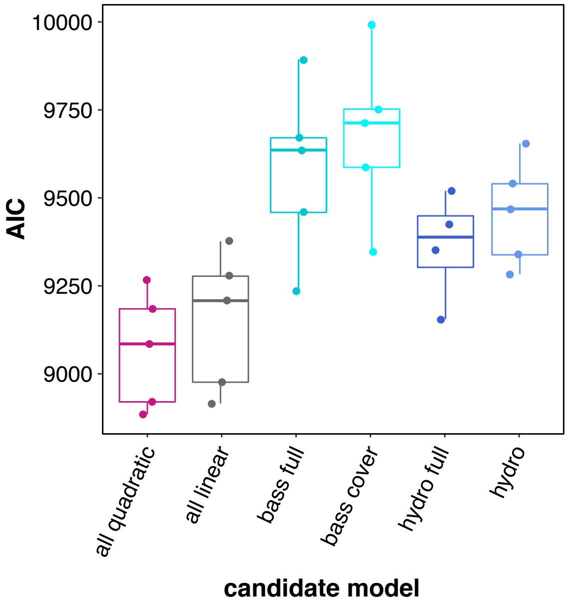


Figure 2: Akaike information criterion (AIC) for the five fit of each candidate models

The proportion of observed fish positions increased with binned RSF scores for the "all quadratic", "bass full", and "bass cover" models (Figure 4). Comparison of Spearman-rank correlations however showed that the "bass full" model performed best (Figure 5). Across folds, correlations between the proportion of observed fish position in the validation set and binned RSF scores from the "bass full" model fit with the calibration set ranged from 0.83 to 0.92. Correlations did not vary for the "bass cover" model. This model included two habitat variables, one of which was binary, potentially limiting the range of RSF scores calculated from the model, thus resulting in very similar binned RSF scores across folds.

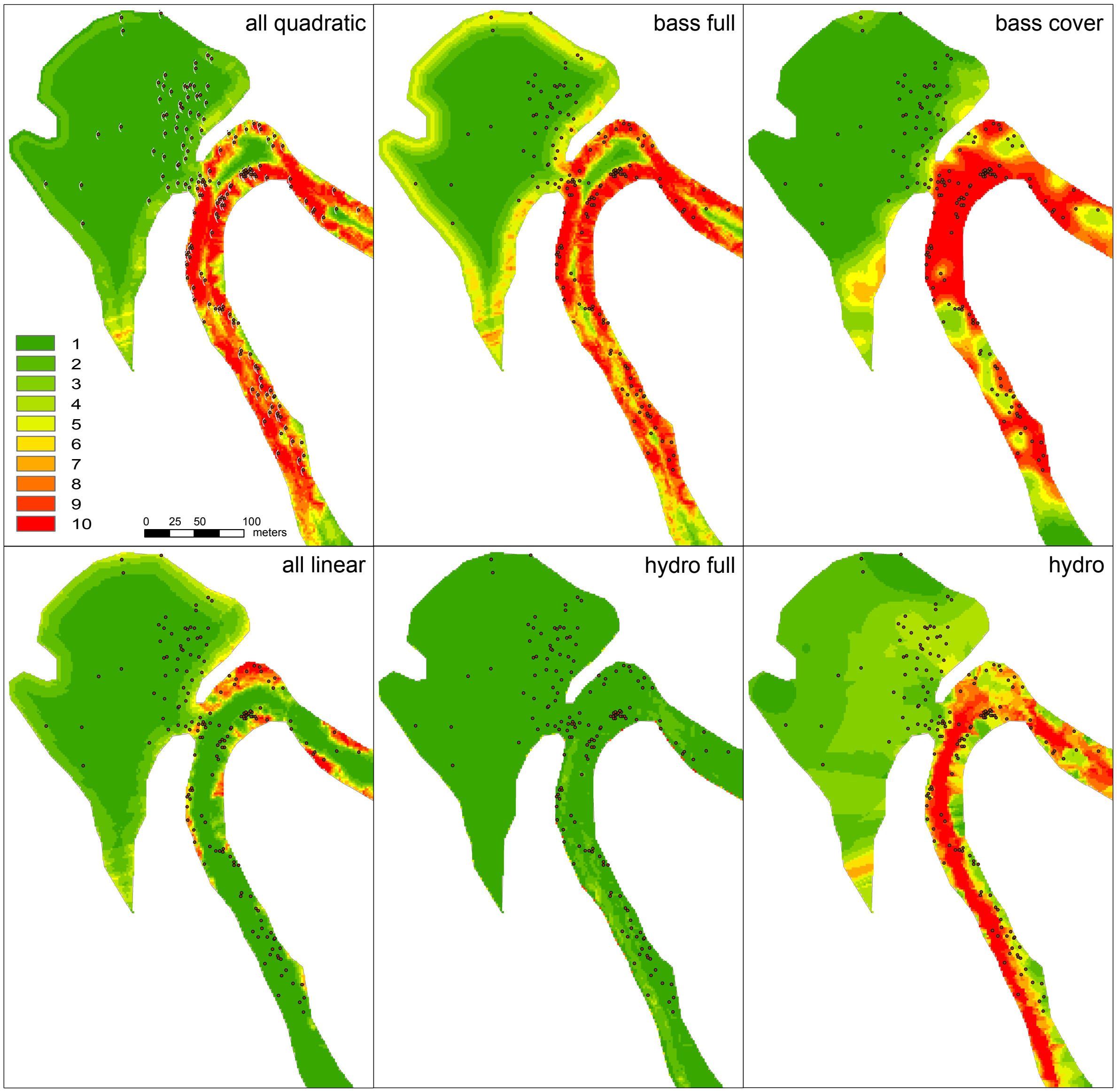


Figure 3: Maps of the binned RSF scores obtained by one calibration for each of the candidate models. Fish locations from tracking by telemetry are overlayed on each map.

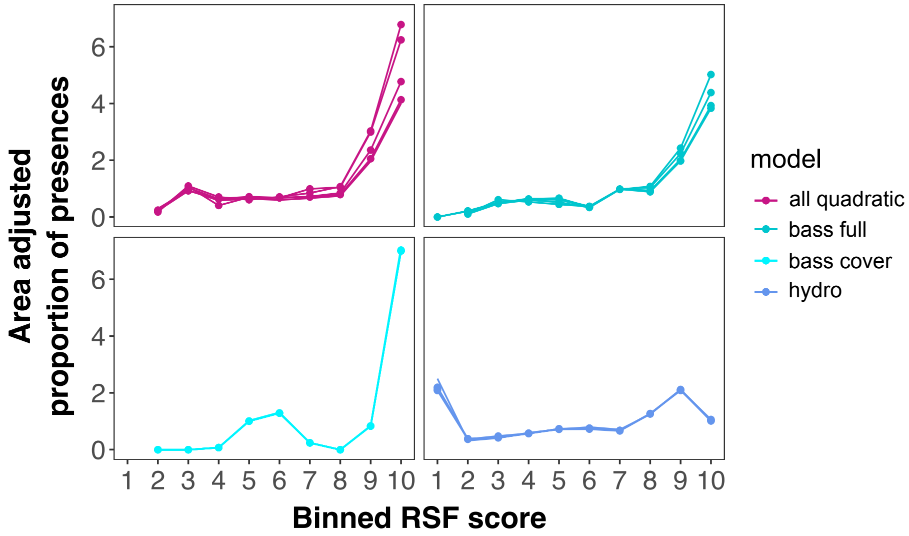


Figure 4: Area adjusted proportion of presence per binned RSF score for the four best candidate models. Each colored line and point represent the 5-fold cross-validation.

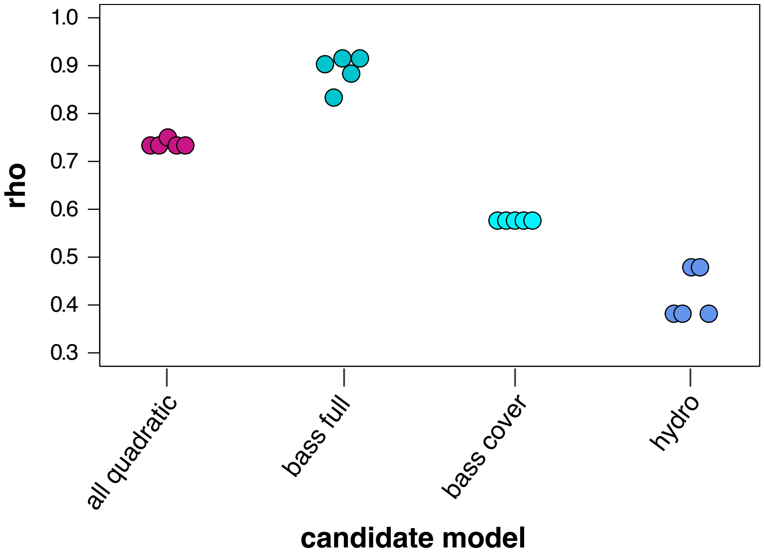


Figure 5: Spearman rank correlations across folds for the four best candidate models.

For most variables, standardized coefficient values were similar regardless of the candidate model and of the calibration set used to fit them (Figure 6). For instance, standardized coefficient values for depth, slope, and macrophyte cover were similar across candidate models and fits. Quadratic terms of flow velocity and distance from shore were the standardized coefficients that varied the most depending on the calibration set (Figure 6). Macrophyte cover coefficients overlapped with zero, indicating that this habitat variable was not a significant correlate of smallmouth bass habitat selection. Woody debris was a significant variable in all candidate models that included it.

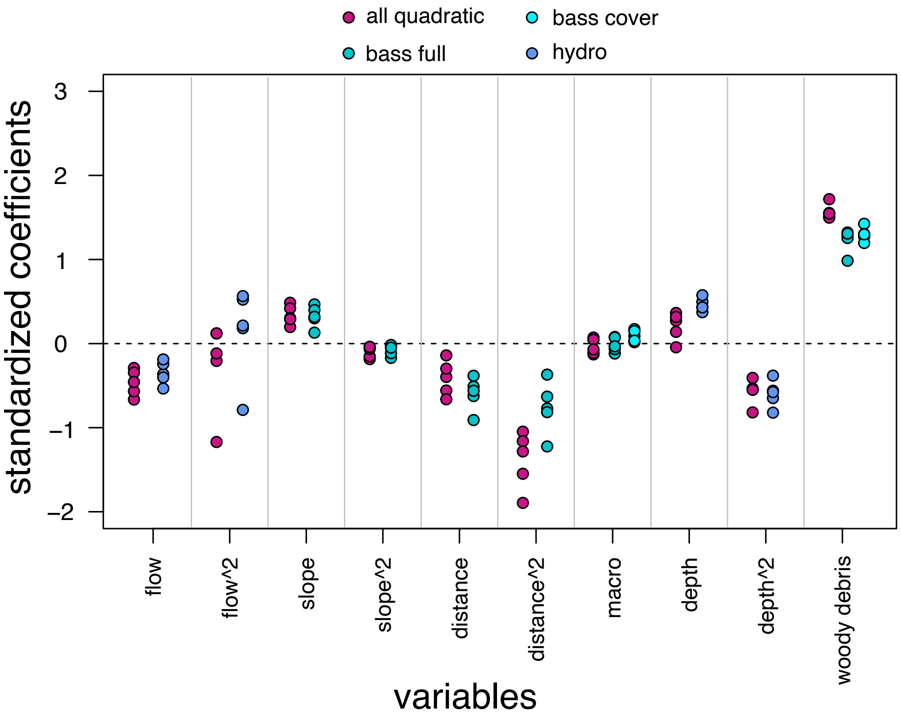


Figure 6: Model standardized coefficients for each fit of the four best candidate models.

Groups defined by their habitat selection

Three groups of fish sharing similarities in habitat selection were revealed by the computation of Gower similarity coefficients and Ward's minimum variance clustering (Figure 7). The largest group contained 12 fish (group 1), the medium sized group contained 8 fish (group 2), and the smallest one included 4 fish (group 3). Number of groups and fish allocation to each group was validated by calculation of silhouette widths. Average silhouette width was of 0.48, and there were no negative individual silhouette width values, indicating that no fish were allocated to the wrong group. The three groups were composed of fish of similar sizes and condition (Figure 7; total length: $F_{2,21}$=0.828, p=0.451; mass: $F_{2,21}=1.123$, p=0.344, and Fulton condition factor: $F_{2,21}=0.609$, p=0.553).

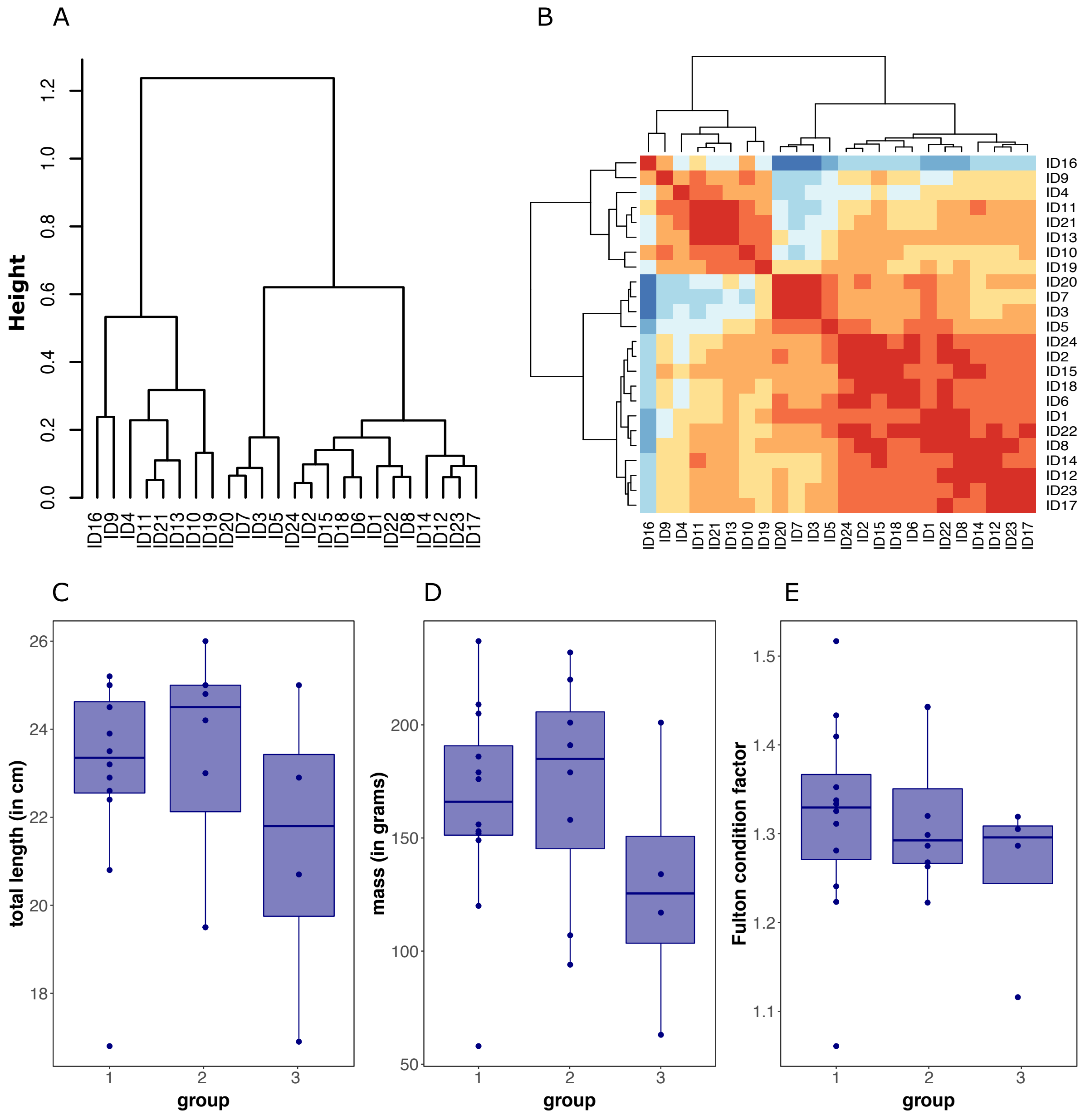


Figure 7: Dendogram of Ward's minimum variance clustering (A) and heat map of Gower similarities (B) among fish. High and low similarity values are represented in red and blue, respectively. Range of total length (C), mass (D), and condition factor (E) of fish assigned to each group. Dots represent individual fish, middle thick line of the boxplots corresponds to the median, lower and upper limits correspond to the first and third quartiles of the data, and whiskers extend to the range of the data.

Fish from group 3 used in general deeper habitats, with steeper slopes and more macrophyte cover than fish from groups 1 and 2 (Table 2). Fish from group 2 used shallower habitats further from shore, indicative of the wetland area represented on the top left of maps (Figure 3) and were not associated with presence of woody debris. Compared to the range of habitat available, all fish used a restricted range of lower flow velocities.

Table 2: Range of habitat variables used by smallmouth bass for each group defined by their habitat selection compared to the range of habitat variables available in the study reach. For each habitat variable except woody debris, mean ± standard deviation are presented. Minimum and maximum values are in brackets. For woody debris, the mode is shown.

Variable	Group 1	Group 2	Group 3	available
Depth (m)	2.2 ± 0.7 *(0.5 - 4.1)*	1.6 ± 0.8 *(0.6 - 3.9)*	3.3 ± 1.3 *(0.8 - 6.6)*	2.1 ± 1.2 *(0.1 - 8.0)*
Flow velocity (m s^{-1})	0.3 ± 0.1 *(0.0 - 0.7)*	0.2 ± 0.2 *(0.0 - 0.9)*	0.2 ± 0.1 *(0.0 - 0.4)*	0.3 ± 0.2 *(0.1 - 1.3)*
Slope (°)	6.1 ± 5.5 *(0.1 - 31.8)*	4.5 ± 4.7 *(0 - 24.8)*	12.1 ± 8.7 *(0 - 32.5)*	4.7 ± 5.4 *(0.0 - 42.2)*
Distance from shore	9.2 ± 5.0 *(2.0 - 33.9)*	14.2 ± 12.6 *(2.0 - 66.0)*	8.4 ± 4.2 *(2.0 - 22.0)*	13.9 ± 11.2 *(2.0 - 80.4)*
Macrophyte cover	40.0 ± 40.0 *(0.0 - 100)*	40.0 ± 40.0 *(0.0 - 100)*	70.0 ± 30.0 *(0.0 - 100)*	39.0 ± 38.0 *(0.0 - 100)*
Presence/absence of woody debris	1	0	1	0

Variables influencing individual to population level habitat selection

High variability among individuals is reflected in univariate marginal responses according to the most complex model (all quadratic; Figure 8). Most individuals showed bell-shaped responses with depth and distance from shore, with highest prediction of selection at average values (around zero on standardized environmental condition). Response for slope was bell-shaped as well, but peaked at values close to two standard deviations higher than average slope. Individual responses were not similar among members of each of the three groups identified by the cluster analysis (Figure 8; Table 3). Most variation in standardized coefficient values was explained by individual fish (Table 3; difference between R^2_c and R^2_m for each model). No variation in standardized coefficient value was explained by group for any variable, except woody debris ($p<0.001$; $R^2_m = 0.482$). Group 3 had the strongest selection for that variable, group 1 showed neutral to positive selection, and group 2 showed neutral to negative selection (Figure 8).

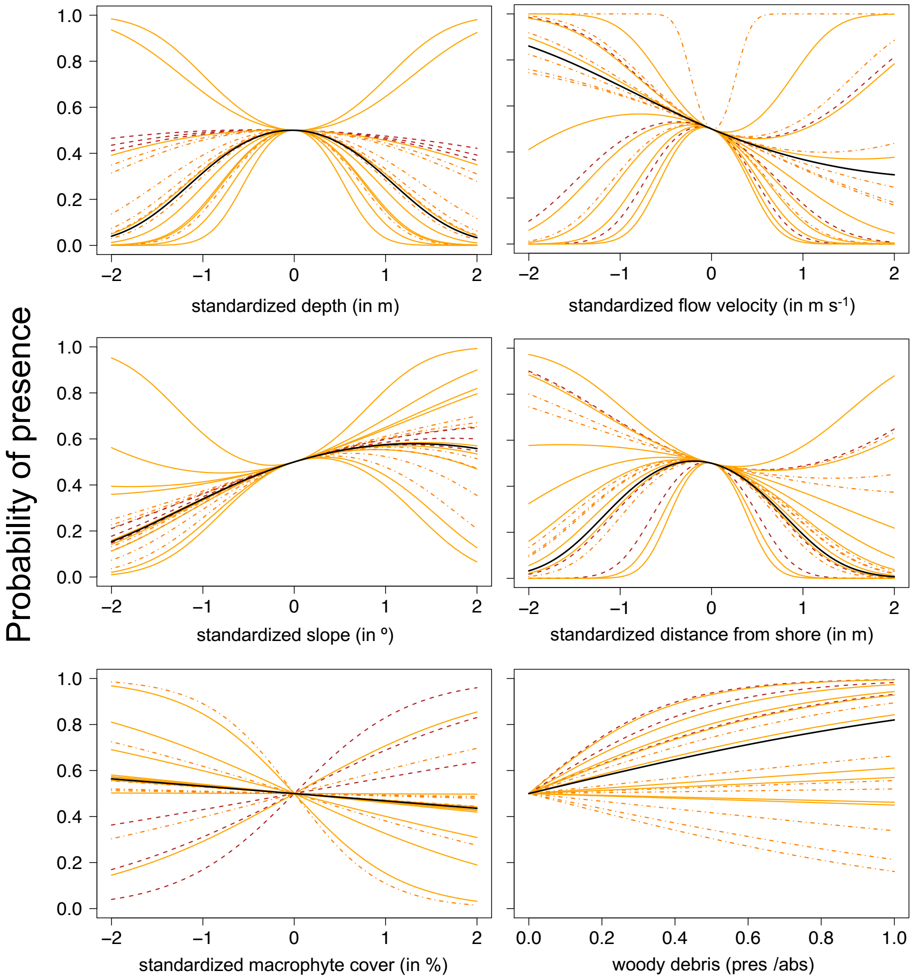


Figure 8: Individual (thin colored lines) and mean (bold black lines) habitat selection by smallmouth bass. Probability of presence are univariate marginal responses according to one fit of the model involving all variables. Full, semi-dashed, and dashed lines represent group 1, 2, and 3 identified by cluster analysis, respectively.

Table 3: Results from LMM relating individual standardized coefficient values to groups defined by habitat selection.

	group			
response variable	**χ^2**	**p-value**	**R^2m**	**R^2c**
coef. depth^2	2.583	0.275	0.097	0.981
coef. flow^2	3.792	0.150	0.138	0.998
coef. slope^2	0.607	0.738	0.023	0.876
coef. distance^2	0.205	0.903	0.008	0.991
coef. macro	4.768	0.092	0.165	0.985
coef. woody debris	22.269	<0.001	0.482	0.991

Discussion

Habitat selection analyses conducted using RSF have been the focus of many methodological papers (Morris et al. 2016, Roberts et al. 2017, Muff et al. 2020) and important syntheses (Matthiopoulos et al. 2020, Northrup et al. 2021) in recent years. They serve as the basis for understanding fundamental ecological relationships and inform habitat management and conservation. In this study, we used some of the best practices identified such as integration of individual variation in models and blocked cross-validation by individual to investigate individual to population level habitat selection. Considering the role of individual variation led to different insight at each step of the habitat selection modelling process. Based on AIC, the best candidate model integrating individual variability was the most complex one ("all quadratic"). However, cross-validation revealed that the "bass full" model had the highest correlation between observed location and RSF scores, suggesting it had the best predictive capacity. Further, while groups defined by habitat selection were identified, variation in response to habitat variable among individuals within groups was higher than that among groups. Finally, even if presence of woody debris was the main correlate of smallmouth bass habitat selection, our results also revealed that this variable influenced individual- and group-level habitat selection.

Habitat selection models

The six candidate models created were based either on previously reported smallmouth bass habitat associations, on hydraulic variables generally used in fish habitat modelling, or on both. Based on AIC, the best candidate model for smallmouth bass habitat selection was the most complex one ("all quadratic"), which included depth, flow velocity, distance from shore, and slope with their quadratic terms, as well as macrophyte cover and woody debris (Figure 2). The "all quadratic" model had high predictive capacity, but it was not the best. The habitat selection model for smallmouth bass with the highest predictive capacity was "bass full" and included distance from shore and slope with their quadratic terms, macrophyte cover, and woody debris (Figure 5). This result suggests that inclusion of depth and flow velocity in models did not contribute to improve their predictive capacity. Interestingly, the "hydro full" and "hydro" models both included depth and flow velocity with their quadratic term and had lower AIC than the "bass full" model. This underscores that using AIC to evaluate fit can lead to inconsistent results (Gerber and Northrup 2020) and does not replace cross-validation.

It was interesting to see that by blocking by individual for cross-validation, it was possible to identify the standardized coefficients that were the most sensitive to the arrangement of individuals that were included in the calibration set (Figure 6). For instance, the standardized coefficient values for the flow velocity quadratic term were positive or negative, depending on the calibration set used to fit models. Standardized coefficient values for distance from shore also varied depending on the calibration set, but to a lesser extent. These results could suggest that selection for flow velocity and distance from shore varied among individuals or that few individuals had very distinct selection for these variables. Since each calibration set included 19 individuals, the latter explanation is more likely. In any case, blocking by individuals allowed to test each fit (19 fish used for calibration) on new individuals (5 fish used for validation), which is thought to provide more accurate estimates of model predictive error than random cross-validation (Roberts et al. 2017). Blocked cross-validation showed that the "bass full" model had the highest predictive capacity, as represented by the highest Spearman-rank correlation results. It would be interesting to test this model on another population of smallmouth bass to confirm its transferability.

Groups defined by their habitat selection

Three groups defined by their habitat selection were identified, and were comprised of fish of similar size and body condition (Figure 7). Based on the range of habitat variables used compared to that of available locations, the largest group (group 1) could be referred to as the "generalists" as fish in this group used locations with mean values of depth, flow velocity, and macrophyte cover similar to the mean conditions in available locations (Table 1). Group 2 could be referred to as the "shallow water specialists" as they used locations with shallower mean depth and less slope than that of available locations. Finally, group 3 could be referred to as the "depth specialists" for their use of locations with deeper water and steeper slopes. Group 2 was the most distinct from the others, while group 1 and 3 were more similar (Figure 7). However, these differences among groups did not exceed individual differences (Figure 8; Table 3), except for selection of woody debris. Only fish in group 2 did not show preference for woody debris. Smallmouth bass are known to occupy a variety of habitats, although their most consistent habitat association is presence of submerged cover, such as large woody debris (Edwards et al. 1983). Smallmouth bass can spend more than half their time near one specific logjam within their home range (Todd and Rabeni 1989). These structures provide overhead cover with lower light intensity useful for sit-and-wait foraging (Warren 2009) so it could be hypothesized that locations with proximity of woody debris represent high quality habitats. If smallmouth bass use woody debris because they provide cover and lower light intensity, other components of the habitat could serve that purpose. Cover could be provided by crevasses, large boulders, metric blocs, or macrophytes. Lower light intensity could be found in deeper waters. We have no information on the type of substrate selected or available for smallmouth bass as it was not possible to get precise substrate composition from the hydroacoustic survey. We found, however, that fish from group 2 were associated with shallow depths and intermediate proportions of macrophyte cover (Table 2). They were therefore not associated to components of the habitat providing cover or lower light intensity. This could suggest that group 2 comprised fish with lower competition abilities and were thus restricted to alternate habitats. It is also possible that fish from group 2 developed a specialized niche and may be using a different foraging strategy, such as actively searching for prey. Based on our telemetry data alone, it is not possible to identify the specific drivers explaining the differences in habitat selection among groups. A longer term study with more individuals tracked using fixed receiver on a finer temporal scale could reveal if such groups persist over time, and if they are associated with specific movement behaviour or home range size.

Variables influencing individual to population level habitat selection

Comparison of standardized coefficients indicated that flow velocity quadratic term was the coefficient that varied the most depending on the arrangement of individuals in calibration sets, suggesting high variability among individuals for this habitat variable (Figure 6). However, comparison of standardized coefficients is not sufficient to identify individual variability as plotting of marginal responses according to the "all quadratic" model and LMMs revealed that the majority of the variability in responses to all habitat variables was attributable to individual fish (Figure 8; Table 3). In particular, individuals showed weak to moderate selection for average depth, while probability of presence at the population level had a clear bell-shaped form, with highest probability at average depth. This is partly in line with previously reported habitat requirement for smallmouth bass. In fact, smallmouth bass have showed preference for intermediate depth (Todd and Rabeni 1989) to deeper pools (Coble 1975, Edwards et al. 1983). Deeper water could provide lower light intensity and thus be an alternative to overhead cover for smallmouth bass. The abundance of woody debris in the study reach could partly explain why smallmouth bass did not select deeper waters. Responses to flow velocity were heterogeneous among individuals while at the population level, probability of presence decreased with flow velocity. Preference for slow (Sechnick et al.

1986) to moderate flow velocity (Coble 1975) have also been reported for smallmouth bass. Depth and flow velocity were not included in the "bass full" model, which had the best predictive capacity, which could indicate that these habitat variables are not strong correlates of population-level smallmouth bass habitat selection.

Probability of presence of smallmouth bass based on slope also varied among individuals although similarly to population-level response, it peaked at values higher than average slope. This is consistent with the previously reported association with steep outer banks (Coble 1975, Warren 2009), where slope in river bed drops drastically close to shore. Relatedly, we were expecting probability of presence to decrease with distance from shore, which we did not observe. There was high variability in response to distance from shore with peak population-level probability of presence at intermediate values. Macrophyte cover was not a significant variable in habitat selection models as the standardized coefficient values obtained for this variable in any candidate model was very close to zero. There was variability in individual responses although fish from group 3 all showed a positive relationship with macrophyte cover (Figure 8). Macrophyte cover may be more important for smallmouth bass of smaller size than that of fish tracked in the present study (Walters and Wilson 1996).

Selection for woody debris varied among individuals and groups (Figure 8; Table 3). Yet, presence of woody debris was the variable with the highest standardized coefficient values in models (Figure 6), suggesting a positive selection. Moreover, candidate models that performed the best included woody debris, which is consistent with previous work that showed that presence of submerged cover is the main habitat variable associated with smallmouth bass in any water body (Warren 2009). Woody debris were present at many depths, at varied distance from shore, and across a range of slopes and flow velocities in the study reach. This further demonstrates that woody debris was the main variable influencing habitat selection for smallmouth bass, in line with previous findings. Smallmouth bass may benefit, among others, from lower light intensity, protection from predator, and abundance of prey in proximity to large woody debris (Bevelhimer 1996). They can potentially also reduce their energy expenditures when sheltering in proximity to woody debris, although support for this proposition is mixed (Chrétien et al. 2021).

Individual variation

Identifying and acknowledging individual variation in habitat selection is the first step. It is then important to investigate the underlying mechanisms explaining this variability and if it has implications for performance or fitness (Bennett 1987). Individual variation in habitat selection can be driven the physiological capacity of an individual. Levels of hormone production, aerobic scope or locomotor performance, among others, will influence individual tolerance to environmental conditions (Ward et al. 2016). The behavioural phenotype (i.e. personality) or dominance rank of an individual could also influence its habitat selection and have implications on that of other individuals (Wolf and Weissing 2012). Some individuals may develop specialized niches while others may be restricted to suboptimal habitats due to lower competitive abilities (Hertel et al. 2020). Understanding the extent of the variability in habitat selection and its fitness consequences may aid identification of critical habitats for conservation and predict resilience and adaptability of populations to changing environments.

Acknowledgements:

We would like to thank the field assistants C. Guéveneux-Julien, G. de Warlincourt, and N. Vanier, and Dr. G. Rose for operating the scientific echosounder. We also thank Dr. L. Plichard and Dr. M. Leclerc for their advice on modelling approaches.

Contributions

E.C., S.J.C., and D.B. designed the research protocol. E.C. planned and conducted the data collection, analyzed the data and wrote the manuscript. All authors contributed critically to the manuscript.

Supplementary information

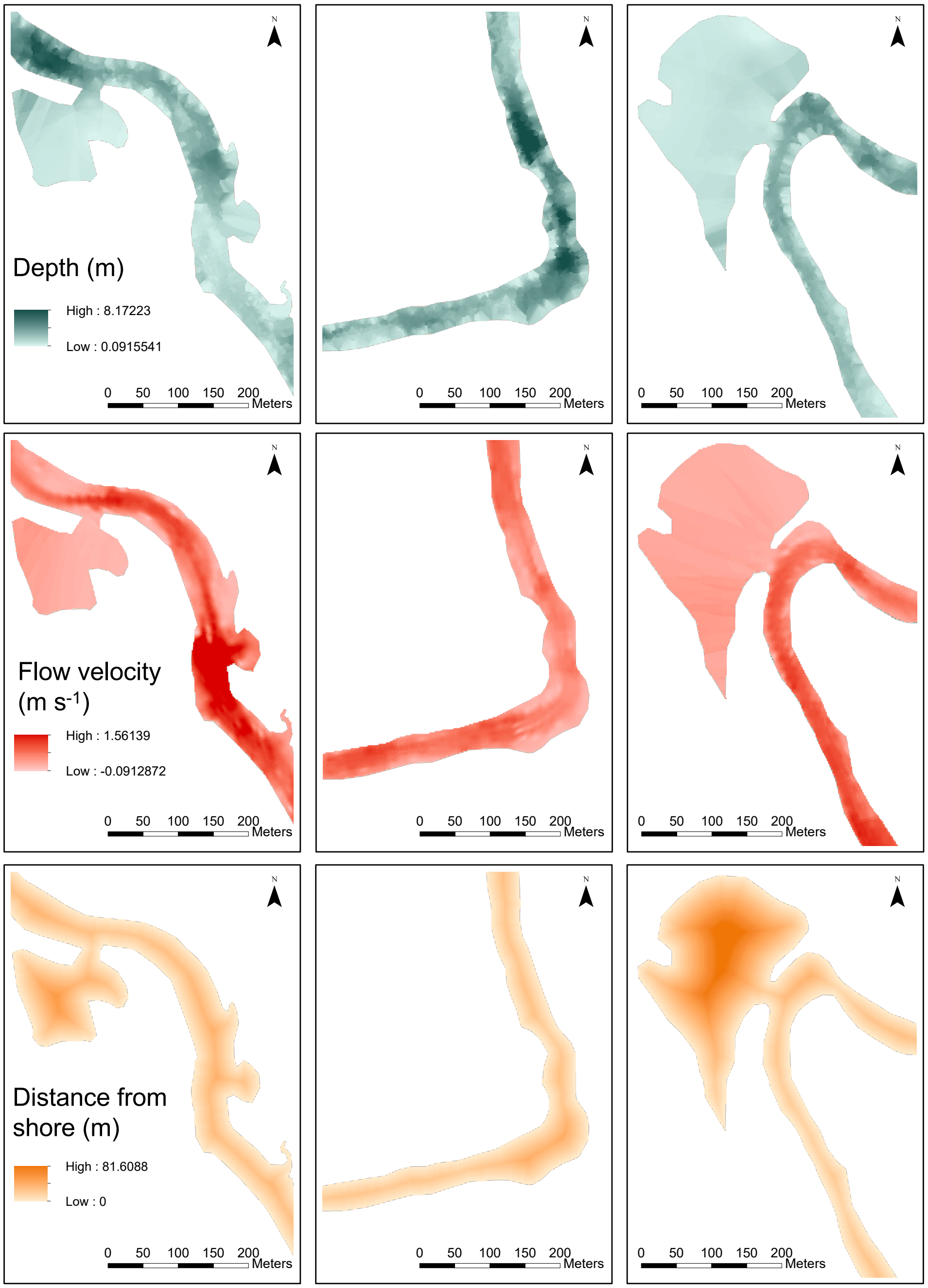


Figure S1: Maps of habitat variables (depth, flow velocity, and distance from shore) at three different locations on Kiamika river reach

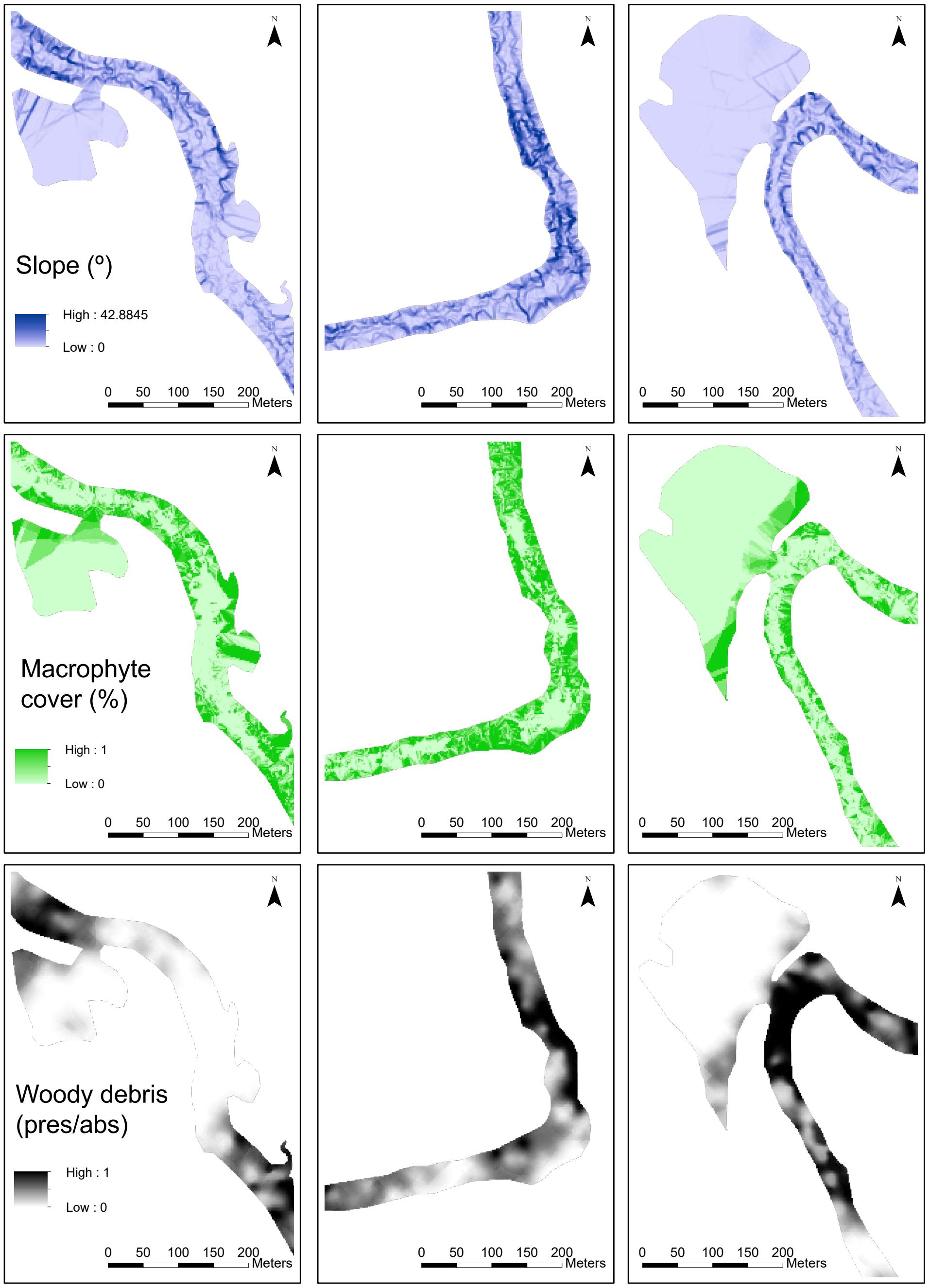


Figure S2: Maps of habitat variables (slope, macrophyte cover, and woody debris) at three locations on Kiamika river reach

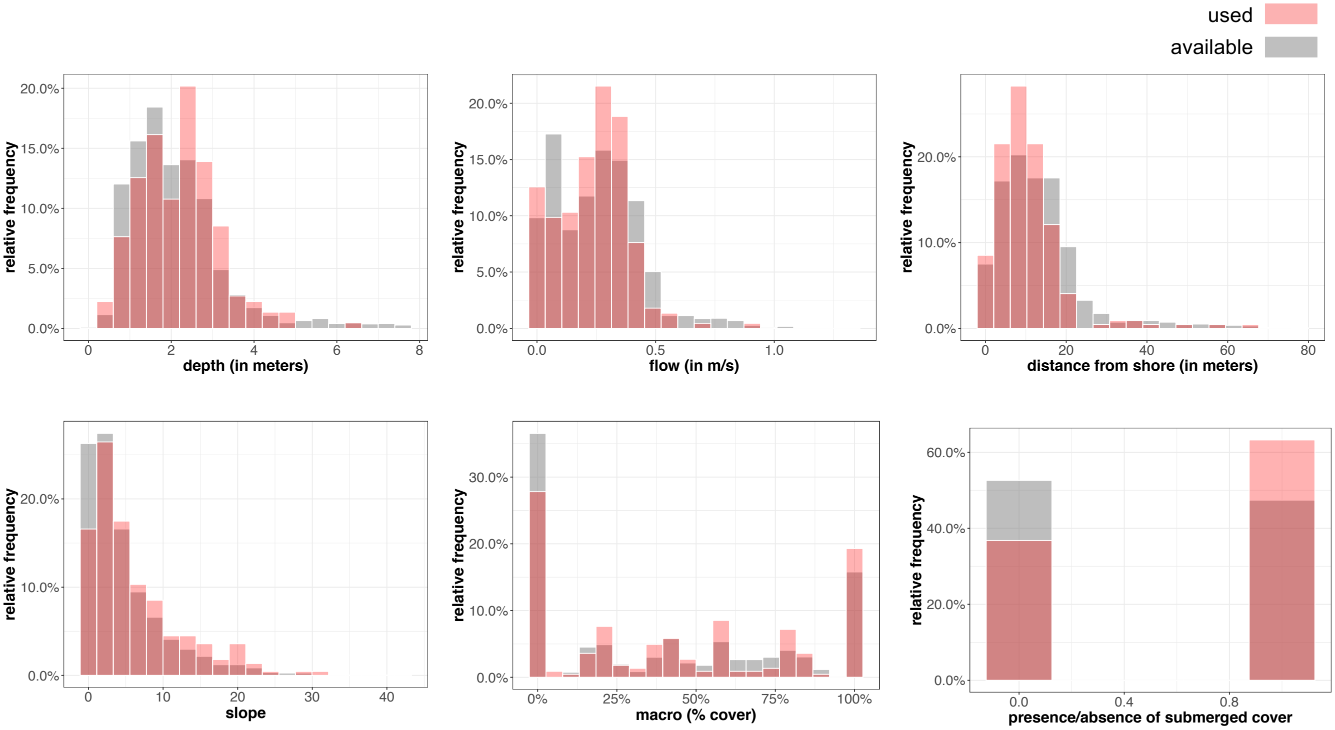
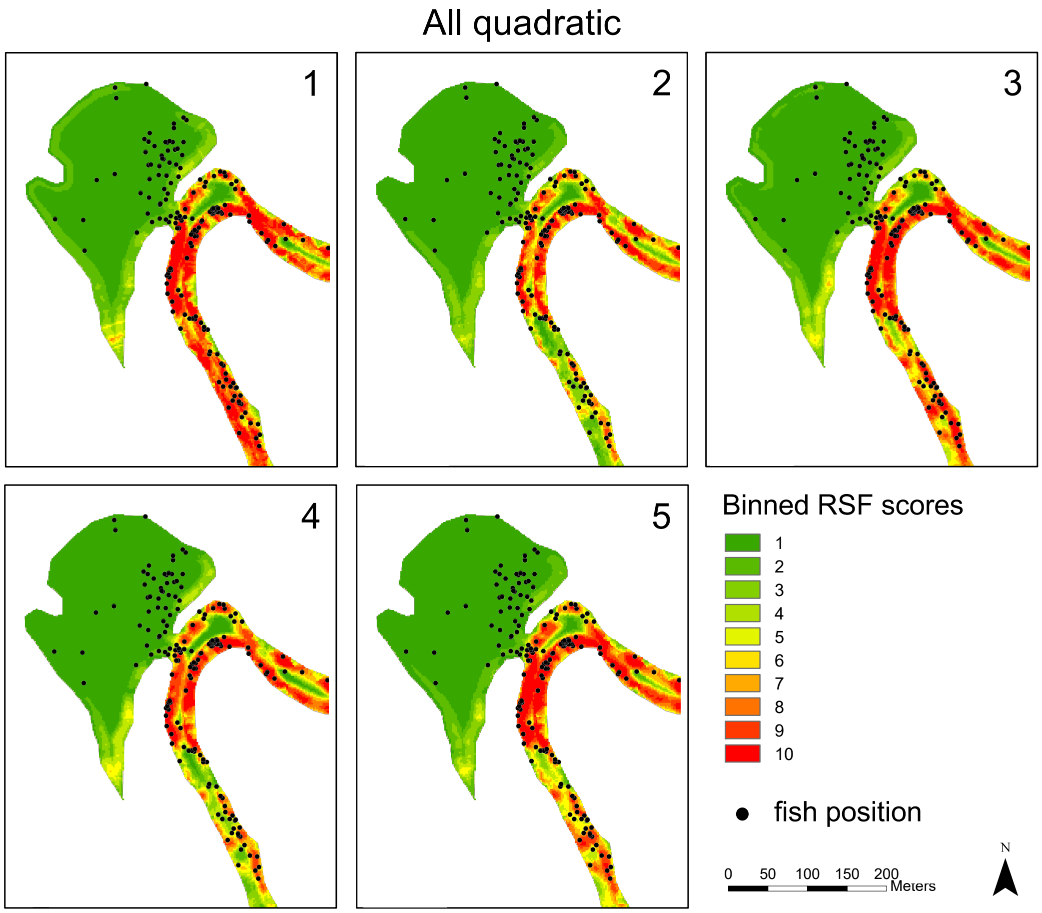
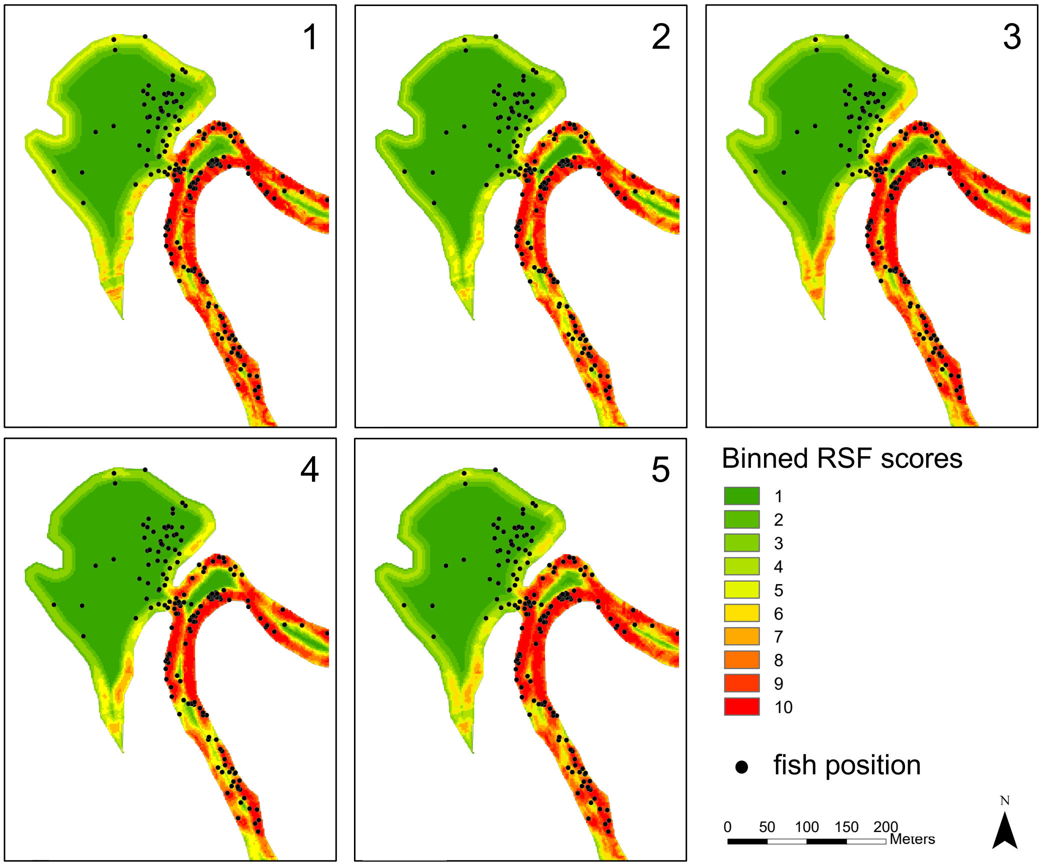


Figure S3: Relative frequency of values of each habitat variable used (red) and available (gray) to smallmouth bass *Micropterus dolomieu* on Kiamika river reach



Figures S4 to S21: Maps of the binned RSF scores obtained from each calibration (5 folds) for each of the candidate models at three locations on Kiamika river reach. Fish locations from tracking by telemetry are overlayed on each map. For each location, models are presented in this order: all quadratic, bass full, bass cover, all linear, hydro full, and hydro cover.

Bass full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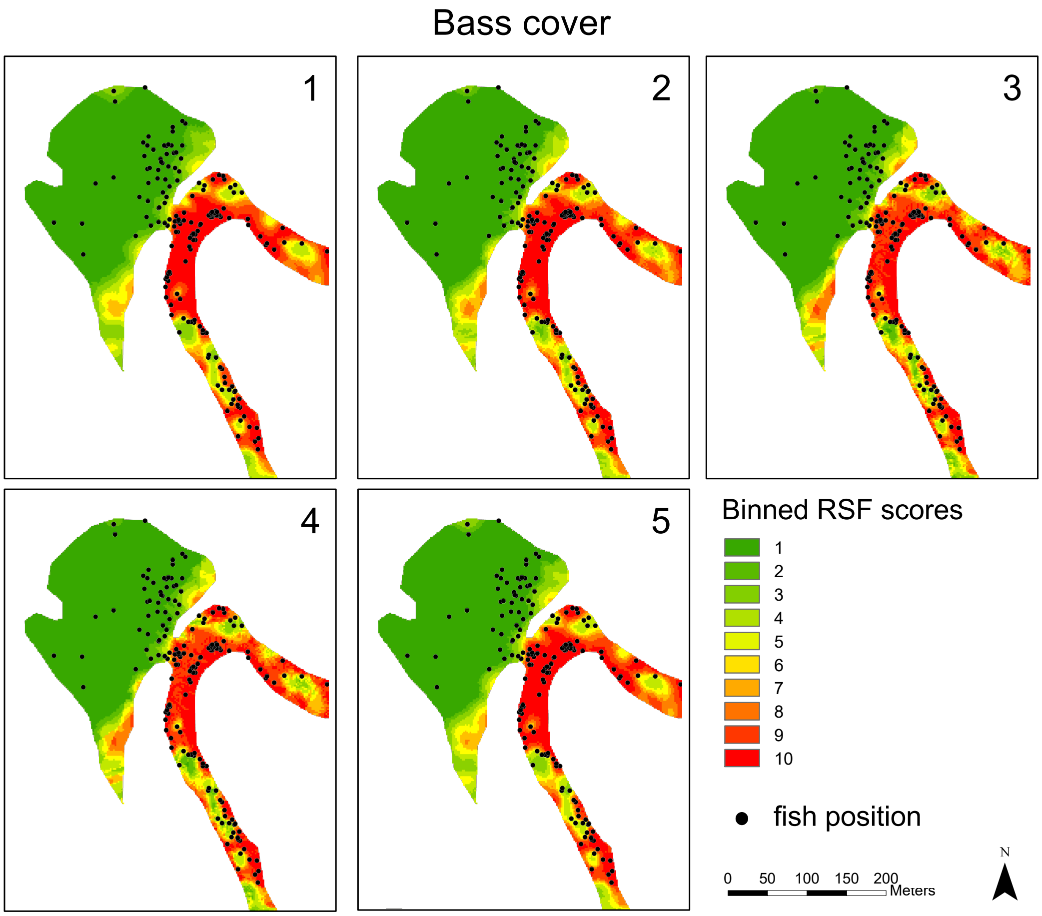
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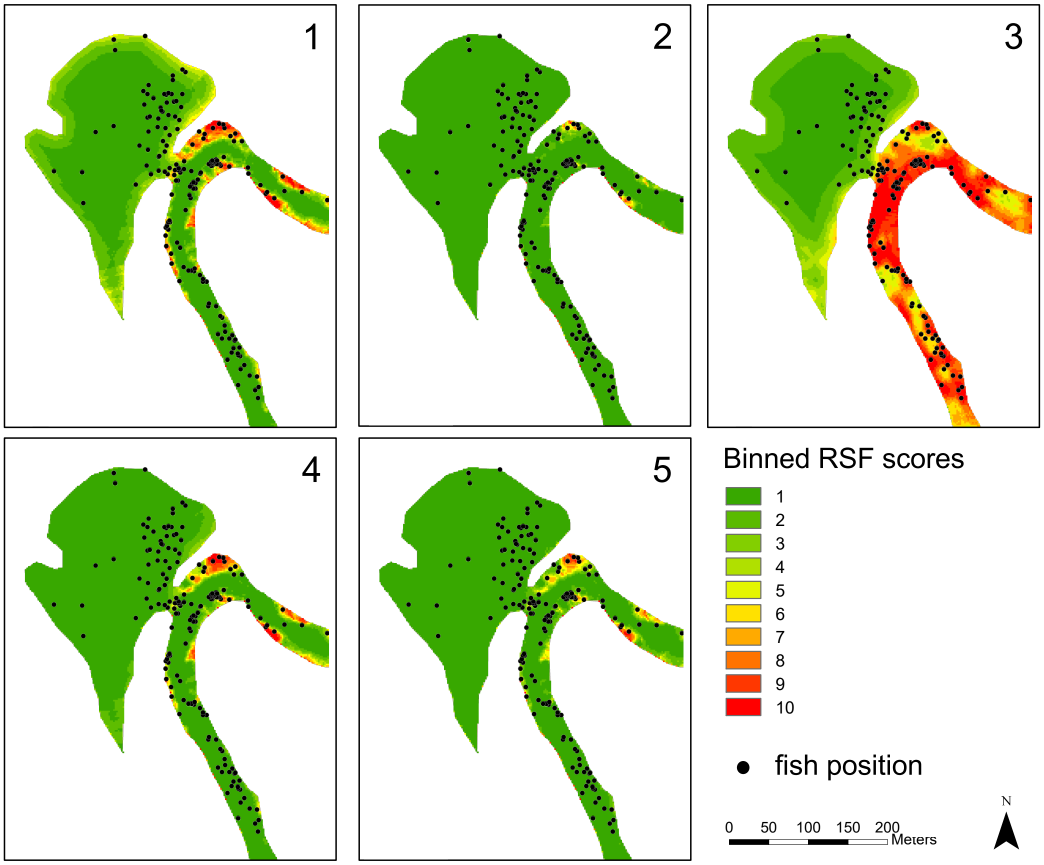
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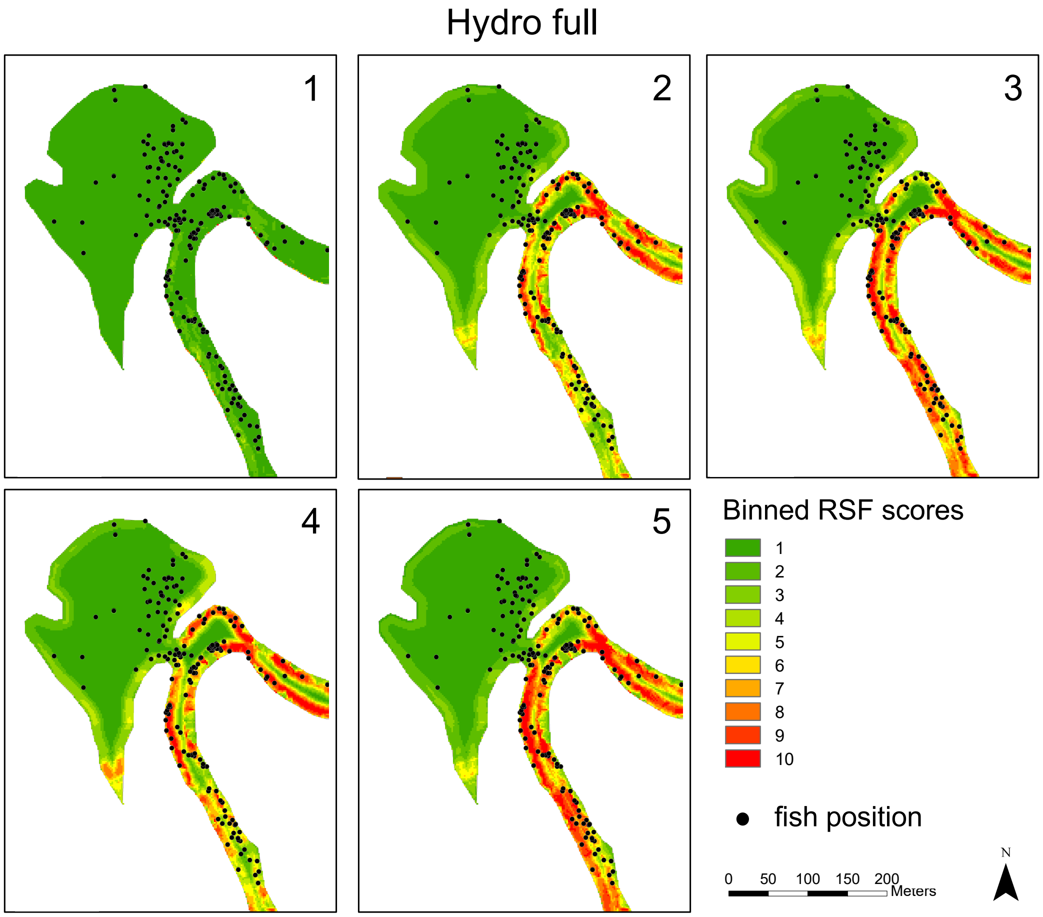
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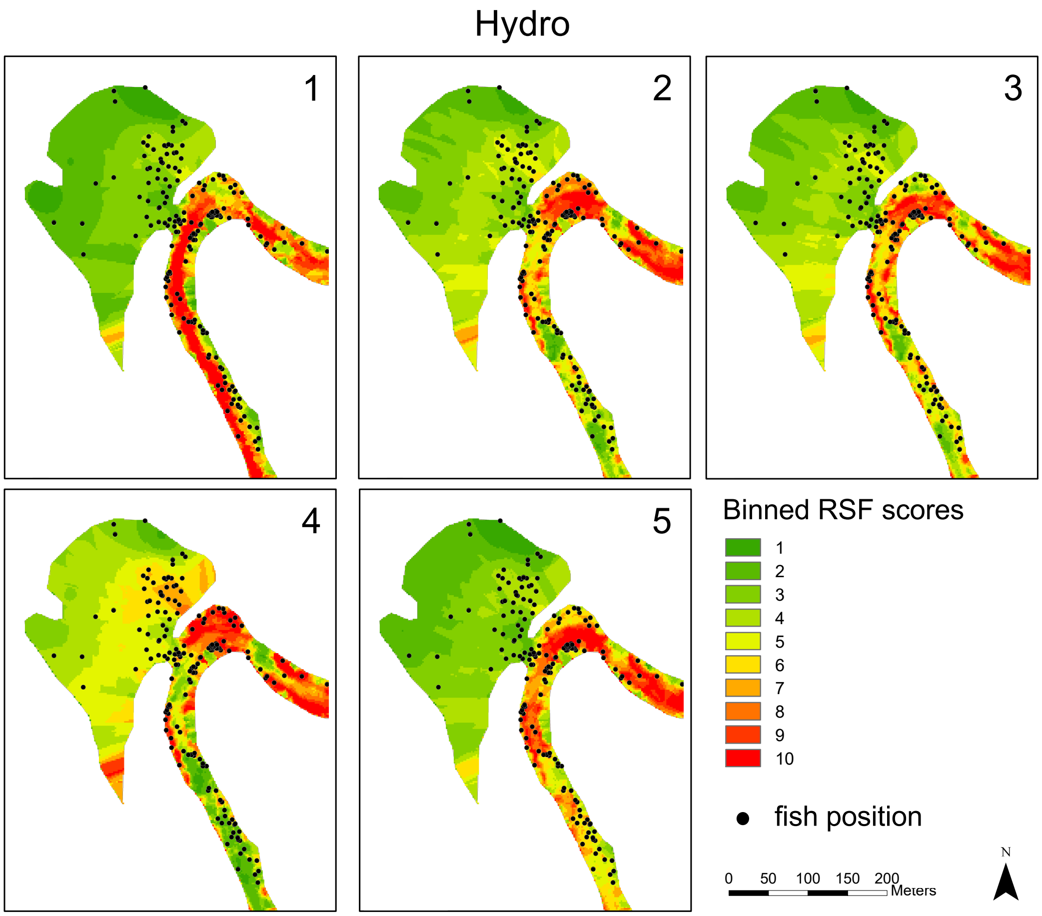
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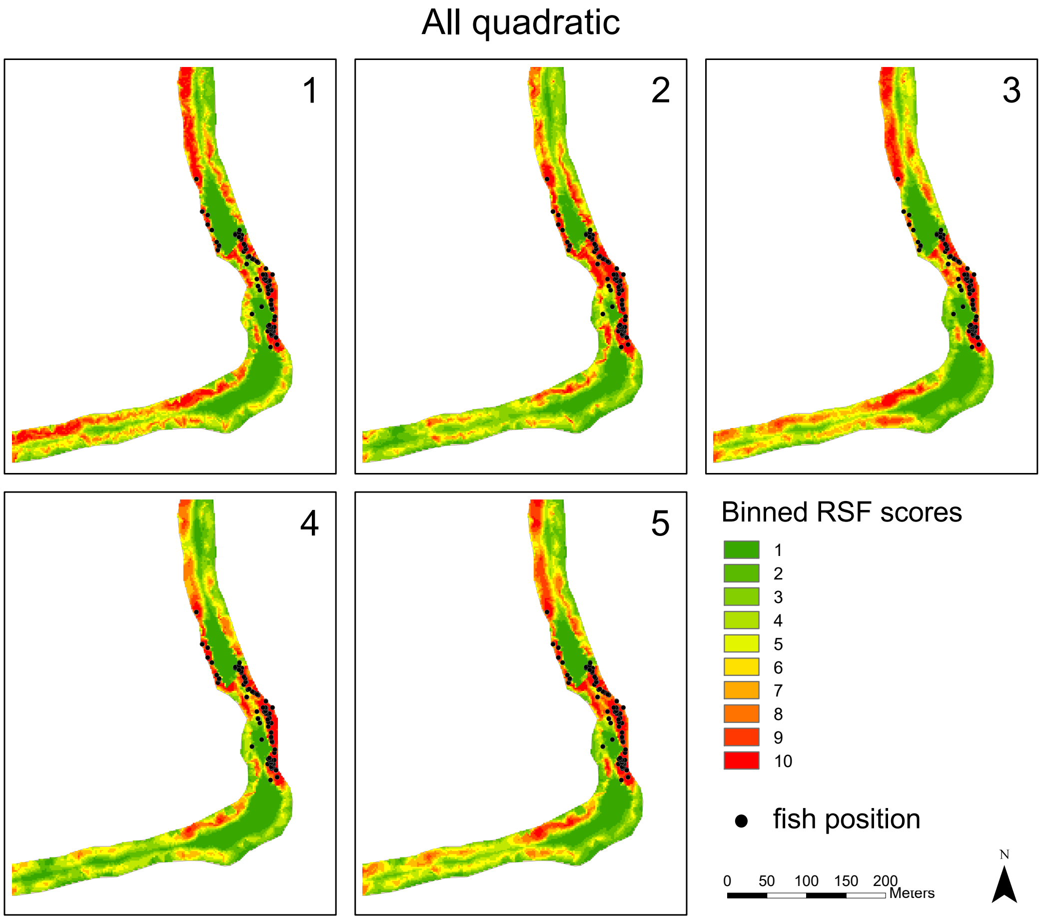
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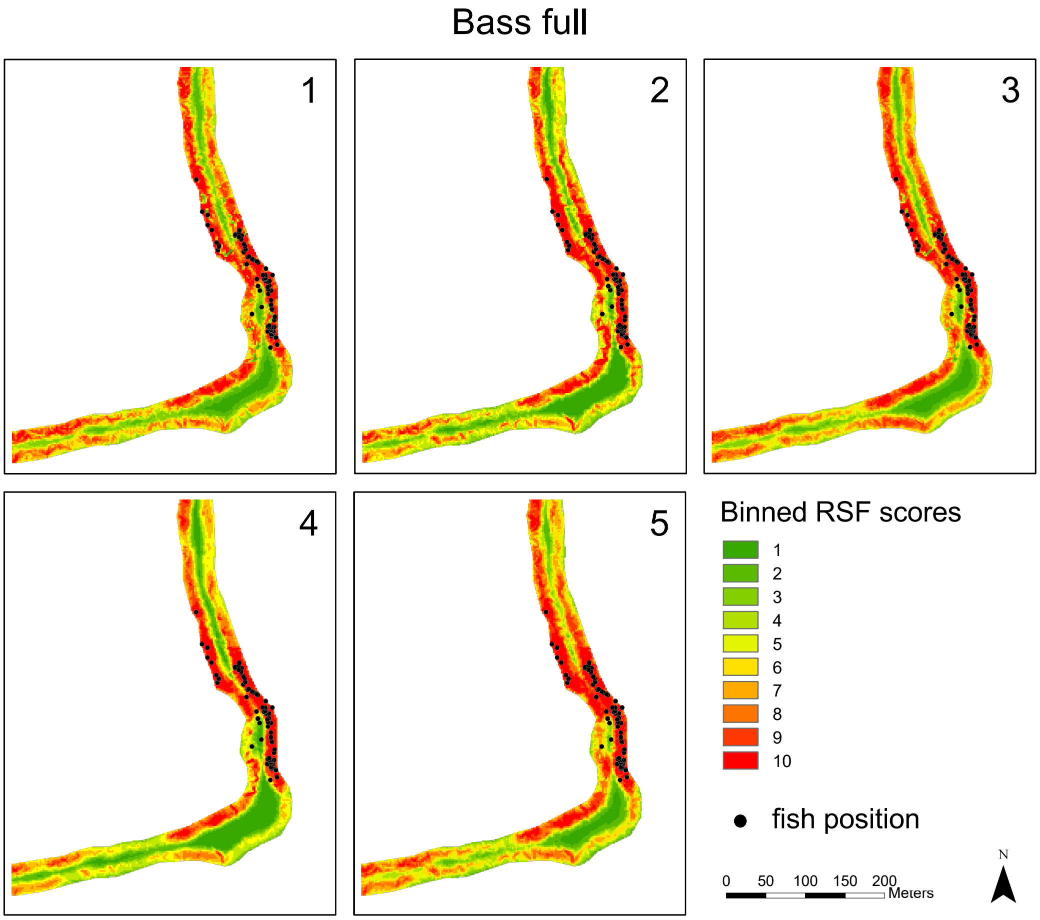
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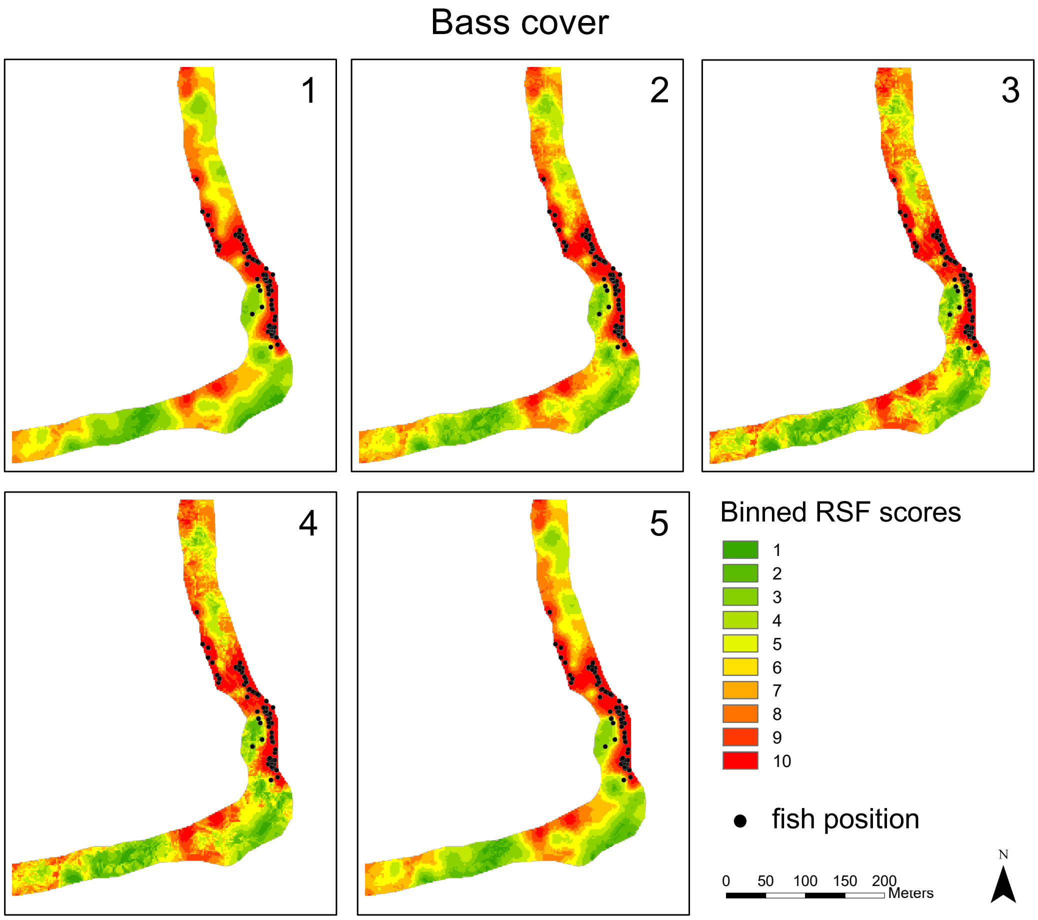
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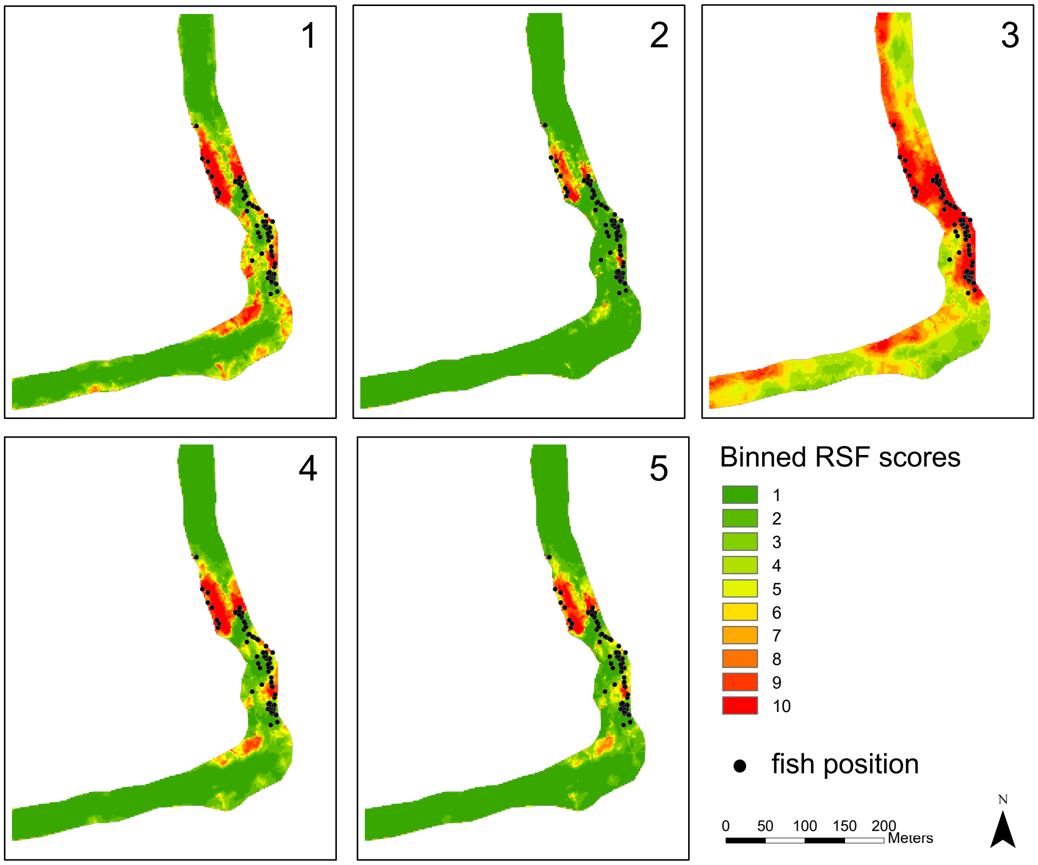
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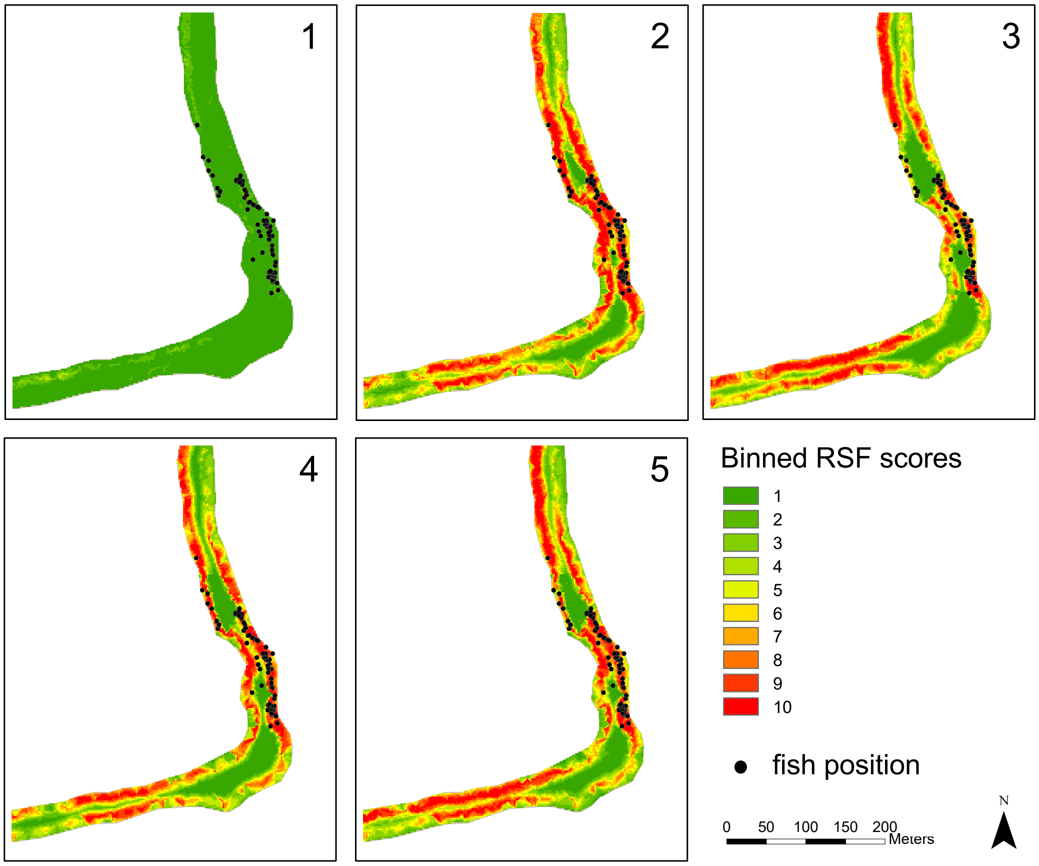
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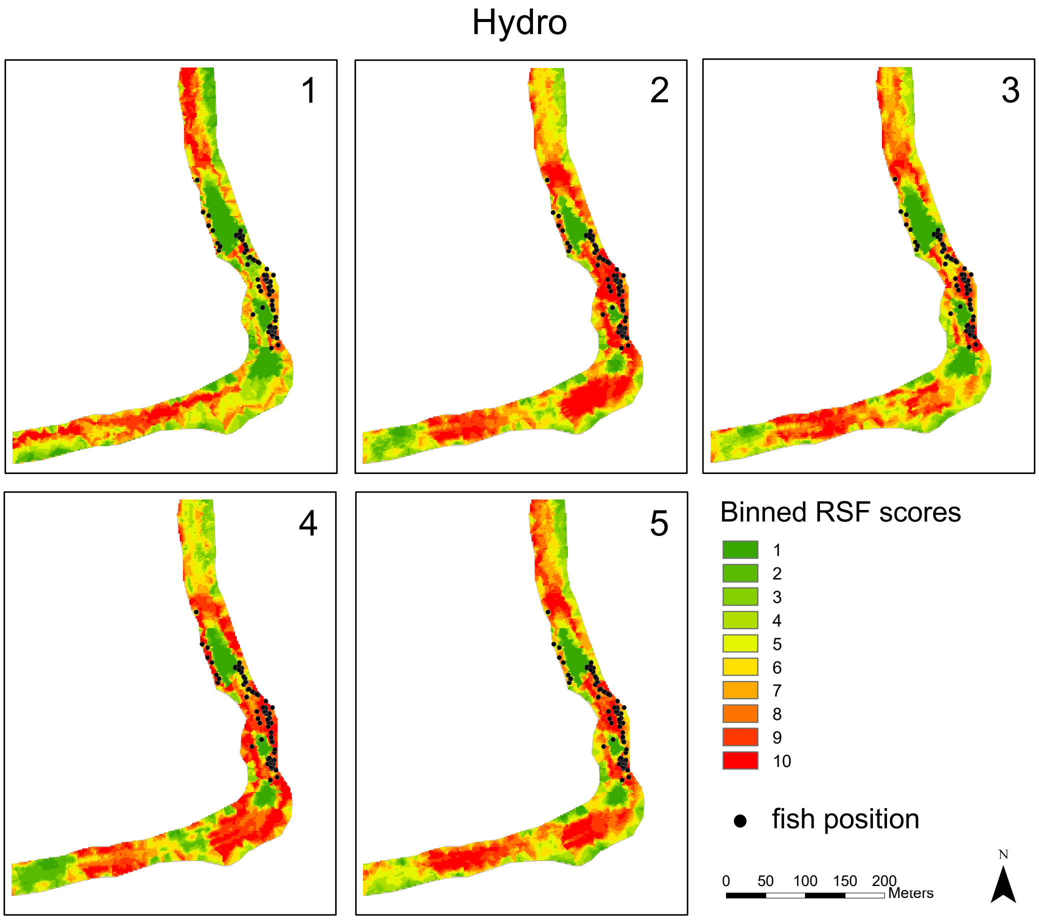
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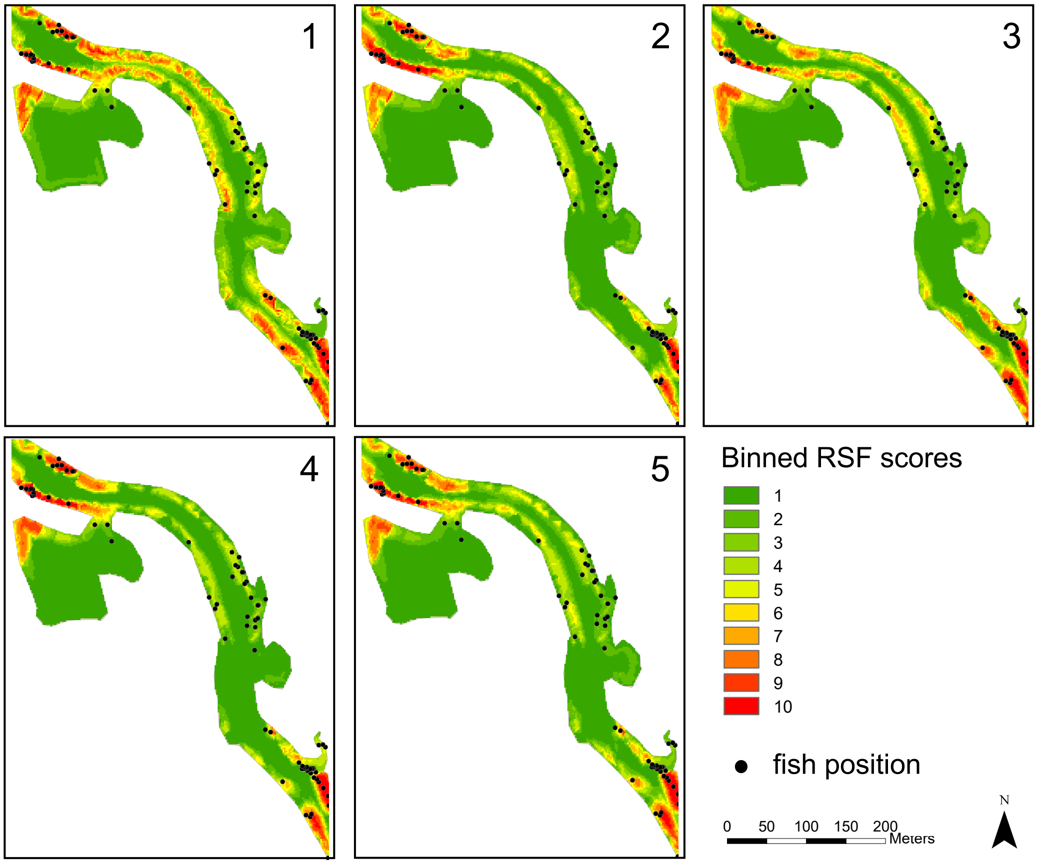

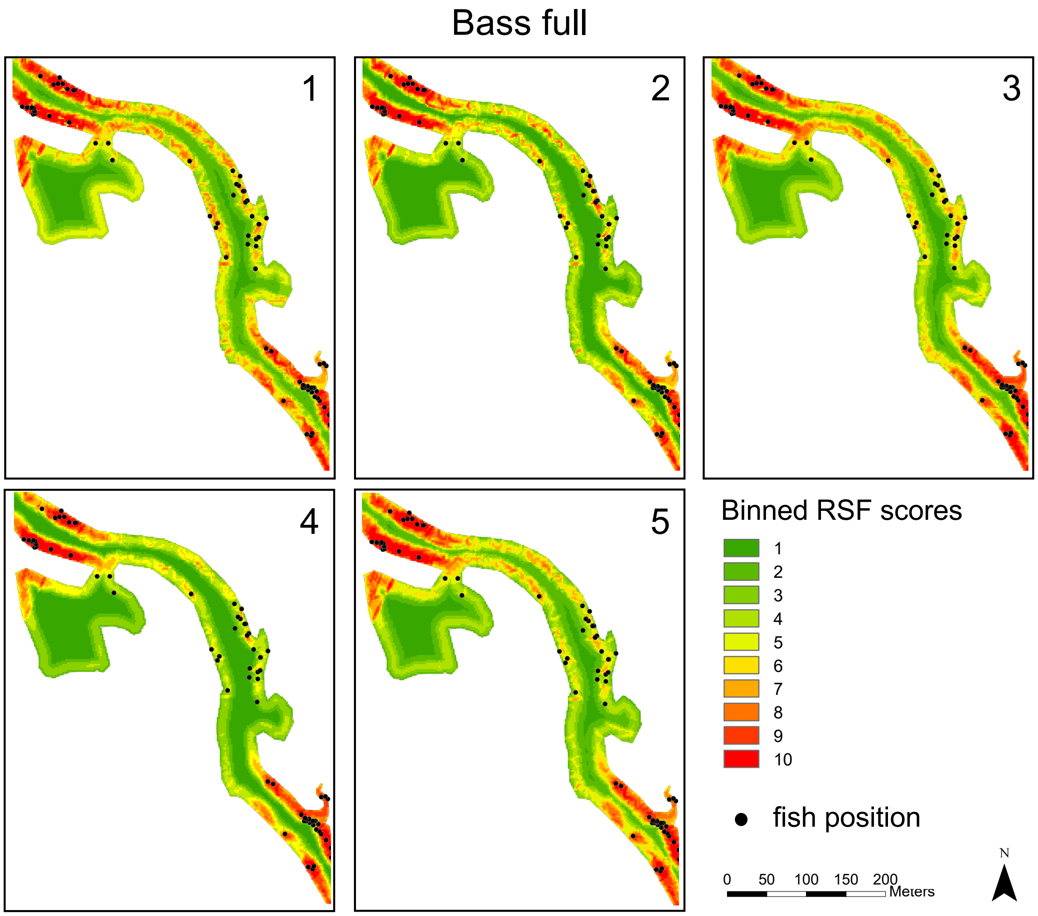
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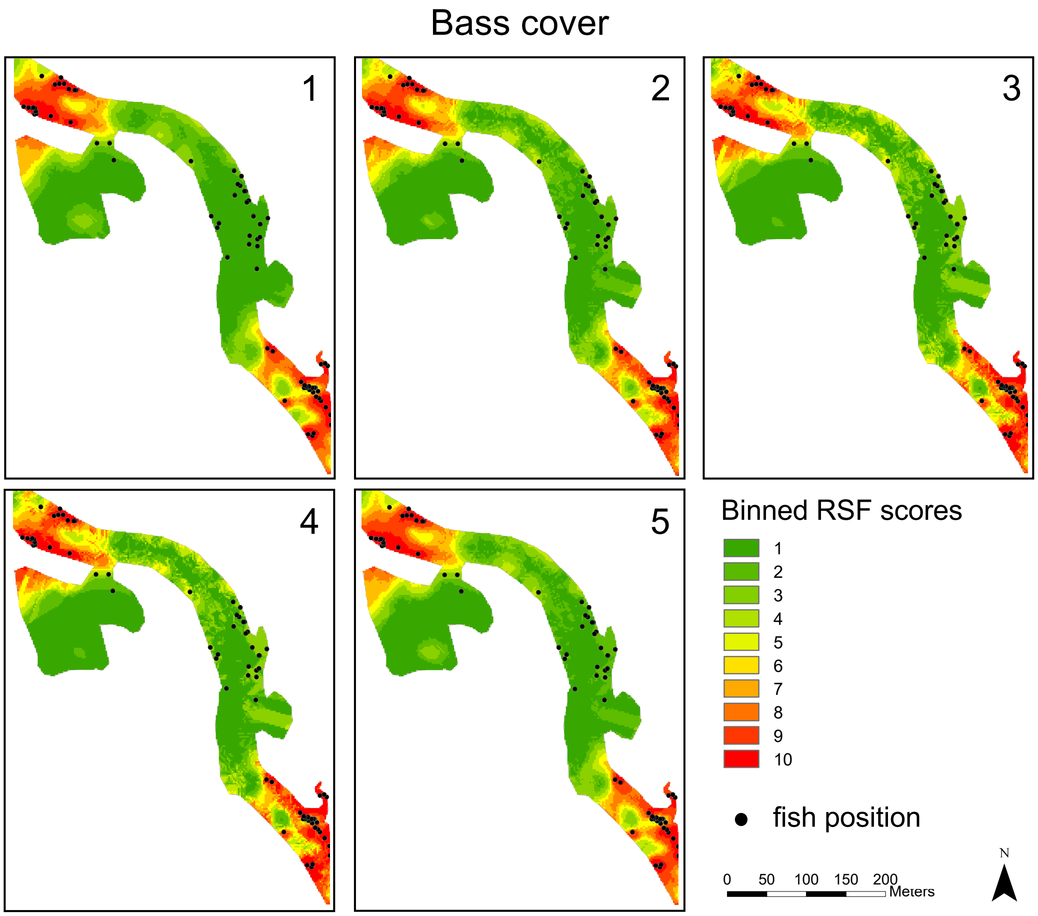

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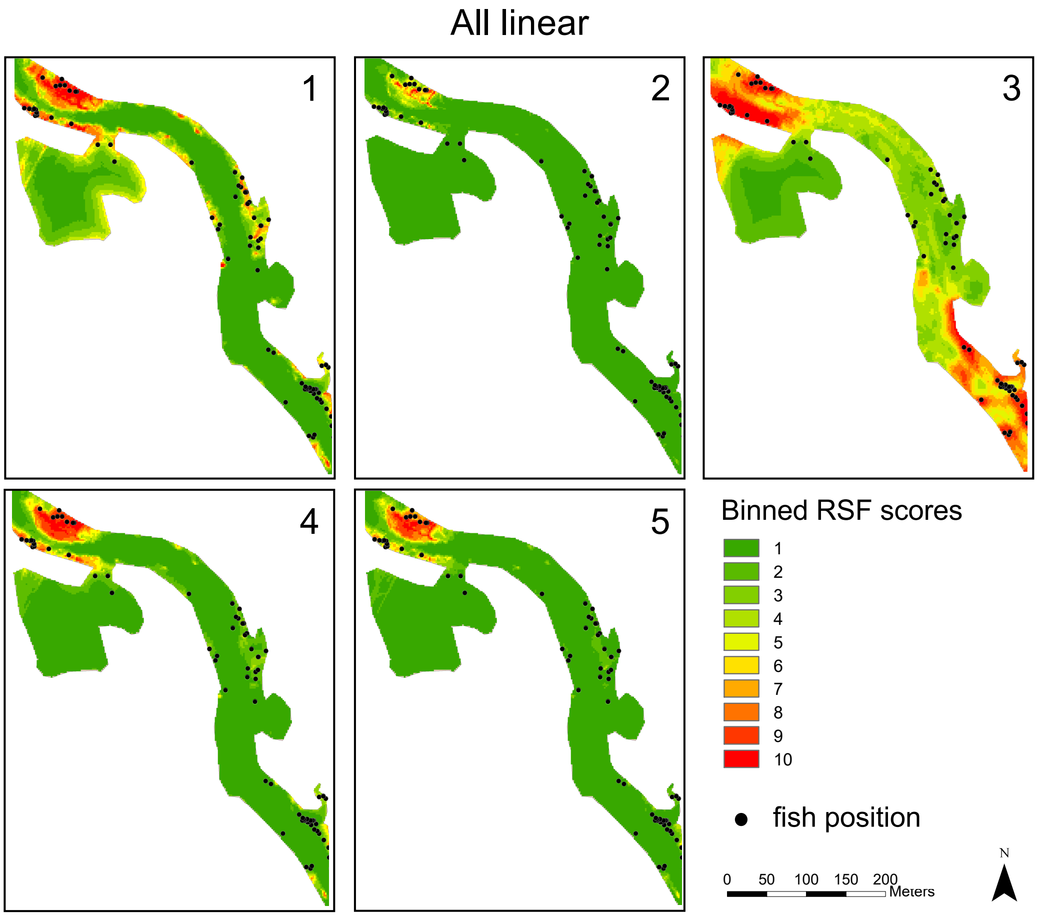
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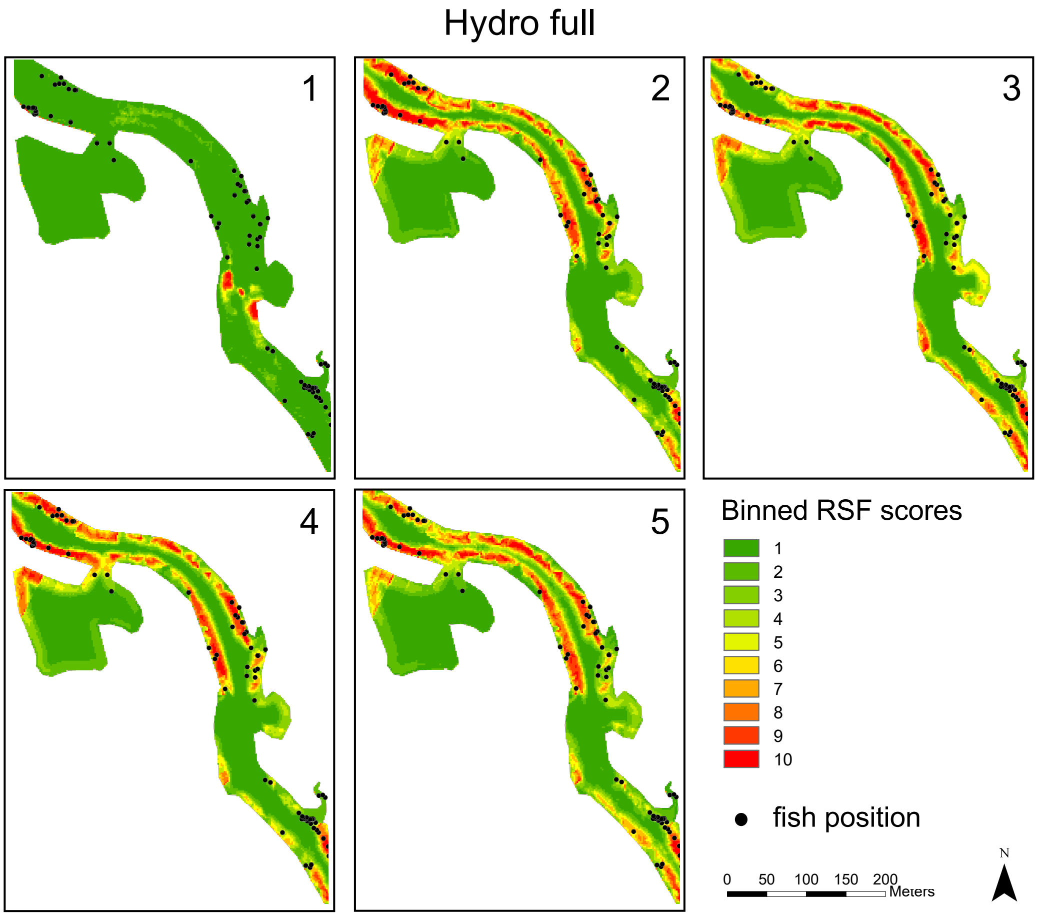
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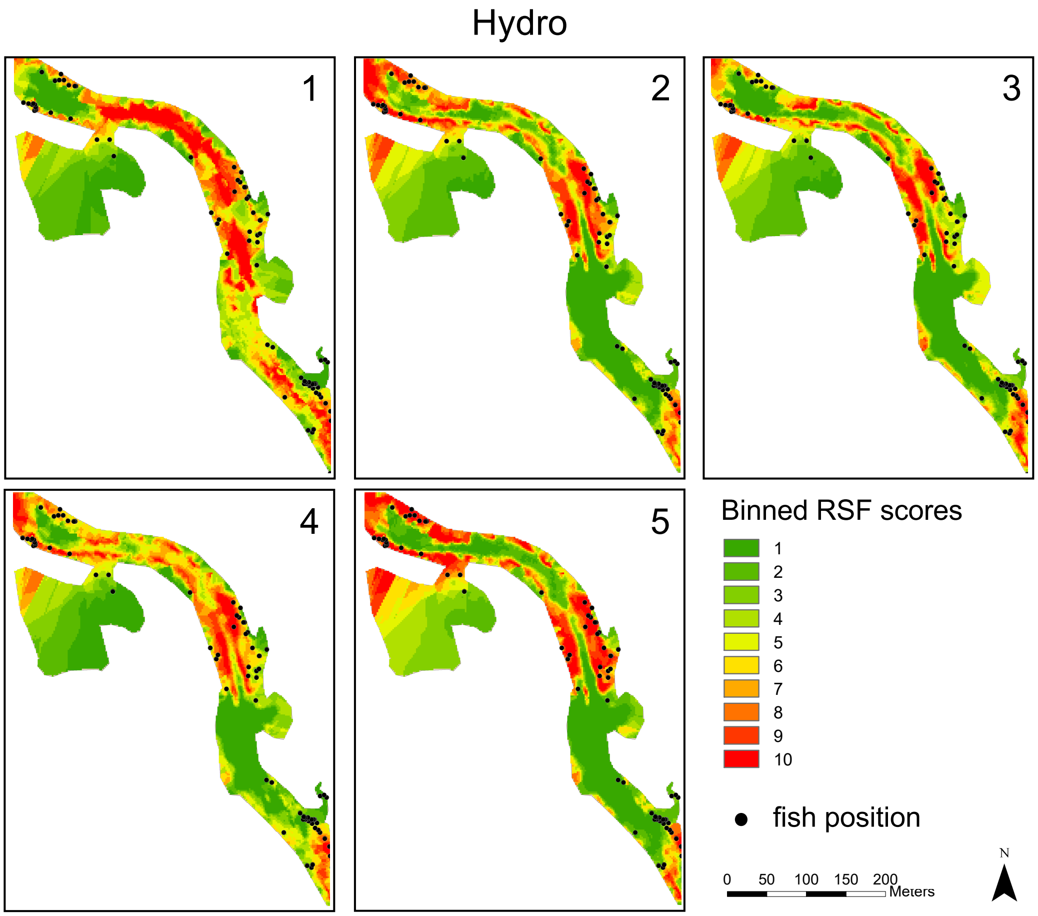
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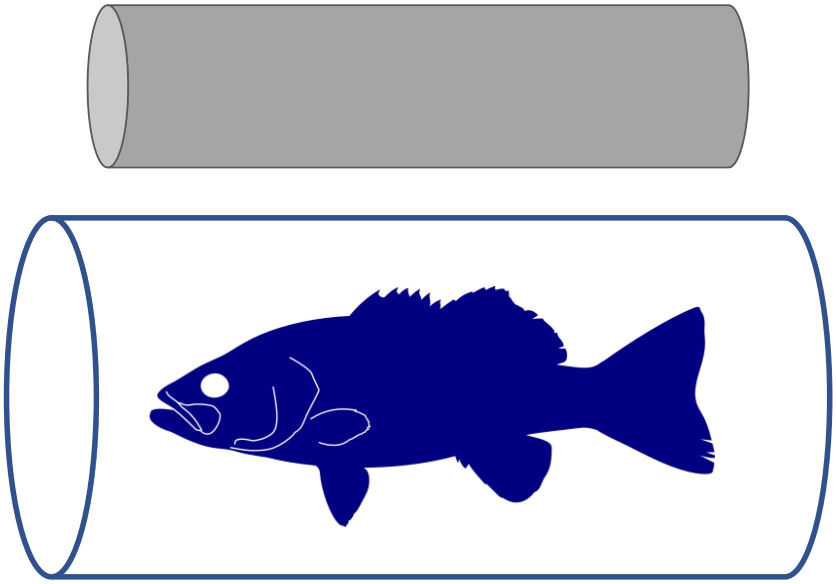

Chapitre 2 :

Est-ce que la présence de refuge influence les traits métaboliques d’un poisson téléoste?

Does shelter influence the metabolic traits of a teleost fish?

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Abstract

Availability of shelter is an important component of habitat selection for animals as it can influence survival (protection against harsh physical conditions and predation) and growth (energy acquisition and expenditure). Few studies address the effect of shelter on metabolic expenditures associated to non-mechanical tasks (excluding station holding or movement). The main goal of this study was to investigate the influence of shelter use on metabolic traits of smallmouth bass (*Micropterus dolomieu*) from two populations (Kiamika River and Lake Long). We conducted respirometry experiments on smallmouth bass to measure standard metabolic rate (SMR), resting metabolic rate (RMR), aerobic scope (AS), recovery time (RT), and excess post-exercise oxygen consumption (EPOC) in presence or in absence of shelter. Presence of shelter did not affect most metabolic traits, except for RMR, which was reduced in presence of shelter for Lake Long fish. Our results also show that larger fish had lower SMR in presence of shelter than when it was absent. When accounting for social hierarchy, there were no differences in most metabolic traits in dominant or subordinate fish in presence or absence of shelter, except for RT, which was significantly lower in presence of shelter for dominant fish. These results do not support the existence of an unequivocal relationship between individual metabolic traits and presence of shelter. If physiological motives may influence the use of shelter, sheltering in itself might not have important consequences on energy expenditures required for non-mechanical tasks.

Key words: energy expenditure, freshwater fish, habitat selection, recovery time, refuge

Introduction

The presence of shelter at a location has important implications for fitness and is therefore a key determinant of habitat selection for animals (Fukui 2001, Michaels and Preziosi 2015). Shelter use improves survival by providing protection from harsh physical conditions and predators (Hughes and Ward 1993, Tufto et al. 1996, Moreno et al. 1996, Millidine et al. 2006, Pollard 2006) and augments reproductive success by increasing progeny survival (Parsons and Chao 1983, Narvarte et al. 2013). Shelter use also has consequences for growth (Walsh and Downie 2005, Finstad et al. 2007), but its net effect depends on the balance between energy acquisition and expenditure (Lind and Cresswell 2005, Brownscombe et al. 2017).

Sheltering is generally thought to reduce energy acquisition due to a "hide and seek trade-off" between curtailed foraging when hiding from harsh physical conditions and predators, and improved foraging when seeking prey (Krause et al. 2000, Lind and Cresswell 2005). Some animals may incur starvation risks if sheltering limits time spent foraging (Hughes and Ward 1993, Krause et al. 2000, Lind and Cresswell 2005). Yet, other animals may augment their foraging efficiency by sheltering (e.g. ambush predators: Kevan and Greco, 2001; Tsairi and Bouskila, 2006). Some animals try to maximize energy acquisition resulting from the hide and seek trade-off by using habitat edges (Fagan et al. 1999). The consequences of sheltering on energy acquisition may depend on animal life stage, feeding strategy, and food availability (Krause et al. 1998, 2000, Ahrenstorff et al. 2009, Hafs et al. 2014).

Sheltering is also expected to reduce energy expenditure (Lind and Cresswell 2005). In particular, sheltering may reduce an animal's energy expenditure associated with conducting mechanical tasks (station holding or movement; e.g. swimming) in a fluid environment. In energetically costly landscapes like rivers, drift-feeding fish do station holding on coarse substrate relative to their size to minimize costs of locomotion and maximize food intake (Fausch 1984, Hafs et al. 2014). Sheltering may also reduce energy expenditure incurred by non-mechanical tasks such as maintaining the physiological integrity of animals (e.g. thermoregulation: Beck and Jennings, 2003; Seebacher and Alford, 2002) or replacing otherwise energetically demanding activities (e.g. camouflage, vigilance, alertness: Lind and Cresswell, 2005; Millidine et al., 2006). No matter if animals seek shelter to lower energy expenditures (e.g. station holding or movement) or if sheltering has consequences on their physiology (e.g. reduce metabolic costs), this relationship between energy expenditure and sheltering merits further investigation.

Energy expenditures incurred by non-mechanical tasks are largely studied by estimating standard metabolic rate (SMR), the minimal energy expenditure required to sustain the life of a post-absorptive ectotherm, like a fish, at a given temperature (Fry 1971, Clark et al. 2013, Chabot et al. 2016). Resting metabolic rate (RMR) is another baseline measure of metabolism that may include low levels of spontaneous activity (Jobling 1994, Burton et al. 2011). A number of studies have identified that, for given physical and chemical conditions, shelter may reduce SMR or RMR of fish by 8 to 30% (Fischer 2000, Finstad et al. 2004, Millidine et al. 2006, Norin et al. 2018) even when mechanical tasks and intra- and inter-specific interactions are absent. Shelters may replace the need for camouflage or vigilance, which may have associated metabolic costs, to remain undetected (Millidine et al. 2006). Relatedly, in the absence of shelter, an increase in metabolic costs could be expected due to increased vigilance rates and mental alertness (Lind and Cresswell 2005). This further emphasizes the importance of shelter for fish fitness as, everything else being similar, a reduction in SMR or RMR increases energy availability for growth and reproduction. Yet, it may be hypothesized that other physiological traits may improve our understanding of the importance of shelter on animal fitness.

Aerobic scope (AS) is the difference between maximum metabolic rate (MMR: the maximum energy expenditure that can be incurred by an animal; Fry, 1971; Norin and Clark, 2016) and SMR. AS corresponds to the animal's metabolic range for aerobic activities (Fry 1971). Thus, AS may have long-term consequences on growth and reproduction. This perspective is consistent with the suggestion that AS may be a useful fitness indicator for fish (Claireaux and Lefrançois 2007, Farrell et al. 2008). High MMR and/or low SMR may allow fish to have a larger scope for aerobic activity above maintenance levels, depending if this fish's AS is more driven by MMR or SMR (Clark et al. 2013). The potential for shelter to increase AS through its effect on SMR has important implications for our understanding of the determinants of habitat selection, especially for fish.

Recovery time (RT) represents the delay for metabolic rates to return to SMR from exhaustive exercise, and excess post-exercise oxygen consumption (EPOC) is the amount of oxygen required to recover from MMR (Hancock and Gleeson 2008). Long RT and high EPOC constitute metabolic traits that can limit an animal's capacity to resume or perform repeated mechanical tasks and thus have important fitness consequences (Zeng et al. 2010). It has been demonstrated that RT correlates positively to vigilance in fish, suggesting that energy expenditure incurred by vigilance increases RT after exercise (Killen et al. 2015). Since sheltering may replace the need for vigilance, it might be hypothesized that shelter use may reduce RT. In an experiment on lizard metabolic recovery, Hailey et al. (1987) observed that lizards (*Podarcis spp.*) recovering from exercise used shelters for longer durations than unexercised lizards. It is unclear if exhausted lizards used shelter longer because they did not recover enough to engage in new activity or if sheltering was beneficial for their recovery. These studies nevertheless lead to the hypotheses that shelter use may affect RT and EPOC.

The main objective of this study was to quantify the effects of the presence of shelter on five metabolic traits in fish: SMR, RMR, AS, RT, and EPOC. Since metabolic traits may vary within species due to population-level physiological adaptations to local environmental conditions (Burton et al. 2011, Eliason et al. 2011, Metcalfe et al. 2016), we quantified the effects of the presence of shelter on metabolic traits of smallmouth bass (*Micropterus dolomieu*, Lacépède) collected from two populations with contrasting ecosystems (i.e., a river and lake). We hypothesized: 1) that SMR and RMR would be lower in the presence of shelter; 2) that AS would be higher in the presence of shelter; 3) that RT and 4) EPOC, would be reduced in the presence of shelter, and; 5) that the effects of shelter on metabolic traits of fish from the two populations would be similar.

Methods

Study species

We studied the effects of the presence of shelter on metabolic traits of smallmouth bass from a river (Kiamika River; 46.61631, -75.21021) and a lake (Lake Long; 45.99755, -74.00023) situated in the Laurentians region (Quebec, Canada). Smallmouth bass naturally dwell in rivers and lakes, which provides the opportunity to test individuals of the same species that differ in the energetic challenges they face in their natural habitat. These fish are also known to use submerged structures (e.g. sunken logs, big rocky substrate, macrophytes) that serve as shelter in rivers, lakes, and reservoirs (Coble 1975, Warren 2009), but the effect of such structures on SMR, RMR, AS, RT, and EPOC remains to be tested.

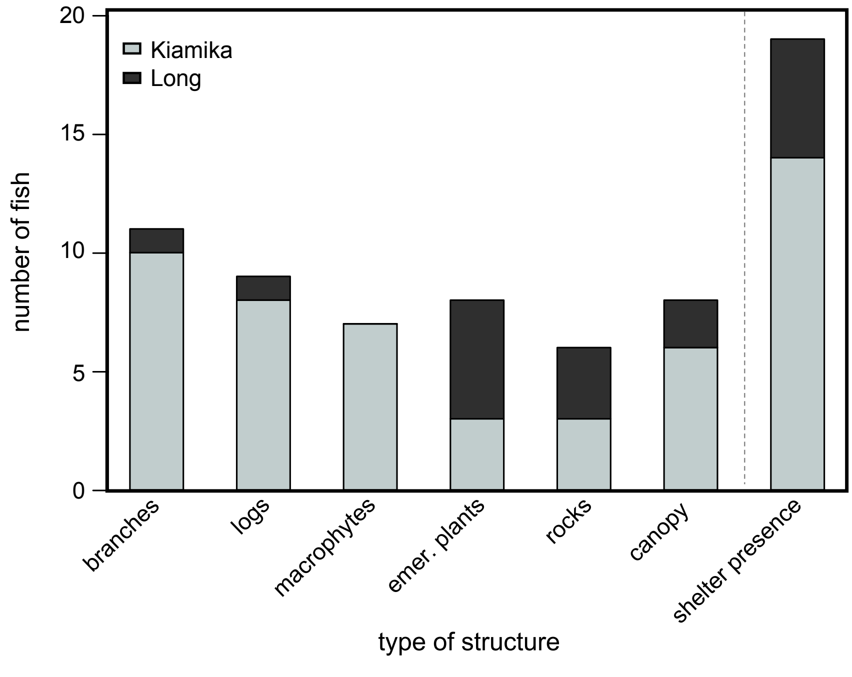

Figure 1: Type of sheltering structures found near smallmouth bass *Micropterus dolomieu* capture locations in Kiamika River (gray) and Lake Long (black). Each bar represents the number of fish captured near each type of structure and the far right bar shows the total number of fish captured near any sheltering structure.

Fish capture and holding

We captured smallmouth bass from Kiamika River and Lake Long by angling using barbless circle hooks to minimize injuries (Cooke and Suski 2005) between 25-Jun and 3-Aug 2018. All fish (except one individual from Lake Long) were captured within 5 meters of structures that could be used as shelter (e.g. logs, emergent plants, rocks; Figure 1). We transported fish captured in Kiamika River by truck to Station de biologie des Laurentides (SBL) affiliated to Université de Montréal in insulated containers filled with oxygenated river water (175 km, approx. 2.5-hour drive). The use of insulated containers ensured water temperature did not vary during transport, and dissolved oxygen was maintained at air saturation (>95%) with air-bubblers connected to a deep cycle battery. Lake Long is on SBL territory, thus we transported by boat fish captured in that lake to the laboratory in the same type of containers (approx. 500 m, 15-min ride). All fish were given a tag with visual implant elastomer (Northwest Marine Technology, Anacortes, WA, USA) for later identification of individuals for respirometry experiments.

Holding conditions consisted in two large opaque flow-through tanks (2.1 m x 0.6 m x 0.6 m, 0.7 m^3 total, 0.6 m^3 of water) that could be separated in three sections with dark mesh dividers. A maximum of 8 fish were held in each tank at the same time and dividers were added to separate fish by size and population. Holding tanks were continuously supplied with filtered and UV-treated freshwater pumped from Lake Croche (adjacent to the laboratory on SBL territory), at a rate of 0.14 m^3 hr^{-1}, which allowed complete water replacement every 4 hours. Dissolved oxygen was maintained at air saturation (>95%) with a recirculating pump and air-bubblers. Acclimation temperature was set at 20°C, which corresponds to the average temperature measured in smallmouth bass locations in Kiamika River for a separate telemetry study (unpublished data), and is comprised within the summer thermal regime of both populations. Water temperature was maintained at 20°C by adjusting the water intake level in the lake (Table 1). Fish were held at an ambient light regime (14h day / 10h night). Large opaque plastic tubes (30 cm long, 10 cm in diameter) were available for fish to hide in holding tanks (one tube per fish). Fish were fed small minnows daily, but were starved for 48h prior to respirometry experiments. All fish were held for three or four days before the first respirometry experiment was conducted.

Table 1: Holding conditions of smallmouth bass *Micropterus dolomieu* at Station de biologie des Laurentides (Quebec, Canada). Water temperature and dissolved oxygen were measured twice daily during summer 2018. For each variable, values presented are mean ± standard deviation.

Variable	Basin 1	Basin 2
water temperature (°C)	19.8 ± 0.5	19.7 ± 0.5
dissolved oxygen (mg l^{-1})	8.7 ± 0.3	8.7 ± 0.2
dissolved oxygen (% air saturation)	98.8 ± 2.3	99.0 ± 2.0

Respirometry experiments

We calculated fish metabolic rates using estimates of oxygen consumption rates, which are taken to represent accurate measures of overall aerobic metabolism (Fry and Hart 1948, Cech 1990). Oxygen consumption rates ($\dot{M}O_2$: mg O_2 hr^{-1}) were estimated using intermittent flow-through respirometry equipment and software (Loligo Systems, Tjele, Denmark). The respirometry set-up comprised four rectangular chambers (37.5 cm x 14.7 cm x 12.7 cm; chamber + tubing volume: 5.45 l) submerged in large coolers (hereafter water basin) (78 cm x 33 cm x 36 cm, 80 l of water) supplied constantly with filtered and UV-treated freshwater. Each chamber was fitted with two sets of airtight tubing and water pumps, the first forming a closed circulation loop on which an oxygen probe was connected, the second allowing a complete flushing and refreshing of water inside the chambers. Flush pumps were automated to run for 7 minutes of every 12-min loop. Dissolved-oxygen levels were maintained above 80% at all times with the constant supply of freshwater and air-bubblers in the water basin. Temperature in the water basin was controlled with a Pt100 temperature probe and TMP-REG instrument (Loligo Systems, Tjele, Denmark) relayed to a hot and a cold water bath. Water temperature was held at 20 °C during all respirometry experiments.

We tested the effect of shelter on SMR, RMR, AS, RT, and EPOC by conducting respirometry experiments while any given fish was held in a chamber covered (treatment "with shelter") or not covered (treatment "without shelter") with the same type of plastic tube as available in holding tank. We assigned treatment order randomly and respirometry experiments conducted for a given fish under different treatments were separated by 3 days, during which fish were returned to their holding tank. All but four fish (two from each population) were tested in both conditions (presence or absence of shelter). One trial involving two fish was interrupted by a power outage due to a storm. Two fish also had to be removed because they were fed by mistake before the trial. Our final dataset comprises 36 observations on 14 and 6 smallmouth bass from Kiamika River and Lake Long, respectively.

Each respirometry experiment started mid-day (~ between noon and 3pm) with a 3:30-minute chase + 1-minute air exposure protocol to induce fish exhaustion following the method described in Roche et al. (2013). Chase duration was set to 3:30 minutes after a pilot experiment on a different sample of smallmouth bass from the two study populations. Recording of oxygen consumption started immediately after transferring the fish into the chambers and continued until oxygen consumption stabilized. Respirometry experiments lasted 21 ± 2 hours (mean ± standard deviation). Within an hour before the onset – and after the termination – of each respirometry experiment, background oxygen consumption (BO_2) was recorded in the empty chamber by a single 20-min long measurement. During the experiments, fish were exposed to the same ambient light regime (14h day / 10h night) as during holding. After experiments, fish were euthanized with clove oil. This research was conducted with the approval of Université de Montréal's animal care committee (CDEA 18-032) and Canadian Council on Animal Care.

Calculations of metabolic traits

BO_2 was subtracted from $\dot{M}O_2$ measurements, assuming a linear change in $\mathrm{BO_2}$ over time. We adjusted metabolic rates ($\dot{M}O_{2\mathrm{adj}}$) to the mean body mass of our sample

(0.152 kg) using the slope *b* of the log-log relationship between $\dot{M}O_2$ and mass (eq.1, Steffensen *et al.*, 1994; Ultsch, 1995). There was no interacting effect of population on the log-log relationship between $\dot{M}O_2$ and mass ($p_{pop \times mass}$= 0.829 and $p_{pop \times mass}$= 0.293 for SMR and MMR, respectively), thus Kiamika River and Lake Long fish shared the same slopes *b* of increase in $\dot{M}O_2$ with mass (SMR: *b*= 0.810, R^2_a= 0.958; MMR: *b*= 0.785, R^2_a= 0.857).

$$\dot{M}O_{2\text{adj}} = (\text{mean fish mass})^{b-1} \text{ x } (\text{individual fish mass})^{1-b} \text{ x individual fish } \dot{M}O_2 \quad \text{(eq.1)}$$

We estimated SMR (mg O_2 kg^{-1} hr^{-1}) using the 0.2 quantile of the $\dot{M}O_2$ data with the package *fishMO2* in R (Chabot 2016, Chabot et al. 2016, R Foundation for Statistical Computing 2018). SMR was estimated over a distribution of, on average, 47 $\dot{M}O_2$ values (from 21 to 73 $\dot{M}O_2$ values). The range of data used for its calculation started when $\dot{M}O_2$ stabilized to a minimum level. In our study, this minimum level generally occurred during the night and ended at sunrise, the moment at which fish activity and respiration started to rise. If the effect of shelter on metabolism requires that an individual be visually hidden, it may be hypothesized that the effect of shelter on SMR estimated during the night (when it is dark) may be difficult to assess. We estimated resting metabolic rate (RMR) as the minimum metabolic rate during day-time (after 7:30 am until the end of the experiment) using the same 0.2 quantile method. RMR was determined over a distribution of, on average, 13 $\dot{M}O_2$ values (from 4 to 33 $\dot{M}O_2$ values). MMR (mg O_2 kg^{-1} hr^{-1}) was estimated as the highest rate of oxygen consumption recorded over any 12-min loop. We calculated AS (mg O_2 kg^{-1} hr^{-1}) as the difference between MMR and SMR. Recovery time (RT) was the duration (in minutes) required until $\dot{M}O_2$ levels stabilized to SMR. Excess post-exercise oxygen consumption (EPOC; mg O_2 kg^{-1}) is the amount of oxygen required to recover from MMR and was calculated as the area under the $\dot{M}O_2$ curve estimated by the sixth-order polynomial recovery function, until the values of the curve were equal to SMR (Killen et al. 2014).

Statistical analyses

All data analyses were computed in R v. 3.5.1 (R Foundation for Statistical Computing 2018). We used linear mixed models (LMM) with the package *lme4* (Bates et al. 2014) to test the effects of shelter and population on all metabolic traits. Linear mixed models are appropriate tools to deal with non-independence in data such as repeated measures on the same individual (Zuur et al. 2009). Fish ID and chamber number were included as potential random effects. Fish body mass, experimental order, and all two-way interaction terms were included as fixed effects in case they contributed to variation in metabolic traits, but dropped from models if non-significant. For each metabolic trait, we created a full model with all descriptors and their interaction, as well as both random effects. First, the best random structure was selected based on the smallest Akaike information criterion (AIC), then the fixed effects component was simplified by backward elimination (Zuur et al. 2009). In all cases, the only random effect retained in models was fish ID. For each model, marginal R^2 (R^2_m: proportion of variance explained by fixed effects) and conditional R^2 (R^2_c: proportion of variance explained by fixed and random effects) were obtained from the models fitted through restricted maximum likelihood analysis. The difference between R^2_c and R^2_m for each model represent variability among individual fish. Model assumptions were confirmed by visual inspection of residual-fits plots.

Results

Metabolic traits varied by 10% (EPOC) to 38% (AS) among combinations of treatments and populations (Table 2). SMR of smallmouth bass from Lake Long was 20% higher than that of Kiamika River fish ($p < 0.001$; Figure 2) but did not vary with presence of shelter ($p = 0.709$; Table 3). Despite metabolic rates being adjusted to fish mass, SMR was significantly affected by the interaction between fish mass and treatment ($p = 0.021$; Table 3): there was no relationship between SMR and mass in the treatment with shelter while SMR increased with fish mass in absence of shelter (Table S1; Figure

S1). SMR was negatively related to experiment order (*p*= 0.034; Table 3; Table S1): rates were on average 6% lower during the 2nd experiment. RMR was 18% higher for fish from Lake Long than for fish from Kiamika River (*p*< 0.001; Figure 2). There was an interacting effect of treatment and population on RMR (*p*= 0.044; Table 3): RMR was 9% higher for Lake Long fish in absence of shelter than in its presence but treatment had no significant effect on RMR for Kiamika River fish (Figure 2). RMR was negatively related to experiment order (*p*= 0.043; Table 3; Table S1). The estimates were 5% lower during the 2nd experiment. LMMs explained a total of 75.3% and 59.3% of SMR and RMR variation, respectively, and most of it was associated to fixed effects (50.3% and 44.1% for SMR and RMR, respectively; Table 3).

Table 2: Metabolic traits of smallmouth bass *Micropterus dolomieu* estimated by respirometry experiments for each combination of treatments and populations (mean ± standard error). SMR, RMR, MMR, and AS are adjusted to the mean body mass of our sample (0.152 kg).

Response	Kiamika		Long	
variable	with shelter	without shelter	with shelter	without shelter
SMR ($mg\ O_2\ kg^{-1}\ h^{-1}$)	98.43 ± 9.83	94.43 ± 9.95	115.68 ± 14.00	116.00 ± 10.81
RMR ($mg\ O_2\ kg^{-1}\ h^{-1}$)	101.63 ± 10.02	98.98 ± 12.64	114.12 ± 13.57	124.15 ± 14.52
MMR ($mg\ O_2\ kg^{-1}\ h^{-1}$)	285.27 ± 48.90	296.83 ± 48.70	242.01 ± 57.75	260.35 ± 40.39
AS ($mg\ O_2\ kg^{-1}\ h^{-1}$)	186.84 ± 46.53	202.40 ± 47.77	126.33 ± 48.90	144.36 ± 39.61
RT (minutes)	402.00 ± 123.12	447.31 ± 132.39	529.20 ± 128.75	503.80 ± 232.93
EPOC ($mg\ O_2\ kg^{-1}$)	379.90 ± 141.11	415.37 ± 162.87	424.83 ± 72.93	389.08 ± 156.31

MMR was on average 16% higher in Kiamika River fish than in fish from Lake Long (Table 2, Figure 2) but this difference was not significant (*p*= 0.057; Table 3). MMR did not vary with presence or absence of shelter (*p*= 0.320). AS of smallmouth bass from

Lake Long was 30% lower than that of Kiamika fish (*p*= 0.004; Table 3, Figure 2) but did not vary with presence of shelter (*p*= 0.212; Table 3). LMMs explained a total of 61.7% and 69.6% of MMR and AS variation, respectively, and most of it was associated to the random effect (47.9% and 40.1%, respectively; Table 3).

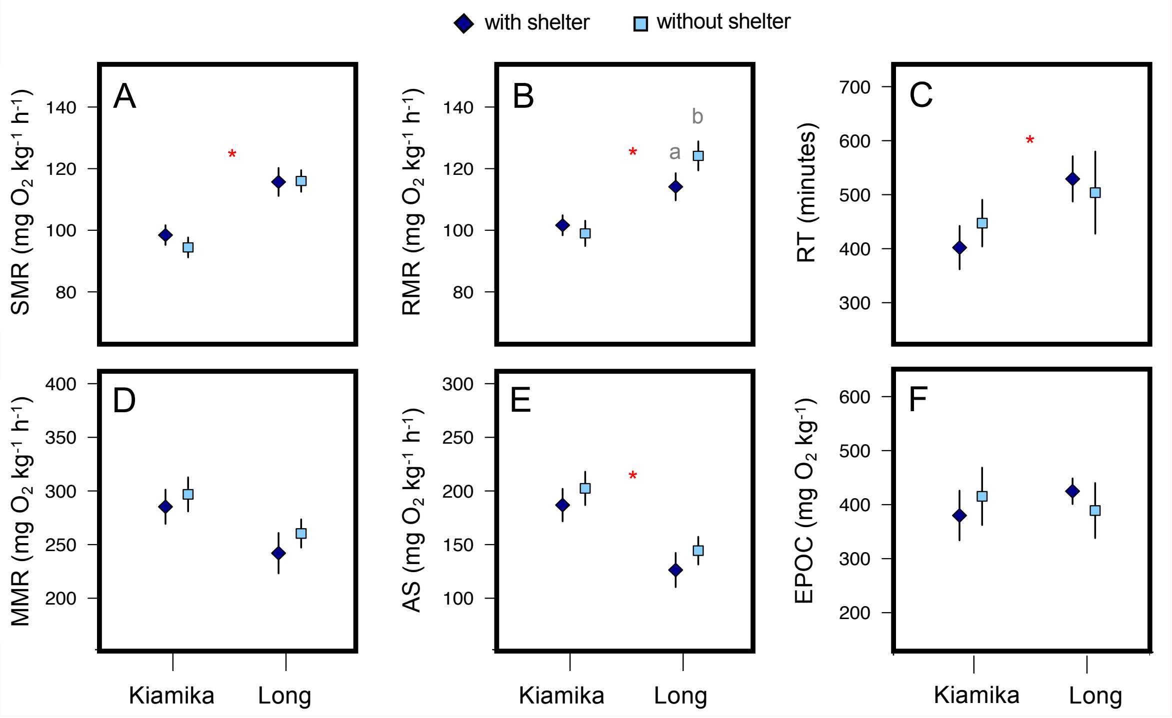

Figure 2: Mean ± standard error values of a) standard metabolic rate (SMR), b) resting metabolic rate (RMR), c) maximum metabolic rate (MMR), d) aerobic scope (AS), e) recovery time (RT), and f) excess post-exercise oxygen consumption (EPOC) of smallmouth bass *Micropterus dolomieu* from Kiamika River and Lake Long during respirometry experiments in presence (dark diamonds) or in absence of shelter (light squares). Red asterisks and grey letters indicate significant differences between populations and treatments, respectively.

Table 3: Results of linear mixed models relating metabolic traits of smallmouth bass *Micropterus dolomieu* to mass, treatment, population, experiment order, and interactions between these variables. Random effect of fish ID was included in models. R^2_m is the marginal R^2 (proportion of variance explained by the fixed effects) and R^2_c is the conditional R^2 (proportion of variance explained by the fixed and the random effects).

Response	Effect	Chi-square	d.f.	p-value	R^2_m	R^2_c
SMR	Mass	1.7361	1	0.1876	0.503	0.753
	Treatment	0.1389	1	0.7094		
	Population	19.0737	1	0.0001***		
	Order	4.4994	1	0.0339*		
	Treatment * mass	5.3495	1	0.0207*		
RMR	Mass	1.0831	1	0.2980	0.441	0.593
	Treatment	0.6140	1	0.4333		
	Population	14.2823	1	0.0002***		
	Order	4.1087	1	0.0427*		
	Treatment * mass	3.5399	1	0.0599		
	Population * treatment	4.0625	1	0.0438*		
MMR	Treatment	0.9872	1	0.3204	0.138	0.617
	Population	3.6159	1	0.0572		
AS	Mass	0.0592	1	0.8078	0.295	0.696
	Treatment	1.5567	1	0.2121		
	Population	8.4447	1	0.0037**		
	Treatment * mass	2.7546	1	0.0970		
RT	Mass	11.9141	1	0.0006***	0.475	0.58
	Treatment	2.3985	1	0.1214		
	Population	3.9285	1	0.0475*		
	Order	5.3229	1	0.0210*		
	Population * order	5.3196	1	0.0211*		
EPOC	Mass	17.809	1	<0.0001***	0.467	0.689
	Treatment	1.1704	1	0.2793		
	Population	0.0599	1	0.8066		
	Order	1.1205	1	0.2898		
	Order * mass	6.7581	1	0.0093*		

RT varied among populations, fish from Lake Long showing on average 18% longer RT than fish from Kiamika River (*p*= 0.048; Table 3, Figure 2). RT did not vary with treatment (p= 0.121; Table 3, Figure 2) but was negatively related to fish mass (p< 0.001; Table 3; Table S1). RT was influenced by the interaction between population and experiment order (p= 0.021; Table 3): RT was 17% shorter for all fish on the 2nd compared to the 1st experiment but, during the 2nd experiment, fish from Lake Long recovered 5% faster than fish from Kiamika River (Table S1). EPOC did not vary between populations nor across treatment (Table 3), but was negatively related to fish mass (p< 0.001; Table 3; Table S1). EPOC was also influenced by the interaction between experiment order and fish mass: slope of decrease of EPOC with fish mass was steeper during the 2nd experiment (p= 0.009; Table 3; Table S1). Most of the variation in RT and EPOC was explained by fixed effects of the LMMs (47.5% and 46.7%, respectively), and total variation explained was of 58% and 68.9%, respectively (Table 3).

Dominance

The experimental and statistical design used in this study were based on the assumption that all experimental fish were similar except for their mass and population. However, observations in the holding tanks suggest that some fish may have potentially been characterized as subordinate or dominant. Dominance in a fish was determined as exhibition of aggressive behaviour (e.g. pecking, chasing) towards other fish. A fish was identified as “subordinate” if it was subjected to pecking, chasing, etc. When aggressive behaviour was not witnessed in a group of fish, each fish dominance was defined as “unknown”. We acknowledge that these characterizations of dominance are simplistic, as we did not design our study to measure dominance ranks. We decided nonetheless to test if the effect of shelter on metabolic traits would be influenced by dominance status identified in our sample. No dominant behaviour could be identified for any fish from Lake Long, and it could not be assessed for two fish of the Kiamika River. Therefore, the dataset for dominance comprises 12 fish only from Kiamika River (5 dominants, 7 subordinates).

Dominant (0.08-0.23 kg) and subordinate (0.05-0.25 kg) fish were of similar size range. Dominance had no significant effect on metabolic traits (Table S2, Figure 3).

Metabolic traits did not vary in presence or absence of shelter for either dominant or subordinate fish, except for RT. Dominant fish had 26% shorter RT in presence of shelter than in its absence (p= 0.050; Table S2, Figure 3). Comparison of R^2_c and R^2_m for each model using this dominant-subordinate subset of data reveals different trends than that of models created with the full data set for SMR and RMR (Table S2). For this subset, individual fish accounted for 52.7 and 31.1% of explained variation in SMR and RMR, respectively. In comparison, 25% and 15.2% of explained variation in SMR and RMR was attributable to individual fish in the full dataset (Table 3).

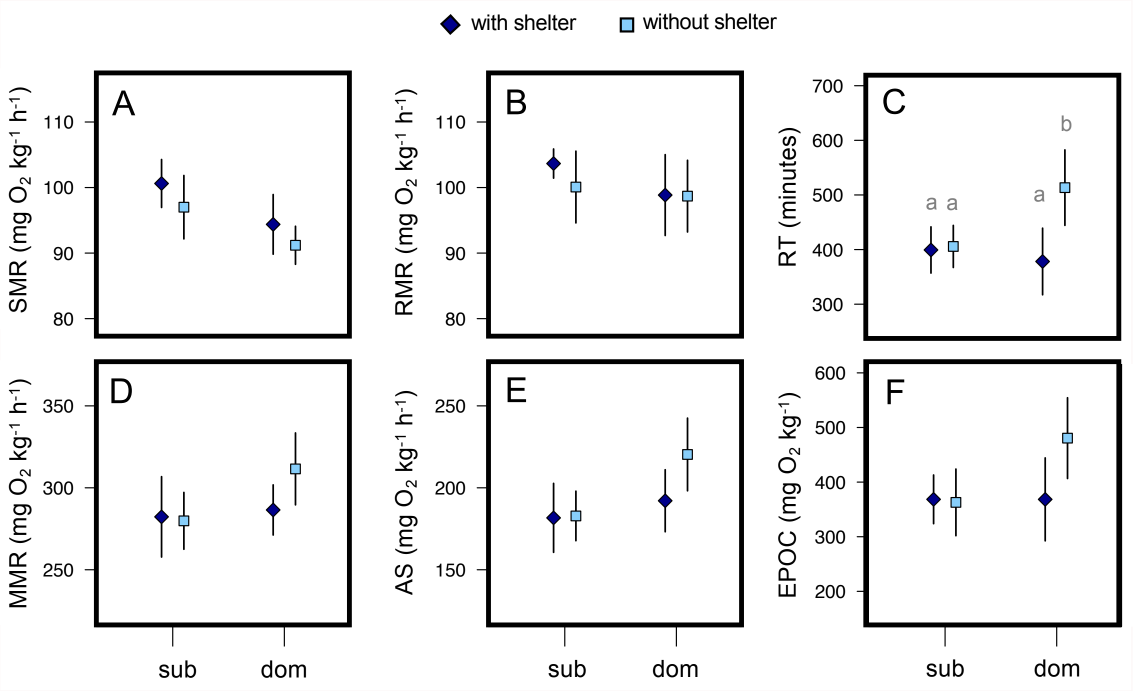

Figure 3: Mean ± standard error values a) standard metabolic rate (SMR), b) resting metabolic rate (RMR), c) maximum metabolic rate (MMR), d) aerobic scope (AS), e) recovery time (RT), and f) excess post-exercise oxygen consumption (EPOC) of subordinate (sub) or dominant (dom) smallmouth bass *Micropterus dolomieu* measured by respirometry experiments in presence (dark diamonds) or in absence of shelter (light squares). Grey letters indicate significant differences between dominance status.

Discussion

Metabolic traits and presence of shelter

Our study revealed no reduction in SMR of smallmouth bass with presence of shelter. However, presence of shelter had a significant effect in reducing RMR for Lake Long fish. It may be expected that presence of shelter would have no effect on metabolic rates estimated during the night (in the dark) if the main goal of sheltering is for the fish to be visually hidden. It is therefore important to account for light levels when comparing our results to that of other studies. Orange-fin anemonefish *Amphiprion chrystopterus* showed 8% lower SMR, measured in the dark during the night, in presence of healthy anemones compared to bleached anemones, while day-time metabolic rates did not differ (Norin et al. 2018). In contrast, no differences in SMR or RMR were observed when shelter was present or absent in a closely related species of clown fish *A. ozellaris* (Kegler et al. 2013). In Atlantic salmon *Salmo salar*, RMR measured during the day were 30 % lower when shelter was available (Millidine et al. 2006) or under simulated ice cover (Finstad et al. 2004). Presence of shelter also resulted in 30 % lower RMR measured during the day in burbot *Lota lota*, but had no effect on that of stone loach *Barbatula barbatula* (Fischer 2000). Comparison of results on two *Amphiprion* spp. – and that of the other studies listed above – highlight that there is no consistent lowering effect of shelter presence on SMR or RMR, nor any trend to be drawn by the light level at which measurements were made.

Presence or absence of shelter did not affect AS. This metabolic trait is the difference between MMR and SMR, and both traits did not vary with presence of shelter. We were not expecting MMR to change with presence of shelter. The chase and air exposure protocol used in our study simulates fisheries stress (Cooke et al. 2013a, 2014b) and is effective to induce maximal fish exhaustion, and thus to measure MMR (Roche et al. 2013). If the fish is completely exhausted, and has reached MMR, there should be no change in MMR with presence of shelter.

Presence of shelter did not reduce RT (except in dominant individuals, discussed below) and EPOC of smallmouth bass. To our knowledge, no other study has investigated the potential for shelter to reduce RT or EPOC, so direct comparisons with our results are not possible. However, a previous study showed that latency to fast start escape response (a proxy for vigilance) were negatively related to RT (Killen et al. 2015). In other words, more vigilant individuals had longer RT. Vigilance is thought to be energetically costly due to higher brain activity (Moss et al. 1998). As sheltering can be a cost effective strategy to replace vigilance (Millidine et al. 2006), we were expecting that RT would be faster and that EPOC would be reduced in presence of shelter. Animals often seek shelter after intense activity to recover and tend to stay hidden longer after being active than resting (Hailey et al. 1987, Krause et al. 1998), although there is some evidence that finding shelter may be more difficult for exhausted organisms (Brownscombe et al. 2014). Despite this apparent need for sheltering for recovery, "forced" shelter presence vs absence during the respirometry experiments in our study did not unequivocally affect RT or EPOC. Physiological motive may lead an animal to use shelter, but the hypothesis that shelter use may have consequences on energy expenditures required for non-mechanical tasks is not supported by our results.

It is also important to note that fish may have a different conception of what a shelter is than what we expected. A respirometry chamber is a confined space placed in a water basin in which there are other chambers and obstacles (pumps, tubing). Fish may feel there is high structural complexity in their surroundings that may act as shelters. In fact, Millidine et al. (2006) found that use of shelter was not necessary for Atlantic salmon to lower their metabolic rates, only the availability of the shelter in the chamber was important: fish rested near the shelter and not inside it during most of the experiments. Moreover, the shelter used in Millidine et al. (2006) study was made from clear material, which means that sheltering did not provide different light level to the fish, but its presence still resulted in 30% lower RMR in Atlantic salmon. It is possible that smallmouth bass considered their surroundings in the respirometry experiment (pumps, tubings, etc.) as available shelters, even if not placed over the chamber. Nonetheless, none of these provided the shade and direct overhead shelter common in a field setting (e.g., under a log). If the main goal of sheltering is for the fish to be visually hidden, no effect on SMR measured in the dark should be expected. However, fish had on average 6 h ± 1.5 h to acclimate to the presence of shelter over the respirometry chamber from the onset of the respirometry experiment until lights were turned off, and had knowledge of being hidden. The extent at which this knowledge may indeed affect fish respiration remains to be fully assessed.

The interaction between body mass and treatment had a significant effect on SMR. Larger fish had lower SMR in presence of shelter than when it was absent. The same trend was also observed in RMR but the effect was not significant (Figure S1). This could indicate that shelter had a more calming effect on larger fish than on smaller ones, or that sheltering is more common in larger individuals. Presence of shelter is the most reported habitat association for adult smallmouth bass, while juveniles are more associated to large substrate relative to their size (Edwards et al. 1983, Todd and Rabeni 1989, Warren 2009). Male and female smallmouth bass mature minimally at >20 and >22 cm, respectively (Warren, 2009), which indicates our dataset comprises sub-adults and adults. It is possible that the interacting effects of body mass and treatment on SMR reflects different habitat associations within the size range of individuals in our sample as the shelter provided during the experiment (similar to a log) is more in line with the type of shelter used preferentially by larger individuals in nature (in contrast to macrophytes or rocks). However, this is not supported by our data. We saw no relationship between body mass and the type of physical structure in proximity of capture areas. We also observed that RT and EPOC were negatively related to body mass. The opposite trend was observed in other studies on freshwater fish (Zhang et al. 2014) while no relationship between body mass and recovery was found in reptiles or amphibians (Gleeson 1991).

Experiment order had a significant effect on SMR and RMR, and its interaction with population or fish mass affected RT and EPOC, respectively. The time that fish were held in captivity represented a compromise between the minimum time necessary to recover from capture and transport to the field station, and the maximum time to avoid stress from prolonged captivity in wild-caught fish. Previous work demonstrated that no differences were observed in performance of wild caught smallmouth bass measured within 1 and 7 days in captivity (Peake 2004). Fish were kept in captivity for three or four days before the first experiment, and another three day period separated the first and second experiment. Despite short captivity duration, habituation to husbandry conditions and respirometry chamber may explain the lower rates measured during the 2nd experiment.

Lentic vs lotic smallmouth bass

There were significant differences in SMR, RMR, AS and RT between the two smallmouth bass populations. Fish from Kiamika River had a 20% lower SMR, a 30% higher AS and a 22% shorter RT than lake fish. These differences may be inherent to the type of natural environment these fish usually dwell in. It may be more important for river fish to have a low SMR and a higher AS due to the high costs of swimming in moving water. Relatedly, shorter RT after intense activities may be necessary to river dwelling fish. There was an interaction between population and treatment for RMR, Lake Long fish having lower RMR in presence of shelter while there were no difference in Kiamika fish. We were expecting presence of shelter would lower SMR/RMR of all fish, regardless of population. For the river population, however, benefits of sheltering may be more related to protection from the physical environment than to reduce energy expenditures for non-mechanical tasks. We cannot rule out that benefits associated with shelter use by these fish were not detected in our study because we did not manipulate flow velocities, restrict food consumption or simulate predator presence (although the chase protocol used to induce MMR simulates a fishing stress; Cooke et al., 2013). While our results are consistent with expected differences in metabolic traits between fish inhabiting rivers and lakes, our study compares a small number of fish from one river and one lake. Experiments involving fish from a large number of rivers and lakes are needed before drawing any formal conclusion.

Dominance

Metabolic rates (SMR, RMR, MMR and AS) did not vary in presence or absence of shelter for either dominant or subordinate fish. Dominance can facilitate access to shelter if that important resource is limited. In crayfish *Orconectes rusticus*, even when shelters are in abundance, dominant individuals generally occupy the preferred shelters and are less likely to be evicted from them than subordinates (Martin and Moore 2008). A dominant smallmouth bass would even prevent subordinates from using shelters in holding (personal observation). It is possible that subordinate smallmouth bass did not feel less vulnerable in presence of shelter by fear of dominant individuals, even if they were not harassed by an aggressive conspecific during the respirometry experiment. Jolles et al. (2016) observed that recent social conditions could affect repeatability of behaviour or expression of personality in three-spined sticklebacks *Gasterosteus aculeatus*. One could expect that recent social conditions could also affect physiological responses. This is in line with the hypothesis that presence of highly dominant individuals or hierarchy could mask variations in physiological traits among subordinates (Killen et al. 2013). While we did not see differences in metabolic rates in presence or absence of shelter in subordinate fish, we did not observe significant differences with treatment among dominant fish either. We cannot conclude that dominance status had a modulating effect on metabolic rates estimated in presence or absence of shelter. We did observe that dominant smallmouth bass had 26 % shorter RT in the presence of shelter than when it was absent, while no difference was observed between treatment in subordinate fish. This result may be related to the cost of vigilance or other metabolic costs to maintain the hierarchy when shelter is absent (Castro et al. 2006, Millidine et al. 2006). Presence of shelter (e.g. dense canopy cover) has been associated with reduced vigilance rates (Griesser and Nystrand 2009) in the Siberian jay *Perisoreus infaustus*. Killen et al. (2015) observed that RT after exercise were positively correlated to vigilance. Our results might then suggest that dominant fish were more vigilant than subordinates. Additional work on smallmouth bass dominance structures is necessary to confirm this trend, and could reveal other relationship between dominance and metabolic traits not detectable in our exploratory analysis.

Individual variability

We observed inter-individual variability in responses, expressed by the difference between R^2_m and R^2_c in models, regardless of population and treatment. For MMR and AS, variance explained by the random effects exceeded that of the fixed effects. This could indicate that MMR and AS are more plastic than SMR, RMR, RT and EPOC. However, SMR and MMR have been reported to vary similarly between individuals of the same species (by about three-fold: Burton et al., 2011; Norin and Clark, 2016; Norin and Malte, 2011). This could also indicate that the chase and air exposure protocol may not have always successfully achieved complete exhaustion. However, we are confident that our method was robust as the chase duration was determined after a pilot experiment on smallmouth bass from the same populations as that of the present study, and that the air exposure following the chase is thought to be an effective way to ensure complete fish exhaustion (Roche et al. 2013, Norin and Clark 2016). Inter-individual variability could be related to genotypes, maternal effects, early developmental conditions, social environment in holding or personality (Burton et al. 2011, Killen et al. 2013). We have no pedigree on our wild-caught smallmouth bass, so we cannot explore the potential effects of genetics, maternal effects or early developmental conditions. In addition, no differences in metabolic rates with treatment were revealed when accounting for the social environment in holding (i.e. dominance), except for RT, which was lower for dominant fish in presence of shelter. However, a more formal quantification of dominance status would be necessary to generalize our results. While it is possible that some inter-individual variability could be attributable to personality in the present study, our design does not allow us to estimate repeatability of responses adequately, as it would have required multiple measures in both treatments (with or without shelter; Roche et al., 2016).

Acknowledgments

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Contributions

E.C., S.J.C., and D.B. designed the experiments. E.C. performed the experiments, analyzed the data and wrote the manuscript. All authors contributed critically to the manuscript.

Supplementary information

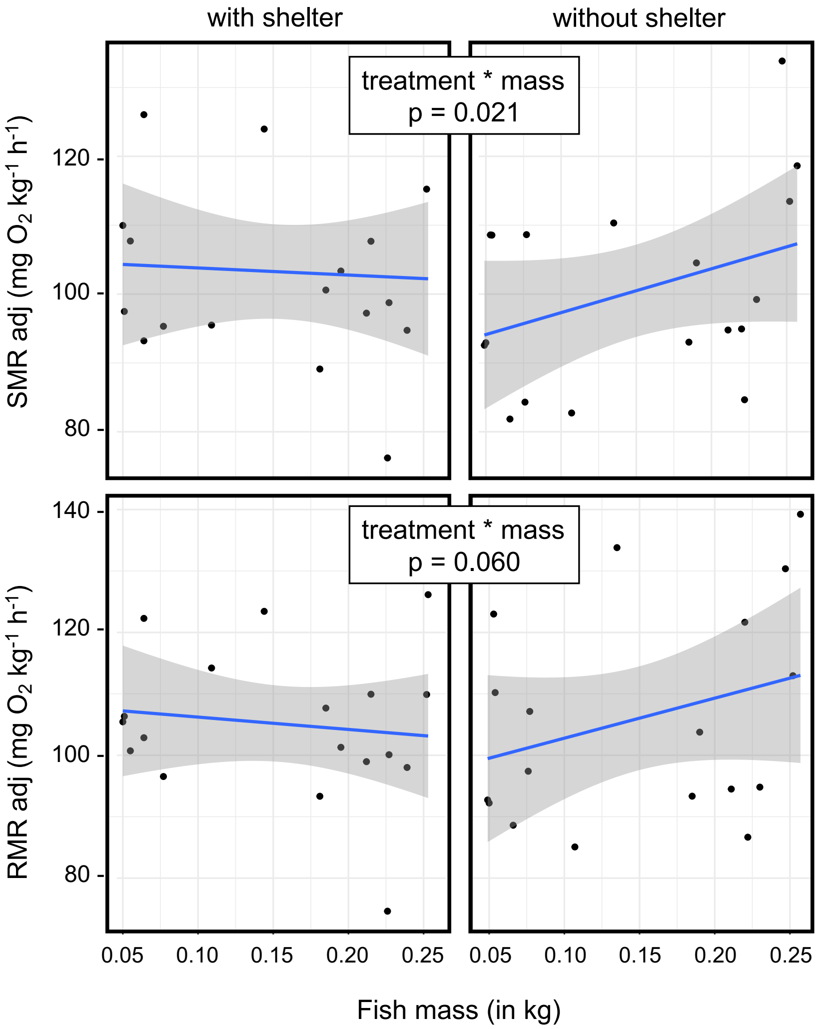


Figure S1: Mass-adjusted standard metabolic rate (SMR) and resting metabolic rate (RMR) of smallmouth bass *Micropterus dolomieu* estimated in both treatments (with or without shelter) as a function of fish mass. Points represent individual metabolic rates. Line and shaded area show a linear regression fit and confidence interval, respectively, between metabolic rate and body mass.

Table S1: Summary of effects retained in linear mixed models relating smallmouth bass *Micropterus dolomieu* metabolic traits to mass, treatment, origin, experiment order and interactions between these variables. For factorial variables Treatment, Population and Order, a + sign indicated a significantly higher coefficient for "without shelter", Lake Long and 2nd experiment, respectively. Random effect of fish ID was included in models. R^2_m is the marginal R^2 (proportion of variance explained by the fixed effects) and R^2_c is the conditional R^2 (proportion of variance explained by the fixed and the random effects).

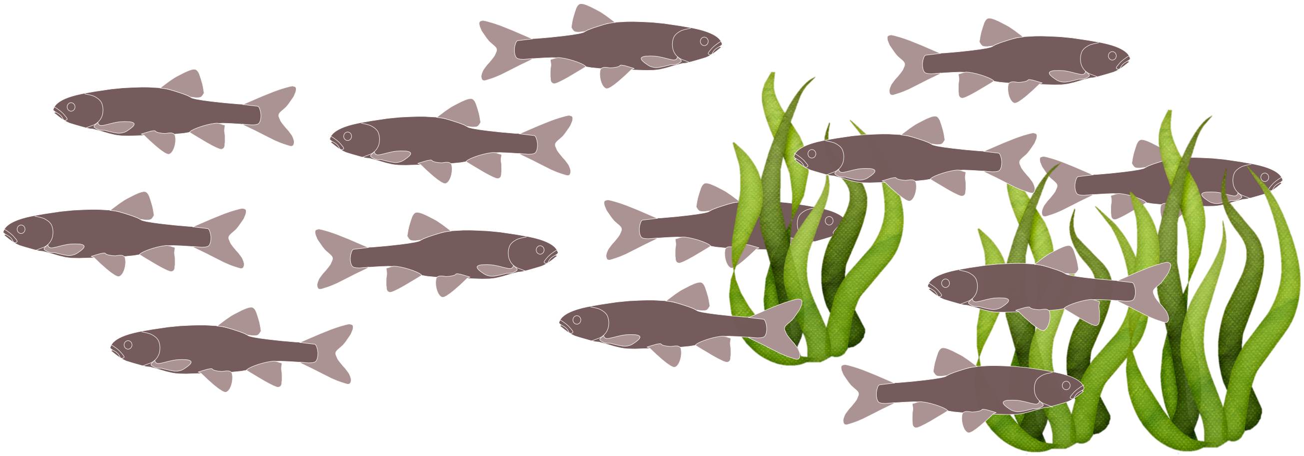
					Interaction term							
Response variable	**Mass (in g)**	**Treatment**	**Population**	**Order**	**M * T**	**M * P**	**M * O**	**T * P**	**T * O**	**P * O**	**R^2_m**	**R^2_c**
SMR (mg O_2 kg^{-1} h^{-1})	n.s.	n.s.	+	-	+						0.503	0.753
RMR (mg O_2 kg^{-1} h^{-1})	n.s.	n.s.	+	-	n.s.			+			0.441	0.593
MMR (mg O_2 kg^{-1} h^{-1})	NA	n.s.	n.s.	NA							0.138	0.617
AS (mg O_2 kg^{-1} h^{-1})	n.s.	n.s.	-	NA	n.s.						0.295	0.696
R_T (minutes)	-	n.s.	+	-						-	0.475	0.580
EPOC (mg O_2 kg^{-1})	-	n.s.	n.s.	n.s.			-				0.467	0.689

Table S2: Results of linear mixed models relating metabolic traits of smallmouth bass *Micropterus dolomieu* to mass, treatment, dominance, experiment order and interactions between these variables. Random effect of fish ID was included in models. R^2_m is the marginal R^2 (proportion of variance explained by the fixed effects) and R^2_c is the conditional R^2 (proportion of variance explained by the fixed and the random effects).

Response	Effect	Chi-squared	d.f.	Pr(> Chi-sq)	R^2_m	R^2_c
SMR	Treatment	0.9951	1	0.3185	0.234	0.761
	Dominance	1.4189	1	0.2336		
	Order	12.2242	1	0.0005***		
RMR	Treatment	0.0048	1	0.9445	0.25	0.561
	Dominance	0.3523	1	0.5528		
	Order	11.8115	1	0.0006***		
MMR	Mass	0.0152	1	0.9018	0.11	0.766
	Treatment	0.0235	1	0.8782		
	Dominance	0.4281	1	0.5129		
	Order	0.4233	1	0.5153		
	Mass * order	6.8337	1	0.0089**		
AS	Mass	0.096	1	0.7566	0.295	0.696
	Treatment	0.1407	1	0.7076		
	Dominance	0.9339	1	0.3338		
	Order	1.7417	1	0.1869		
	Mass * order	5.9836	1	0.0144*		
RT	Mass	9.494	1	0.0021**	0.449	0.668
	Treatment	3.5824	1	0.0584		
	Dominance	1.7797	1	0.1822		
	Dominance * treatment	3.8466	1	0.0498*		
EPOC	Mass	19.5625	1	<0.0001***	0.535	0.634
	Treatment	1.3099	1	0.2524		
	Dominance	3.444	1	0.0635		

Table S3: Summary of effects retained in linear mixed models relating metabolic traits of smallmouth bass *Micropterus dolomieu* to mass, treatment, dominance, experiment order and interactions between these variables. For factorial variables Treatment, Dominance and Order, a + sign indicated a significantly higher coefficient for "without refuge", "dominant" and 2nd experiment, respectively. Random effect of fish ID was included in models. R^2_m is the marginal R^2 (variance explained by the fixed effects) and R^2_c is the conditional R^2 (total variance explained by the fixed and the random effects).

					Interaction term							
Response variable	**Mass (in g)**	**Treatment**	**Dominance**	**Order**	**M * T**	**M * D**	**M * O**	**T * D**	**T * O**	**D * O**	**$R^2{}_m$**	**$R^2{}_c$**
SMR adj. (mg O_2 kg^{-1} h^{-1})	NA	n.s.	n.s.	-							0.234	0.761
RMR adj. (mg O_2 kg^{-1} h^{-1})	NA	n.s.	n.s.	-							0.25	0.561
MMR adj. (mg O_2 kg^{-1} h^{-1})	n.s.	n.s.	n.s.	n.s.			-				0.111	0.766
AS adj. (mg O_2 kg^{-1} h^{-1})	n.s.	n.s.	n.s.	n.s.			-				0.162	0.741
R_T (minutes)	-	n.s.	n.s.	NA				+			0.449	0.668
EPOC (mg O_2 kg^{-1})	-	n.s.	n.s.	NA							0.535	0.634



Chapitre 3 :

La taille du groupe social et la présence de refuge influence les traits métaboliques individuels d’un poisson social

Social group size and shelter availability influence individual metabolic traits in a social fish

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Abstract

Group living is widespread among animal species and yields both costs and benefits. Presence of conspecifics can restrict or enhance the expression of individual behaviour, and the recent social environment is thought to affect behavioural responses in later contexts, even when individuals are alone. However, little is known about how social group size influences the expression of individual physiological traits, including metabolic rates. There is some evidence that shoaling can reduce fish metabolic rates but this variable may be affected by habitat conditions such as shelter availability via density-dependent processes. We investigated how social group size and shelter availability influence Eurasian minnow *Phoxinus phoxinus* metabolic rates estimated by respirometry. Respirometry trials were conducted on fish in isolation before and after they were housed for three weeks in a social treatment consisting in a specific group size (n= 4 or 8) and shelter availability (presence or absence of plant shelter in the experimental tank). Plant shelter was placed over respirometers for half of the duration of the respirometry trials, allowing estimation of minimum day-time and night-time metabolic rates in both conditions (in the presence or absence of plant shelter). Standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (AS) were also estimated over the entire trial. Minimum day-time and night-time metabolic rates estimated while in presence of plant shelter were lower than when estimated in absence of plant shelter, both before and after individuals were housed in their social treatment. After the social treatment, SMR were higher for fish that were held in groups of four as compared to that of fish held in groups of eight while MMR showed no difference. Plant shelter availability during the social treatments did not influence SMR or MMR. Our results suggest that social group size may directly influence energy demands of individuals, highlighting the importance of understanding the role of group size on variations in physiological traits associated with energy expenditure.

Key words: density, maximum metabolic rate, shelter, social group, standard metabolic rate

Introduction

An animal social group is any set of socially interacting individuals that remain together in space and time (Krause and Ruxton 2002). Group living can provide a number of benefits, such as reduced predation risk, improved foraging, increased mate choice, and reduced energetic cost of movement or thermoregulation (Krause and Ruxton 2002, Evans et al. 2016, Jolles et al. 2020). Conversely, group living can be associated with increased conspicuousness or attack rates from predators, reduced individual growth if food resources are limited, and increased parasite or disease burden (Altizer et al. 2003, Hoare et al. 2004, Guénard et al. 2012). Social structures emerge in groups from variability in individual behaviour and interactions among groupmates. Some behavioural responses are influenced by the number of groupmates present (Krause and Ruxton 2002). For example, group size has been negatively correlated with foraging in novel contexts (Day et al. 2001) but positively correlated with exploration (Ward 2012). Presence of conspecifics can restrict or enhance the expression of individual behaviour through processes like conformity or facilitation (Ward 2012, Jolles et al. 2016, Ward and Webster 2016). Consequently, individuals may express a different suite of behaviours and different degrees of their full behavioural capacity while in group compared to when they are alone (Jolles et al. 2020). Further, there is some evidence that the recent social environment can affect behavioural responses in later contexts, even when individuals are alone (Jolles et al. 2016). This suggests that the social environment could modulate an individual's behavioural expression or capacity, yet the ways in which the phenotype of individual animals interact with their social environment remains largely unknown, including how social dynamics affect individual physiological traits.

The interplay between the social environment and individual physiological traits may be especially complex due to the effects of social dynamics on individual stress, energy intake, and energy use (Webster and Ward 2011). For instance, standard metabolic rate (SMR), the minimum rate of energy use needed to sustain life at a given temperature in an ectotherm (Burton et al. 2011, Chabot et al. 2016), generally correlates with dominance, aggression, and tendency to take risks among individuals (Biro and Stamps 2010, Redpath et al. 2010, Metcalfe et al. 2016, Arnold et al. 2021). However, there is also evidence that individual stress can influence SMR over various temporal scales. In brown trout *Salmo trutta*, holding in pairs led to an increase in SMR of subordinate individuals, probably due to social stress, while SMR of dominant individuals did not change (Sloman et al. 2000). This is an example of how dominance can modulate relationships between metabolism and behaviour (Killen et al. 2013), though whether such effects occur in larger or more complex social systems than dyads requires further investigation. There is evidence, however, that shoaling can reduce SMR in fish through "calming effects" (Nadler et al. 2016). Like SMR, maximum metabolic rate (MMR) and aerobic scope (AS; the difference between MMR and SMR) can correlate with dominance (Killen et al. 2014), boldness, or aggression (Redpath et al. 2010). However, to our knowledge, there is no evidence to date that social stress can influence MMR or AS (Killen et al. 2016a), despite their potential to constrain energetically costly behaviours and other aerobically fueled activities (Metcalfe et al. 2016). In any case, SMR and MMR are often positively correlated (Killen et al. 2016b, Norin and Clark 2016, Auer et al. 2017) within and across species. As such, any effects of social dynamics on metabolic rates at rest may also affect aerobic capacity, or vice versa. The potential for social dynamics to influence either SMR or MMR could be reflected in AS, and thus influence the capacity to perform aerobically fueled activities. Yet, few studies have investigated how group living affects interactions between behavioural and physiological traits (Huang et al. 2020), aside from studies looking at effects of dominance in dyads (Sloman et al. 2000).

Habitat may further modulate interactions between individual traits and social dynamics (Jolles et al. 2020). Habitat conditions such as temperature or oxygen concentration influence metabolic rates, which in turn may affect performance among individuals within groups (Fry 1971, Huey 1991, Claireaux and Lefrançois 2007, Horodysky et al. 2015). Conversely, social stress can reduce tolerance to thermal stress (LeBlanc et al. 2011) and hypoxia (Thomas and Gilmour 2012). Other habitat conditions such as food and shelter availability may exert density-dependent influences on relationships between metabolism and behaviour. A number of studies have revealed that SMR or RMR estimated while in presence of shelter were reduced compared to when shelter was absent, probably due to decreased stress or reduction of alertness or vigilance when individuals are visually hidden (Fischer 2000, Finstad et al. 2004, Millidine et al. 2006, Norin et al. 2018, Chrétien et al. 2021). However, little is known about the effects of long-term shelter availability on individual metabolic rates and interactions with an animal's social environment. Increased competition for a limited resource, like availability of shelter, could strengthen social hierarchies and increase stress experienced by subordinates, and these effects could be greater in larger social groups. As such, group size and long-term shelter availability may have interacting effects that carry over and influence individual metabolic rates.

We investigated whether exposure to a given group size and shelter availability could influence metabolic rates of Eurasian minnows *Phoxinus phoxinus,* a small Cyprinid naturally living in social groups (Magurran 1986). We held fish in groups of four or eight, in tanks with or without plant shelter. The combination of group size and plant shelter availability in experimental tanks generated social treatments that differed in fish density and potential competition intensity for use of shelter. Respirometry trials were conducted before and after fish were housed for three weeks in these different social treatments, to measure metabolic rates ($\dot{M}O_2$). Furthermore, during respirometry trials, metabolic rates were estimated in two conditions which both lasted about half the duration of the trial: while respirometerss were covered by plant shelter and while respirometers were not covered by such plant shelter. This design allowed us to get estimates of minimum day-time and night-time metabolic rates ($\dot{M}O_{2min}$) in presence or in absence of plant shelter, as the importance of being visually hidden by a shelter may vary with light intensity, as well as estimates of SMR, MMR, and AS. We hypothesized that the recent social environment, in the 3-week social treatment, would have metabolic effects that carry over, even when individuals are alone (Jolles et al. 2016), and be reflected in estimates of metabolic rates. Consequently, we predicted that presence of plant shelter during respirometry trials would lower day-time $\dot{M}O_{2min}$, but that the magnitude of this effect would be smaller after the fish were held for three weeks in their social treatment (Killen et al. 2013). Given that minnows are social fish, we also predicted that SMR would vary with group size, due to the potential for social dynamics to modulate SMR (Sloman et al. 2000). We also predicted that fish held without access to plant shelter in their social treatment would have higher SMR, due to chronic effects of stress (Huey 1991). The potential for group size and plant shelter availability to influence MMR is unclear. One the one hand, MMR is generally thought to be less plastic than SMR (Norin and Metcalfe 2019), but on the other hand, SMR and MMR are thought to be positively correlated (Killen et al. 2016b, Norin and Clark 2016). We nonetheless expected to see changes in AS due to predicted changes in SMR.

Materials and Methods

Experimental animals

Juvenile Eurasian minnows (*Phoxinus phoxinus* Linnaeus) were captured in spring 2018 from River Kelvin (55.86667, -4.31667; Glasgow, United Kingdom) using dip-nets. The sampling location was an artificial side channel along the River Kelvin where small minnows are trapped as they pass over a weir and are unable to return to the main river. Fish were transported to the nearby University of Glasgow aquarium facilities and held at 15 ºC in two large stock tanks (100 x 40 x 30 cm) each filled with 100-150 individuals (density = 833 to 1250 fish m^{-3}) for 11 months before the study, which took place in April and May 2019. During this holding period, fish were fed *ad libitum* a combination of pellets and blood worms and were on a 12 h light: 12 h dark photoperiod.

Experimental design

Experiments were conducted on a total of 80 fish. Since the capacity of the respirometry set-up was of 16 fish (each such group is hereafter referred to as a "batch"), five batches were subjected to respirometry before and after exposure to the social treatments (combination of group size and shelter availability). Each experiment consisted of an initial respirometry trial, a 3-week social treatment, and a final respirometry trial (Fig. 1). Before the onset of an experiment, a group of 16 minnows were haphazardly picked from the two stock tanks and isolated for 48 hours in a rearing tank (40 x 40 x 30 cm). During that period, fish were fasted to ensure they were in a post-absorptive state before the respirometry trial.

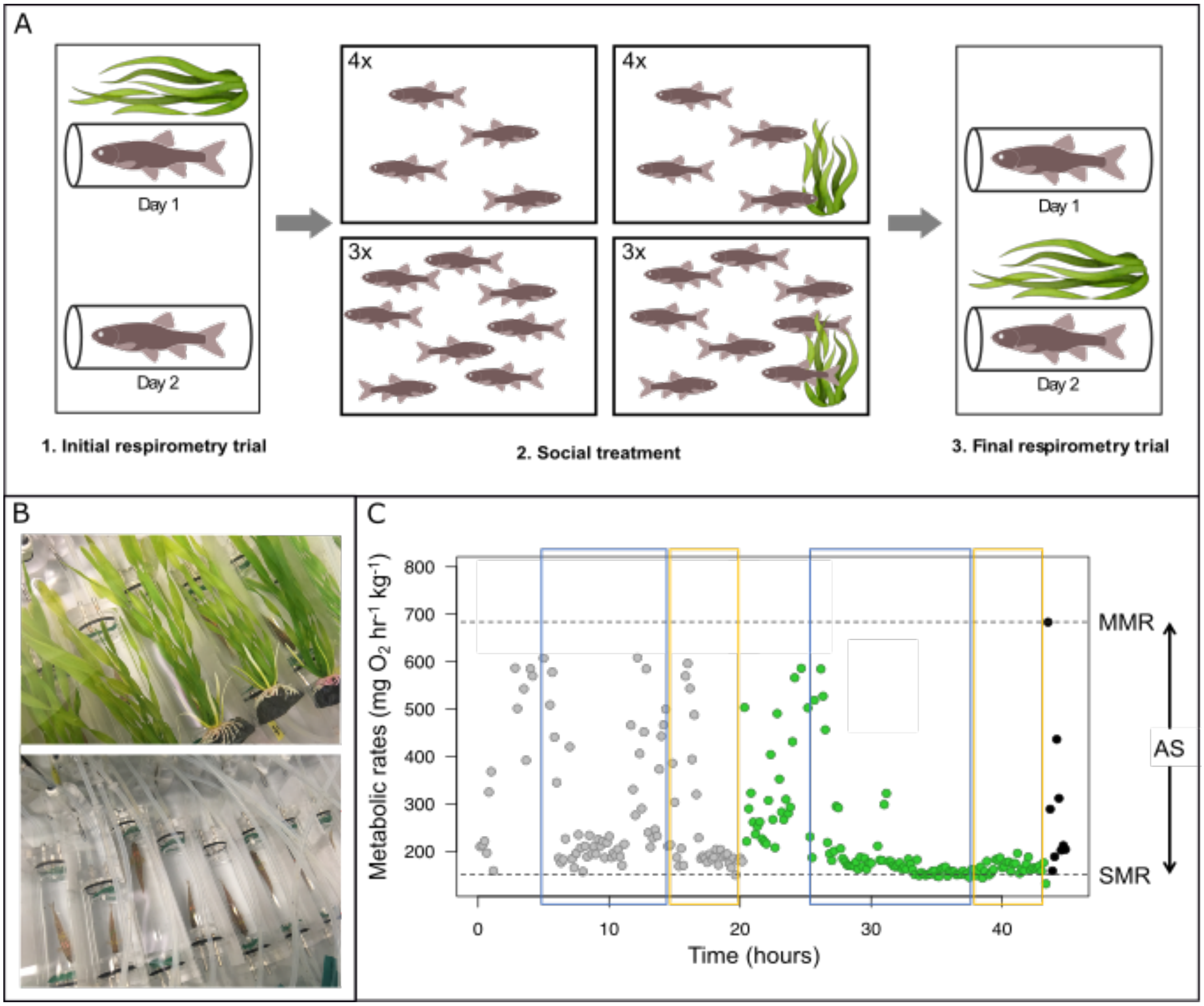

Figure 1: Experimental design of the study. A) Each experiment consisted of an initial respirometry trial, a 3-week social treatment, and a final respirometry trial. 1. Initial respirometry trial: Fish oxygen uptake was measured for ~45h during which chambers were covered with artificial plant shelter for approximately half of the trial duration. 2. Social treatment: After the initial respirometry trial, fish were allotted in groups of four or eight fish and placed in experimental tanks containing artificial plant shelter or not, thus forming different social treatments. Fish stayed in their social treatment for 3 weeks. 3. Final respirometry trial: After the social treatment, fish oxygen uptake was measured again by respirometry, in chambers covered with artificial plant shelter for half of the trial duration. B) Photograph of respirometry trial setup with fish in individual chambers covered with plant shelter (top) or not (bottom). C) Experimental protocol to obtain $\dot{M}O_2$ data for the Eurasian minnow. The example shows a 48-h long respirometry trial which started with the condition "without plant shelter" (chamber not covered with plant shelter; grey points). The condition was changed to "with plant shelter" (green points) the next day at around noon. On the last day at noon, fish was removed from the respirometry chamber, chased, and immediately placed back into the chamber to obtain MMR (black points). Blue and yellow rectangles represent the range of data used for estimation of night-time and day-time minimum $\dot{M}O_2$, respectively, with or without plant shelter. Top and bottom horizontal dotted lines show estimates of MMR and SMR.

Each respirometry trial was conducted to estimate fish metabolic rates in the presence or absence of artificial plant shelter. Fish were placed in individual glass chambers (~100 ml) separated by opaque white dividers to prevent fish from seeing each other. Respirometry trials lasted ~45h during which chambers were covered with artificial plant shelter for approximately half of the trial duration (Fig. 1). The presence of an artificial plant over the chamber was randomly set to occur during the first or the second half of the initial respirometry trial (Fig. 1B), and order was reversed for the final respirometry trial. At the end of the initial respirometry trial, fish were weighed, measured and injected with a unique combination of visible implant elastomer (Northwest Marine Technology, Anacortes, WA, USA) in the dorsal body surface to allow individual identification. The 16 fish within a given batch were afterwards allotted in groups of four or eight fish (e.g. the first batch was allotted in four groups of four fish, the second batch was allotted in two groups of eight fish, and so on) and placed in experimental tanks (40 x 40 x 30 cm) containing artificial plant shelter or not, thus forming different social treatments. After the three week social treatment, the 16 fish were weighted and measured again, and the final respirometry trial was conducted. Testing the five batches, from the beginning of the initial respirometry trial with the first batch to the end of the final respirometry trial with the last batch, required 41 days.

Social treatments took place in 14 experimental tanks of identical dimensions (40 x 40 x 30 cm). In eight of these experimental tanks, the social treatment was defined by a group size of four fish (density = 83 fish m^{-3}) either with, or without, artificial plant shelter (four experimental tanks each). In the remaining six experimental tanks, the social treatment was defined by a group size of eight fish (density = 166 fish m^{-3}) either with, or without, artificial plant shelter (three experimental tanks each).

Fish were fed daily *ad libitum* a combination of pellets and blood worms, scattered throughout their experimental tank, during the 3-week social treatment to minimize potential effects of density on individual food intake and growth. Daily specific growth rate (SGR: in % day^{-1}) during the 3-week social treatment was calculated for each individual using the following equation:

$$SGR = \frac{[\log(\mathrm{Mf}) - \log(\mathrm{Mi})]}{t} \text{ x } 100 \qquad \text{(eq.1)}$$

where M_f is the observed mass at the time of the final respirometry trial, M_i is the observed mass at the time of the initial respirometry trial, and t is the number of growth days.

Respirometry trials

Metabolic rates were estimated using oxygen uptake rates ($\dot{M}O_2$: mg O_2 hr^{-1}; Killen et al., 2021; Svendsen et al., 2016), determined via intermittent flow-through respirometry equipment and software (Firesting, PyroScience, Aachen, Germany). Water was continuously mixed through each chamber with a peristaltic pump and gas impermeable tubing. Automated flush pumps refreshed the chambers with UV-treated and oxygenated water for 2 min of every 7-min cycle. Dissolved oxygen concentrations were maintained above 80% air saturation at all times with air-bubblers. Temperature was measured with a Pt100 temperature probe and maintained at 15 ºC with a TMP-REG instrument (Loligo Systems, Tjele, Denmark) by recirculation of water through a stainless coil in a cold bath.

Respirometry trials lasted ~45h (43.8 to 46.1h), and chambers were covered with artificial plants for about half of their duration (~ 21.5 ± 2 hours; Fig. 1). Respirometry trials started mid-afternoon, and condition (with or without artificial plant shelter) was changed at around noon the next day (~21h after the onset of the respirometry trial). Approximately 43h after the onset of the respirometry trial, fish were taken out of their chamber one by one for a 2-min chase protocol (Roche et al. 2013) and returned in their chamber for immediate measurement of $\dot{M}O_2$ to estimate their maximum metabolic rate MMR (Fig. 1C). Respirometry resumed for another hour, and fish were removed from the chambers and transferred to their original experimental tank. Background oxygen consumption in each empty chamber was recorded over three 7-min cycles at the start and end of each respirometry trial.

Calculation of metabolic rates

Metabolic rates were calculated by multiplying the slopes of decline in oxygen concentration in the chamber during closed measurement cycles, excluding the first 30 seconds, by the volume of the chamber (corrected for the volume of fish, assuming a density of 1 kg l^{-1}) using the package *FishResp* in R (R Foundation for Statistical Computing 2018, Morozov et al. 2019). Background oxygen consumption was subtracted from $\dot{M}O_2$ measurements, assuming a linear change between measures taken at the start and end of each trial. Day-time and night-time minimum metabolic rates ($\dot{M}O_{2\text{min}}$; mg O_2 kg^{-1} hr^{-1}) were calculated separately to account for the potentially different effect of the presence of shelter during day-time and night-time. $\dot{M}O_{2\text{min}}$ were estimated using the 0.2 quantile of the $\dot{M}O_2$ data with the package *fishMO2* in R (Chabot

2016, Chabot et al. 2016). The range of data used for the calculation of night-time $\dot{M}O_{2\mathrm{min}}$ started 5 hours after fish were put in the chamber (at around 9:30 pm) or 5 hours after the change in condition (presence of plant shelter or not; at around 6:30 pm), and ended in the morning at 7:00 am, moment at which lights were turned on. The range of data used for the calculation of day-time $\dot{M}O_{2\mathrm{min}}$ started at 7:00 am and ended at the change in condition, or when fish were retrieved from the chamber for the chase protocol (Fig. 2). Standard metabolic rate (SMR; mg O_2 kg^{-1} hr^{-1}) was set as the lowest estimate of day-time or night-time $\dot{M}O_{2\mathrm{min}}$ over a trial. MMR (mg O_2 kg^{-1} hr^{-1}) was estimated as the highest rate of oxygen consumption over a 3-minute rolling average regression within a measurement cycle following the chase protocol. Aerobic scope (AS; mg O_2 kg^{-1} hr^{-1}) was calculated as the difference between MMR and SMR. All metabolic rates were adjusted to the mean body mass of the fish in our sample (mean ± s.d.: 1.95 ± 0.57 g) using the slope *b* of the log-log relationship between $\dot{M}O_2$ and mass (Steffensen et al. 1994, Ultsch 1995).

$$\dot{M}O_{2\mathrm{adj}} = (\text{mean fish mass})^{b-1} \times (\text{individual fish mass})^{1-b} \times \text{individual fish } \dot{M}O_2 \qquad \text{(eq.2)}$$

From each respirometry trial, two night-time and day-time $\dot{M}O_{2\mathrm{min}}$ estimates were calculated (one per trial day) per fish, as well as one SMR, MMR, and AS (Fig. 1C). This resulted in one dataset of 320 estimates of night-time and day-time $\dot{M}O_{2\mathrm{min}}$, and in another dataset of 160 estimates of SMR, MMR, and AS, for 80 fish. Some data points were removed in the night-time and day-time $\dot{M}O_{2\mathrm{min}}$ dataset because slopes of decline in oxygen concentration in the chambers did not have sufficiently high R^2 (>0.95), resulting in 306 estimates of night-time $\dot{M}O_{2\mathrm{min}}$ and 312 estimates of day-time $\dot{M}O_{2\mathrm{min}}$, on 80 fish. In addition, two fish did not reach MMR during the initial respirometry trial, therefore the final dataset comprises 158 estimates of MMR, and 158 estimates of AS, on 80 fish.

Statistical analyses

All analyses were computed in R v. 3. 6. 0 (R Foundation for Statistical Computing 2018). Effects of presence of shelter on night-time and day-time $\dot{M}O_{2\text{min}}$ measured during initial and final respirometry trials were tested using linear mixed effects models (LMM) with the package *lme4* (Bates et al., 2014). Full models with night-time or day-time $\dot{M}O_{2\text{min}}$ as a response variable included trial (initial or final), trial day (1st or 2nd), presence or absence of plant shelter covering respirometry chambers during the trial, fish body mass (g), and all two-way interactions as fixed effects. Trial day, fish body mass, and interaction terms were included in models in case they contributed to variation in estimates of metabolic rates, but dropped if non-significant and the models re-run. Models included fish ID and batch number (1 to 5) as random effects in a nested structure (batch number/fish ID). Model assumptions were met when response variables were log-transformed. For all models, assumptions of homoscedasticity, linearity and normality were confirmed by visual inspection of residual plots.

Effects of group size and shelter availability on SMR, MMR, and AS were tested with LMM using data from the initial and final respirometry trials, social treatment conditions (group size: four or eight fish, shelter availability: presence or absence of artificial plant in experimental tank), fish body mass, and all interactions as fixed effects. The SMR model included fish ID and batch number as random effects in a nested structure (batch number/fish ID). The MMR and AS models included only fish ID as random effect. Model assumptions were confirmed by visual inspection of residual plots.

Effect sizes (in %) were calculated using estimated marginal means from final models obtained with the package *emmeans* (Lenth and Hervé 2015). Marginal R^2 (R^2_m: % of variance explained by fixed effects) and conditional R^2 (R^2_c: % of variance explained by fixed and random effects) were calculated from the models fitted through restricted maximum likelihood analysis (Bolker et al. 2009b, Harrison et al. 2018). The difference between R^2_c and R^2_m for each model represent variability due to the random effects (Nakagawa and Schielzeth 2013).

Results

Over the 3-week social treatment, SGR was higher for fish held in groups of four (mean ± standard deviation: 0.64 ± 0.27 % day^{-1}, from -0.07 to 0.99% day^{-1}, Fig. S1) than for fish held in groups of eight (0.50 ± 0.19 % day^{-1}, from 0.09 to 0.99% day^{-1}), and this difference was significant (p=0.004, R^2_{adj} = 0.084). No relationship was found between SGR and metabolic rates measured at the final experiment (see Supplementary Information for details: Tables S1-S2, Fig. S1-S2).

Table 1: Results of linear mixed models relating night-time and day-time minimum metabolic rates ($\dot{M}O_{2\mathrm{min}}$) of Eurasian minnows to respirometry trial (initial or final), trial day, and presence or absence of plant shelter. R^2_m is the marginal R^2 (% of variance explained by the fixed effects) and R^2_c is the conditional R^2 (% of variance explained by the fixed and the random effects).

Response variable	Effect	χ^2	p-value	R^2_m	R^2_c
log Night-time $\dot{M}O_{2\mathrm{min}}$	Trial	9.313	0.002	11.5	42.6
	Day	42.501	<0.001		
	Plant shelter	9.229	0.002		
log Day-time $\dot{M}O_{2\mathrm{min}}$	Trial	111.905	<0.001	16.7	56.2
	Day	7.591	0.006		
	Plant shelter	0.052	0.819		
	Day* Plant shelter	4.051	0.044		

Presence of shelter during respirometry trials

Respirometry timing (initial or final), trial day, and plant shelter (presence or absence during respirometry) had significant effects on night-time $\dot{M}O_{2\mathrm{min}}$ (p=0.002, p<0.001, and p=0.002, respectively; Table 1). Night-time $\dot{M}O_{2\mathrm{min}}$ estimates were on average 8.7% higher during the final trial compared to that of the initial one. They were also 16.2% lower on the 2nd day of trial compared to the 1st day, and 7.9% lower in the presence of plant shelter (Fig. 2A-B) compared to when plant shelter was absent. Day-time $\dot{M}O_{2\mathrm{min}}$ was influenced by respirometry timing (p<0.001; Table 1). Day-time $\dot{M}O_{2\mathrm{min}}$ was on average 26.9% higher at the final respirometry trial (Fig. 2C-D). There was an interaction between trial day and plant shelter on day-time $\dot{M}O_{2\mathrm{min}}$ (p=0.044): in the presence of plant shelter, day-time $\dot{M}O_{2\mathrm{min}}$ rates measured on the 2nd day were 10.0% lower than those of the 1st day.

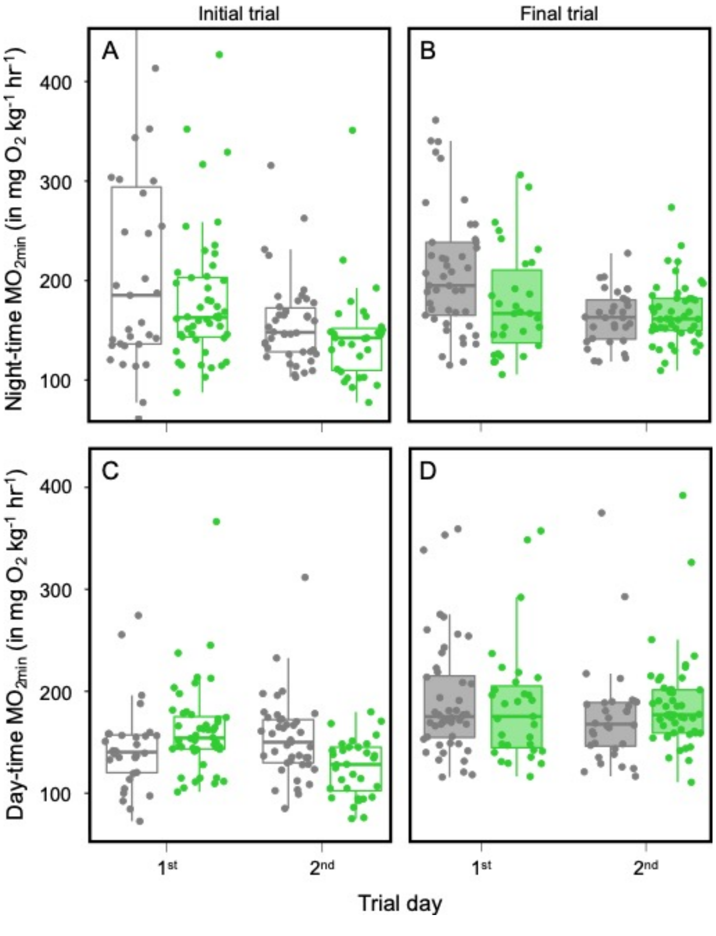

Figure 2: Observed night-time (A, B) and day-time (C, D) metabolic rates in initial (clear) and final (shaded) respirometry trials. Grey and green dots represent estimates in absence or in presence of plant shelter, respectively. Middle thick line of the boxplots corresponds to the median, lower and upper limits correspond to the first and third quartiles of the data, and whiskers extend to the range of the data.

Social treatments and metabolic rates

There was an interacting effect of trial and group size (p=0.006; Table 2) on SMR. Estimates of SMR were 28% higher at the final respirometry trial compared to the initial one for fish held in groups of four, while SMR increased by 13% between the two trials for fish held in groups of eight (Fig. 3A-B). Plant shelter availability in experimental tanks did not influence SMR. MMR did not change between the initial and final respirometry trials (p=0.254). Fish held in groups of four had, however, higher MMR than fish held in groups of eight (p=0.005; Fig. 3C-D). Finally, there was an overall reduction in AS after the 3-week social treatment (p=0.029; Table 2). Group size also negatively influenced AS (p=0.008; Fig. 3E-F). Plant shelter availability in experiment tanks did not influence MMR or AS (Table 2).

Table 2: Results of linear mixed model relating metabolic rates of Eurasian minnows to the moment of the respirometry trials, group size, and shelter availability. Fish ID and batch number were included in the SMR model as random effects. Only fish ID was included as a random effect for MMR and AS models. R^2_m is the marginal R^2 (% of variance explained by the fixed effects) and R^2_c is the conditional R^2 (% of variance explained by the fixed and the random effects).

Response variable	Effect	χ^2	p-value	R^2_m	R^2_c
SMR	Trial	54.646	<0.001	19.6	54.7
	Group size	0.469	0.494		
	Shelter availability	0.009	0.925		
	Trial * Group size	7.567	0.006		
MMR	Trial	1.302	0.254	6.3	24.6
	Group size	7.795	0.005		
	Shelter availability	0.226	0.636		
AS	Trial	4.740	0.029	7.3	24.2
	Group size	6.887	0.008		
	Shelter availability	0.254	0.614		

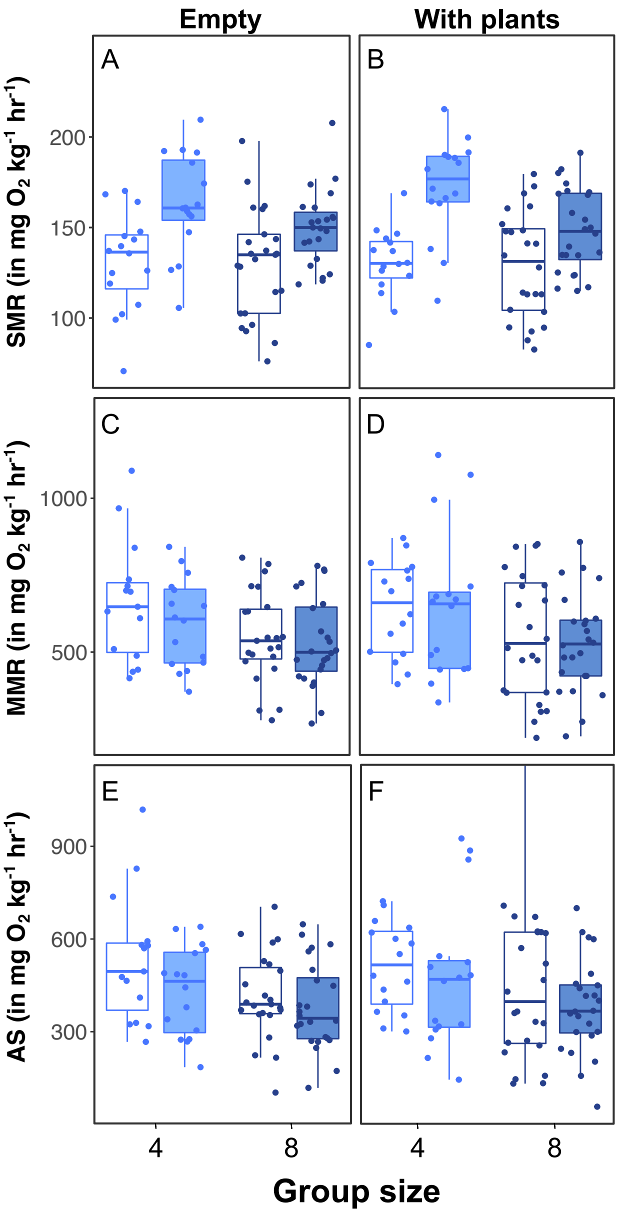

Figure 3: Observed SMR (A-B), MMR (C-D), and AS (E-F) of Eurasian minnow. Light blue and dark blue boxes and points represent estimates for fish held in groups of four and eight, respectively. Clear and shaded boxes represent initial and final respirometry trials, respectively. A-C-E panels refer to experimental tanks without plant shelter, and B-D-F refer to experimental tanks containing plant shelter. Middle thick line of the boxplots corresponds to the median, lower and upper limits correspond to the first and third quartiles of the data, and whiskers extend to the range of the data.

Discussion

The main goal of this study was to assess whether being in a smaller or larger group of conspecifics and having plant shelter available or not could modulate expression of metabolic traits. Minimum metabolic rates estimated in presence of shelter were lower than those estimated in absence of shelter, for both respirometry trial. This indicates that plant shelter availability during respirometry trials has a consistent and robust lowering effect on estimates of minimum metabolic rates in Eurasian minnow, as the recent social treatment did not mask this effect. We did, however, observe an overall increase in estimates of SMR between the initial and final respirometry trial, with the increase in SMR throughout the study being two-fold higher for fish held in groups of four as compared to that of fish held in groups of eight. Availability of plant shelter in experimental tanks during the social treatments did not affect metabolic rates. Whether such effects would be similar if fish could see their conspecifics during the respirometry trials remains to be tested. Nonetheless, our results suggest that recent social group size can have metabolic effects that carry over, even when fish are at rest and in isolation, such as during respirometry trials. This means that group size could have a modulating effect on levels of baseline metabolism, which could in turn have implications on an animal's energy budget, including growth, reproductive investment, and overall performance capacity. In the current study, the presence of more groupmates in the social treatment was associated with lower metabolic rate, suggesting that a reduction in energy demand may be an additional benefit of living in larger social groups.

Presence of shelter during respirometry trials

Presence of plant shelter during respirometry trials lowered estimates of metabolic rates both before and after exposure to the social treatments. Presence of shelter during respirometry trials has been associated with lower metabolic rates in some species (Fischer 2000, Finstad et al. 2004, Millidine et al. 2006, Norin et al. 2018) but not in others (Fischer 2000, Kegler et al. 2013), or to mixed results (Chrétien et al. 2021). Using shelter can reduce the occurrence of otherwise energetically demanding activities, such as those associated with maintaining vigilance against predators (Lind and Cresswell 2005, Millidine et al. 2006). It was surprising that the effect of shelter was stronger for night-time than for day-time $\dot{M}O_{2\mathrm{min}}$, assuming the main reason for sheltering is to remain visually hidden. This pattern was nonetheless observed in another study, where an effect of shelter presence was observed during the night but not during the day (Norin et al. 2018). It is possible that fish showed higher levels of spontaneous activity during day-time which might mask any effect of the shelter on $\dot{M}O_{2\mathrm{min}}$, although no consistent relationship has been observed between activity and light intensity in our study species (Jones 1956). Another potential explanation is that fish had time to acclimate to the presence of shelter before lights were turned off for the night, and therefore anticipated that they could be sheltered at night. In the laboratory, lights were turned off at 7:00 pm, so about 3 to 6 hours after plant cover was placed over the chambers (depending if this condition occurred on the 1st or the 2nd day of the respirometry trial). We predicted that the magnitude of the effect of shelter on metabolic rates would be smaller after the 3-week social treatment. This trend was not observed, suggesting that individuals did not adjust their metabolic response to immediate shelter presence, regardless of the group size or level of shelter availability they received during the social treatment. This indicates that shelter availability has a consistent and robust lowering effect on resting metabolic rates in Eurasian minnow and likely other species with similar social systems and patterns of habitat use.

Social treatments and metabolic rates

There was an overall increase in estimates of SMR throughout the study. Importantly, group size affected the strength of the increase: fish held in groups of four showed a two-fold higher increase in estimated SMR than fish held in groups of eight. Although Eurasian minnows can be found in small groups in the wild (similar to that used during the social treatments of the current study), they can also form much larger shoals (Magurran and Pitcher, 1983; S. S. Killen, University of Glasgow, personal observation). While it is therefore possible that the larger group size has a buffering effect on individual metabolic costs, through improved security or reduced individual vigilance (Nadler et al. 2016, Culbert et al. 2019), caution must be exercised when extrapolating the trends observed here to groups with hundreds of fish in nature. We cannot rule out that conditions may have been more favorable for growth in tanks with groups of four fish, even if food was not a limited resource in any social treatment. However, there was no relationship between final SMR and SGR, nor was there an interaction between SGR and social treatment conditions (Tables S1-S2, Fig. S1-S2), suggesting other mechanisms are more likely to explain the differences observed. Since all experimental tanks were of the same size, densities varied between group size ($\text{density}_{4\text{fish}} = 83$ fish m^{-3}; $\text{density}_{8\text{fish}} = 166$ fish m^{-3}). Therefore, the differences observed could be either due to differences in group sizes or densities. For instance, fish in groups of four potentially had more volume available for individual exploration and an increased need for individual vigilance, potentially increasing the cognitive load and associated metabolic costs that may carry over, even when the fish are at rest, during respirometry for estimates of SMR (Moss et al. 1998). Prolonged changes in locomotor activity level due to social interaction or vigilance may induce changes in muscle enzyme levels and mitochondria density, and thus affect fish minimum energy demand (Killen et al. 2016b).

Intensity of competition and strength of hierarchy structures could also vary with group sizes. For example, Pottinger and Pickering (1992) observed that social hierarchies emerged in rainbow trout *Oncorhynchus mykiss* held for six weeks in pairs or in groups of 5, but not in groups of 10 fish. An increase in aggressive behaviour such as pecking incurs increased activity and metabolic costs (Marchand and Boisclair 1998). With increasing group size, competition for limited resources like shelter may increase but dominance hierarchy tends to weaken, as the cost of interacting with multiple individuals may become too high (Sloman and Armstrong 2002).

We did not observe any statistically significant difference in SMR for fish held in experimental tanks containing plant shelter or not. It is possible that plant shelter in the experimental tanks were considered as a limited resource that stimulated competition, especially for the 8-fish groups. In experimental tanks with plant shelter available, only one artificial plant was provided, meaning that for the 8-fish groups, there was relatively less *per capita* shelter available than for the 4-fish groups, which could have enhanced social stress. Sustained stress in social groups with stronger dominance hierarchies could also carry over and limit our ability to effectively estimate SMR (Sloman et al. 2000, Killen et al. 2014, Metcalfe et al. 2016). Additional research on the effects of social dynamics on fish cognitive abilities or stress indicators could shed light on the mechanisms underlying the results observed here.

We did not expect group size to affect metabolic rates in the initial respirometry trial as fish were all held in the same high-density stock tank beforehand. Yet, fish held in groups of four had significantly higher MMR and AS than fish held in groups of eight before the 3-week social treatment (Table 2). However, this result seems to be driven by a single batch of fish. Groups of four fish were created from the first and the fourth batches while groups of eight fish were created from batches two, three and five. Only the first batch of 16 fish subjected to our experiment reached overall higher MMR (and AS) than the other batches at the initial respirometry trial (Fig. S3). One hypothesis that might explain the observed result is that the first batch may have been composed of individuals with higher susceptibility to capture, a trait that can be associated with higher metabolic rates (Redpath et al. 2010). While this pattern could be interesting to investigate in other studies, we can only interpret it here as a measurement artefact and cannot link this result to the social treatments. We conducted respirometry trials before and after the social treatments first to account for initial differences in metabolic rates, and second to quantify the relative change in metabolic rates after the social treatments. Regardless of initial differences in metabolic rates, that may be driven by the first batch of fish subjected to our experiment, results from models show there was no significant difference in MMR between trials, suggesting no relative change in MMR throughout the experiment. In addition to statistically controlling for effects from initial differences in metabolic rates by including "trial" and its interaction with other effects in full models, we also included "batch number" as a potential random effect in all our models to account for higher similarities in fish from the same batch compared to other fish. Batch number was retained in a nested structure with fish ID for night-time $\dot{M}O_{2\text{min}}$, day-time $\dot{M}O_{2\text{min}}$ and SMR models. It was not, however, kept in models on MMR or AS, because its inclusion resulted in singular fits (Matuschek et al. 2017): no variance was associated to the random effect "batch number". In any case, models using either "fish ID" or "batch number /fishID" as a random component generated similar results (Table S3). We consider that our statistical approach was robust to control for initial differences in metabolic rates, and to higher similarities in fish from the same batch compared to other fish. Our results however illustrate the importance of accounting for unforeseen or unforeseeable initial differences in metabolic rates when designing experiments. For instance, high susceptibility to capture is a trait that can correlate with MMR (Redpath et al. 2010), and might explain the pattern we observed when comparing MMR of the first batch of fish "captured" in the stock tank to MMR of the subsequent ones. One way to overcome this issue would have been to systematically allocate the 16 fish from each batch to two groups of four and one group of eight, instead of randomly assigning all fish from a given batch to a unique group size. Another way would be to avoid using the first batch of fish "captured" in a stock tank for experiments. Testing approaches to control for initial differences in metabolic rates would be useful to improve experimental designs, and should be the focus of further research.

The effect of the social environment on trait plasticity has been widely studied in behavioural ecology, but generally overlooked in comparative physiology (Gilmour et al. 2005). Yet, the social environment can influence individual's stress levels and in turn affect the ability to tolerate additional stressors, like thermal stress (LeBlanc et al. 2011) and hypoxia (Thomas and Gilmour 2012), especially in subordinate individuals. Conversely, group living has been associated with a reduction in overall metabolic demand, likely through a reduced need for individual vigilance (Roberts 1996). Similarly, shoaling has been suggested to have a "calming effect" and to reduce metabolic rates of social fish species, through conspecific visual and olfactory cues (Nadler et al. 2016). There is a need to consider how the social environment may affect physiological responses as, on the one hand, social dynamics may increase individual stress, but on the other hand, living in social groups may buffer physiological responses to some stressors (Culbert et al. 2019). We observed that group size could influence SMR in Eurasian minnows, which can be attributable to increased social stress at lower densities for these social fish. The study of interactions among individuals, dominance ranks, and robustness of dominance structure in the different social treatments could shed light on the results obtained here. It is possible that increased group size and habitat complexity induces metabolic plasticity, which suggests that selection on energy expenditure in animals with strong social systems may be less likely to result in genetic change. Our results highlight the importance of understanding the role of social dynamics on variations in individual metabolic traits and thus on the physiological consequences of habitat selection (Huey 1991).

Acknowledgements

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Contributions:

E.C., D.B., S.J.C., and S.S.K. conceptualized the project. E.C. and S.S.K. designed the experiments. E.C. performed the experiments, analyzed the data and wrote the manuscript. All authors contributed critically to the manuscript.

Supplementary information

Specific growth rate

Fish were fed *ad libitum* a combination of pellets and blood worms in their experimental holding tank during the 3-week social treatment to minimize potential effects of density on individual food intake and growth. We compared daily specific growth rate (SGR: in % day^{-1}) across social treatments and observed that fish held in groups of eight had on average lower SGR (Table S1), but that SGR was overall very variable among individuals (Figure S2).

Further, we tested if SGR could influence metabolic rates. It was not possible to include SGR in the models presented in the results of the manuscript as those models included more than one estimate of metabolic rates per individual (initial vs final respirometry trial), while we have a single SGR per individual. Therefore, we tested if SGR and its interaction with the social treatment could influence metabolic rates estimated at the final respirometry trial. There was no effect of SGR on any metabolic rate (Table S2, Figure S3). In addition, there was no interaction between SGR and group size or shelter availability.

Table S1: Results of linear model relating specific growth rate (SGR) of Eurasian minnows to the social treatment (group size and shelter availability).

Response variable	Effect	Estimate ± standard error	*F*	p-value	R^2_{adj}
SGR	Group size	-0.152 ± 0.051	9.011	0.004	8.4
	Shelter availability	0.025 ± 0.050	0.248	0.620	

Table S2: Results of linear model relating final standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) of Eurasian minnows to the specific growth rate (SGR), the social treatment (group size and shelter availability), and their interaction*.

Response variable	Effect	*F*	p-value
Final SMR	SGR	2.036	0.158
	Group size	12.232	<0.001
	Shelter availability	0.190	0.664
Final MMR	SGR	0.028	0.868
	Group size	4.983	0.029
	Shelter availability	0.285	0.595
Final AS	SGR	0.001	0.972
	Group size	3.182	0.078
	Shelter availability	0.235	0.629

*All interactions were non-significant and were therefore removed from models.

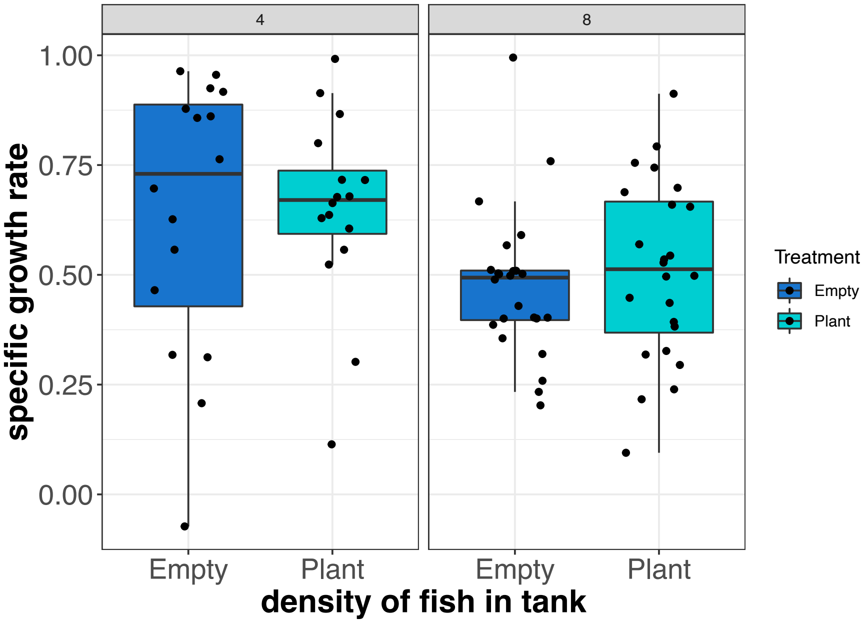

Figure S1: Boxplot of specific growth rate (SGR; in % day^{-1}) of fish in each social treatment consisting in a combination of group size (left: four fish; right: eight fish) and shelter availability (no plant shelter in blue; with plant shelter in turquoise). Middle thick line of the boxplots corresponds to the median, lower and upper hinges correspond to the first and third quartiles of the data, and whiskers extend to the range of the data. Each fish SGR is overlayed on the boxplot (black dots).

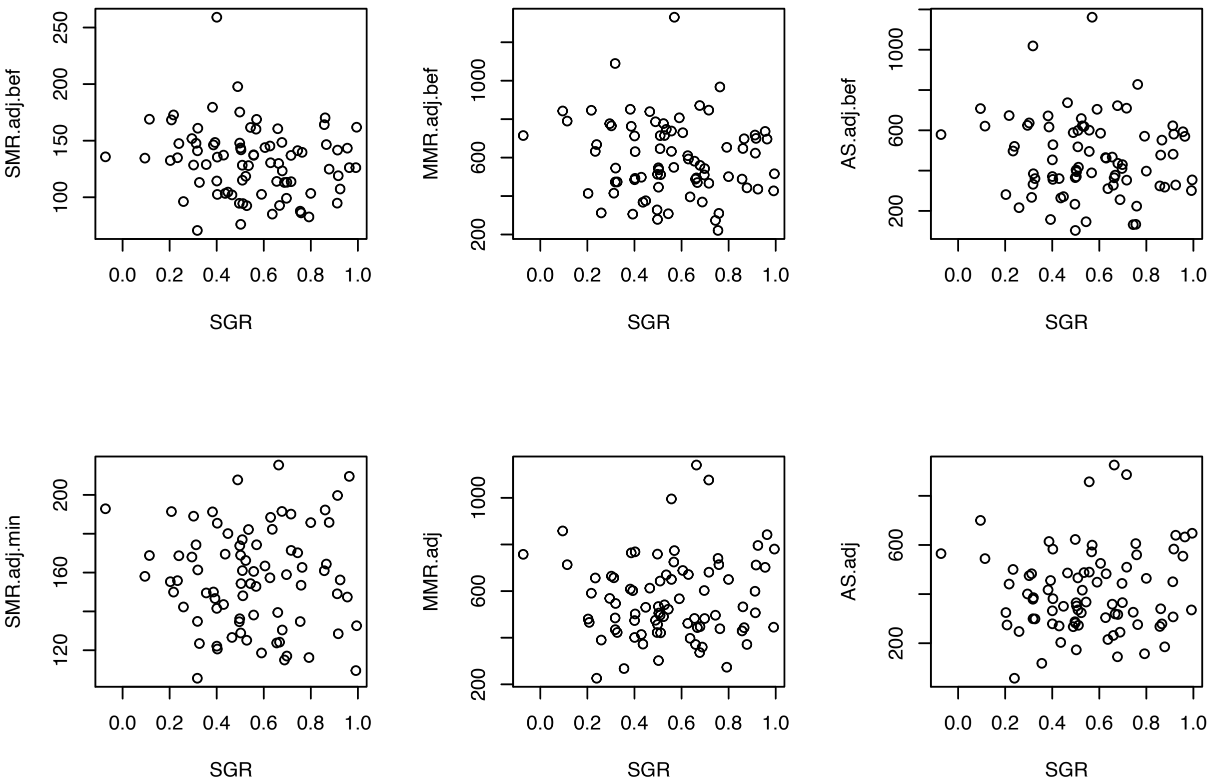

Figure S2: Observed SMR, MMR, and AS of Eurasian minnow (in mg O_2 kg^{-1} hr^{-1}) during the initial (top row) and final (bottom row) respirometry trial in relation to specific growth rate (SGR; in % day^{-1}).

MMR and AS

Table S3: Results of linear mixed model relating maximum metabolic rate (MMR) and aerobic scope (AS) of Eurasian minnows to the moment of the respirometry trials and the social treatment (group size and shelter availability). Fish ID and batch number were included in the models as a random effect in a nested structure (batch number/Fish ID). R^2_m is the marginal R^2 (percentage of variance explained by the fixed effects) and R^2_c is the conditional R^2 (percentage of variance explained by the fixed and the random effects).

Response variable	Effect	χ^2	p-value	R^2m	R^2c
MMR	Trial	1.312	0.252	6.3	24.7
	Group size	6.717	0.010		
	Shelter availability	0.224	0.636		
AS	Trial	4.813	0.028	7.5	23.2
	Group size	7.159	0.007		
	Shelter availability	0.262	0.609		

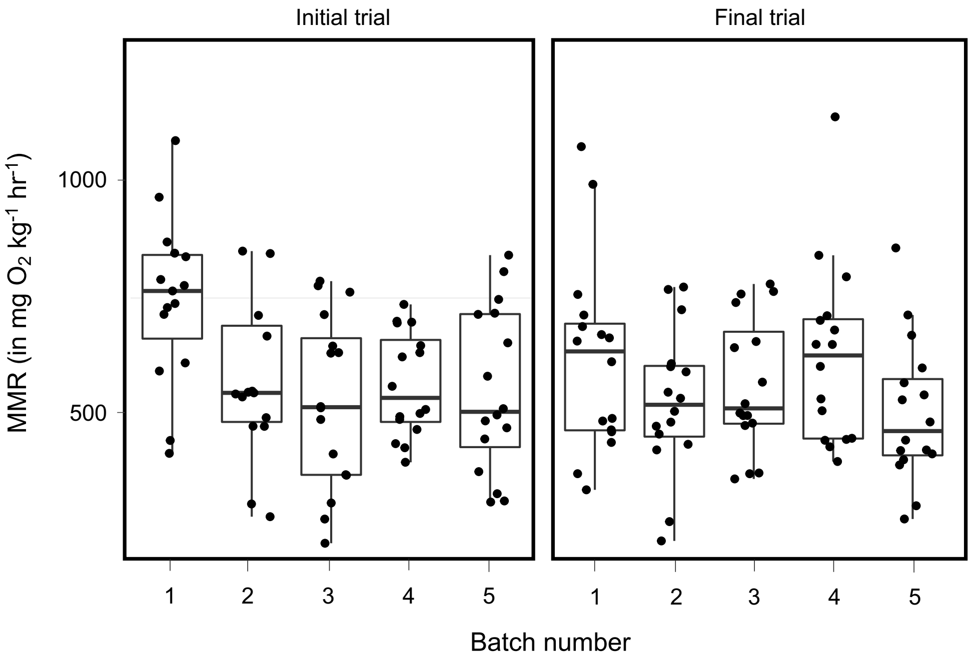

Figure S3: Maximum metabolic rates (MMR) per batch of fish captured together from the stock tank. Left panel shows rates measured in the initial respirometry trial, right panel shows rates measured at the final respirometry trial. Middle thick line of the boxplots corresponds to the median, lower and upper hinges correspond to the first and third quartiles of the data, and whiskers extend to the range of the data. Each fish MMR is overlayed on the boxplot (black dots).

Pêche sur la Rivière Kiamika, Québec (Photo : C. Guéveneux-Julien)

Conclusions

La présente thèse avait comme objectif principal l'étude des déterminants et des conséquences physiologiques de la sélection des habitats chez les poissons. Pour le **Chapitre 1**, une approche corrélative a été utilisée, en associant des données de télémétrie à des conditions environnementales afin d'identifier des associations poissons-habitats et créer des modèles de sélection des habitats. Pour le **Chapitre 2** et le **Chapitre 3**, une approche mécaniste a été utilisée, en quantifiant les réponses physiologiques de poissons à des conditions environnementales et des environnements sociaux contrôlés en laboratoire. La Figure 1 présente les travaux de chaque chapitre dans la perspective écophysiologique de l'étude des associations poissons-habitats. Les prochaines sections soulignent les contributions à la littérature scientifique associées à chaque chapitre et les pistes de recherches futures soulevées par les résultats de la thèse.

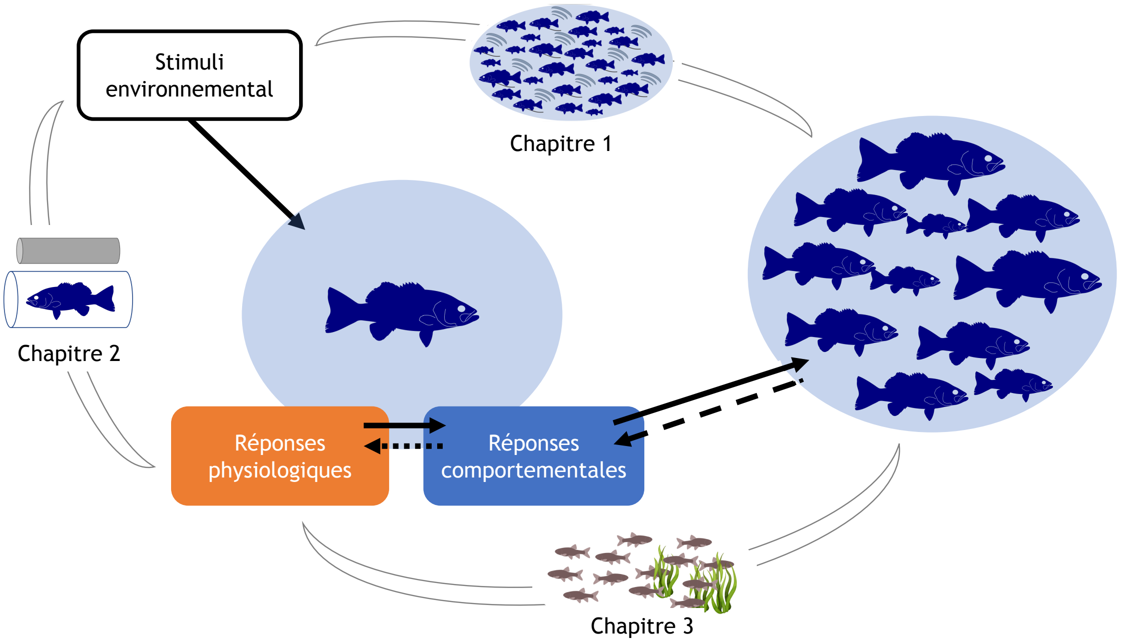

Figure 1 : Schématisation des contributions de la thèse dans la perspective écophysiologique de l'étude des associations poissons-habitats, telle que présentée en introduction.

Sélection des habitats

Pour le **Chapitre 1**, des données de télémétrie et de conditions environnementales dans une rivière ont été combinées afin d'identifier les variables déterminant la sélection des habitats des achigans à petite bouche. Le premier objectif était de comparer la capacité prédictive de modèles de sélection des habitats intégrant la variabilité individuelle. Nous avons créé six modèles à priori combinant différentes variables pouvant expliquer la sélection des habitats chez les achigans à petite bouche basés sur les connaissances préalables des associations achigans-habitats telles que rapportées dans la littérature scientifique et sur les variables hydrologiques caractérisant la rivière. Grâce à la validation croisée, nous avons démontré que les modèles incluant les variables représentant la présence de refuge avaient un meilleur prédictif que ceux qui ne les incluaient pas. Le deuxième objectif était de tester l'existence de groupements de poissons présentant des similitudes dans leur sélection d'habitats. Nous avons identifié trois groupements de poissons définis par leur sélection d'habitats. Bien qu'il y avait un chevauchement entre les conditions environnementales utilisées par chacun des groupements, le groupement 2 se distinguait spécifiquement en n'étant pas associé à la présence de refuge. Le troisième objectif visait à identifier les conditions environnementales influençant la sélection des habitats au niveau individuel, des groupements et de la population. Les résultats ont montré qu'il y a une plus grande variabilité dans la sélection des habitats entre les individus qu'entre les groupements. La sélection des poissons pour chaque condition environnementale a varié au niveau individuel. Seule la préférence pour la présence de refuge a varié entre les groupements, les poissons du groupement 2 ayant sélectionné davantage des habitats sans refuge. Malgré tout, nous avons noté une sélection positive des refuges au niveau de la population.

Les principales contributions à la littérature associées à ce chapitre sont (1) de démontrer les avantages d'intégrer la variabilité interindividuelle dans le processus de modélisation afin d'identifier les meilleurs modèles par validation croisée, (2) d'utiliser la validation croisée afin de distinguer les conditions environnementales expliquant la variabilité dans la sélection des habitats des individus aux populations, et (3) d'identifier des groupements présentant des similitudes dans leur sélection d'habitats. Cette dernière contribution est particulièrement importante. Si des groupements d'individus au sein d'une population diffèrent dans leur sélection d'habitats, plusieurs questionnements peuvent être soulevés. Il est possible que les ressources du milieu soient limitées, restreignant les individus les moins compétitifs dans des habitats alternatifs. Il est possible que les différences soient liées à la personnalité des individus (e.g. timides ou téméraires). Il est également possible que ces différences soient liées à différentes stratégies alimentaires. Des études seraient requises afin de déterminer si ces groupements sont stables temporellement et s'ils sont associés à des taux de survie ou de reproduction différents (Hertel et al. 2020). Dans une perspective de conservation, l'existence de ces groupes pourrait permettre de mettre en lumière la capacité actuelle des habitats à supporter les populations et le potentiel de résilience des populations à des changements environnementaux (Bennett 1987).

Les données de télémétrie nous ont permis de créer des modèles de sélection des habitats intégrant la variabilité interindividuelle mais leur potentiel en écologie comportementale est beaucoup plus vaste (Hertel et al. 2020). Les données de radio-télémétrie peuvent être récoltées par des bornes radio fixes ou par un échantillonnage avec une antenne et un receveur-radio. Les bornes fixes permettent un suivi continu des poissons portant un émetteur mais la précision des positions obtenues dépend du nombre et de la localisation des bornes. Le suivi avec une antenne est discontinu mais il peut être plus précis puisqu'il peut s'effectuer par bateau, ce qui permet de s'approcher très près de chacune des positions de poissons (Cooke et al. 2013b). Puisque nous avons opté pour le suivi avec antenne, nous avons pu associer les positions de poissons aux conditions environnementales très locales. Nous avons également varié les moments de la journée durant lesquels le suivi des poissons sur la rivière s'est effectué, de manière à couvrir la gamme des habitats utilisés par les poissons durant un cycle journalier. Les données obtenues nous ont permis de créer des modèles et d'investiguer la variabilité interindividuelle dans la sélection des habitats. La stratégie d'échantillonnage utilisée ne nous a par contre pas permis de quantifier les taux de mouvements des poissons. La quantification des taux mouvements aurait pu nous indiquer si les poissons faisaient des déplacements répétés dans l'espace ou nous informer sur le type d'utilisation de chaque habitat (e.g. repos, déplacement; Hertel et al. 2020). Des études empiriques suggèrent que les taux de mouvement d'un animal devraient diminuer lorsqu'il traverse un habitat de grande qualité (Kuefler et al. 2012). Une étude comparative des mouvements du grand brochet *Esox lucius* a d'ailleurs montré que les poissons provenant d'une rivière sujette à des fluctuations extrêmes des régimes d'écoulement liées à un barrage en amont bougeaient davantage que ceux provenant d'une rivière à régime d'écoulement naturel (Harvey-Lavoie et al. 2016). En écologie du paysage, l'étude du mouvement des animaux a mené à l'émergence de deux grands cadres conceptuels : le paysage énergétique (sensu *energy landscape*) et le paysage de la peur (sensu *landscape of fear*) (Gallagher et al. 2017). Le paysage énergétique est un cadre conceptuel permettant de comprendre ou de prédire les variations dans les mouvements des animaux par les variations à l'échelle du paysage (Shepard et al. 2013). Le paysage de la peur représente de manière spatialement explicite les risques relatifs de prédation selon les caractéristiques de l'environnement physique (Laundré et al. 2010). Gallagher et al. (2017) suggèrent d'intégrer les paysages énergétique et de peur pour mieux comprendre les mécanismes sous-jacent l'écologie spatiale des animaux.

Le potentiel d'extrapolation des modèles est généralement limité à l'étendue des données qui ont servi à créer les modèles. Une méthode de validation croisée appropriée pour les données structurées (dans l'espace, dans le temps ou par individu) peut toutefois permettre de mieux estimer l'erreur de prédiction des modèles (Roberts et al. 2017). C'est pourquoi nous avons séparé nos données par blocs d'individus pour la validation croisée. De cette manière, nous avons testé plusieurs fois nos modèles sur de « nouveaux » individus. De ce fait, nos modèles pourraient avoir une bonne capacité de prédiction de la sélection des habitats d'autres populations d'achigans dans des rivières similaires pour la même période de l'année. Toutefois, il serait hasardeux de tenter de prédire la sélection d'habitats des achigans au printemps ou à l'automne à partir de nos modèles. Un suivi à long terme des positions de poissons par des bornes fixes aurait pu permettre d'obtenir les données requises pour la création de modèles de sélection d'habitats pour le printemps, l'automne et l'hiver. Ces données sont nécessaires afin d'identifier les habitats critiques pour tout le cycle de vie des poissons et pour caractériser les domaines vitaux (Hertel et al. 2020). Le domaine vital est un espace dans lequel un individu fera la majorité de ses activités, telles se nourrir, se reproduire ou se protéger des prédateurs. Il est attendu que la taille du domaine vital devrait être plus petite dans un habitat de qualité que dans un habitat de moins bonne qualité (Minns 1995).

Conséquences physiologiques de l'environnement physique

Pour le **Chapitre 2**, l'objectif était de quantifier l'effet de la présence de refuge sur plusieurs traits métaboliques des achigans à petite bouche. Nous avons mené des expériences de respirométrie en laboratoire pour estimer les taux métaboliques en présence ou en absence de refuge sur des poissons de la rivière Kiamika, où les travaux pour le **Chapitre 1** se sont déroulés, ainsi que sur des poissons du lac Long. Les RMR estimés en présence de refuge étaient plus bas que ceux estimés en absence de refuge pour les poissons provenant du lac Long. Aucune différence n'a été observée dans les RMR des poissons de la rivière Kiamika estimés en présence ou en absence de refuge. Nous avons également noté que les SMR étaient plus bas en présence de refuge chez les individus plus gros alors qu'aucune différence n'a été observée entre les SMR estimés en présence ou en absence de refuge chez les plus petits individus. Nous avons aussi montré un effet de la présence de refuge sur RT mais seulement lorsqu'on a tenu compte du statut de dominance des achigans. Le RT des individus dominants était plus court en présence de refuge alors qu'aucune différence n'a été observée pour ce trait en présence ou en absence de refuge chez les individus soumis. Les résultats n'ont pas démontré d'effet constant de la présence de refuge sur les dépenses énergétiques, ce qui a inspiré une bande-dessinée réalisée en collaboration avec un illustrateur dans le cadre d'un concours de vulgarisation scientifique (**Annexe I**).

La principale contribution à la littérature scientifique associée à ce chapitre est la quantification des effets de la présence de refuge sur AS, RT et EPOC. Bien que des études aient été menées afin de quantifier les effets de la présence de refuge sur l'estimation de SMR ou RMR (Fischer 2000, Finstad et al. 2004, Millidine et al. 2006, Kegler et al. 2013, Norin et al. 2018), le **Chapitre 2** est, au meilleur de nos connaissances, la première étude visant à quantifier les effets de la présence de refuge sur AS, RT et EPOC chez les poissons. Or, des variations dans ces traits peuvent affecter la performance des poissons dans leur milieu naturel. La capacité aérobique (AS) représente l'énergie métabolique disponible pour l'activité et peut avoir des conséquences à long-terme sur la croissance et la reproduction (Fry 1971, Claireaux and Lefrançois 2007). Le temps de récupération (RT) et la consommation d'oxygène excédentaire post-activité (EPOC) peuvent influencer la capacité d'un organisme à reprendre ses activités après un effort intense (Zeng et al. 2010). Nous nous attendions à une AS plus élevée, à un RT moins long et à un EPOC moins élevé en présence de refuge, en particulier parce que les refuges pourraient remplacer les dépenses énergétiques liés à la vigilance (Lind and Cresswell 2005, Millidine et al. 2008). Nous n'avons pas observé ces effets, sauf pour RT en considérant la dominance.

Durant les expériences de respirométrie, la présence de refuge était contrôlée. Il serait intéressant de mener une expérience durant laquelle les poissons auraient à choisir d'utiliser ou non un refuge après une activité intense. Il serait possible de quantifier la durée d'utilisation des refuges selon l'intensité de l'activité, à différentes températures, en présence de congénères ou non, etc. Les poissons soumis à ce type d'expérience pourraient porter un enregistreur cardiaque, ce qui permettrait de quantifier si les poissons choisissant d'utiliser des refuges diminuent leurs dépenses énergétiques. Ce type d'expérience permettrait de mieux comprendre le comportement et les bénéfices d'utilisation des refuges pour ces poissons.

Conséquences physiologiques de l'environnement social

L'objectif général du **Chapitre 3** était de quantifier et de comparer les effets de la taille des groupes sociaux et de la présence de refuge sur le métabolisme de vairons. Nous avons mené des expériences de respirométrie avant et après une expérience sociale de trois semaines, durant laquelle les poissons étaient gardés en groupes de 4 ou 8 poissons dans des aquariums qui contenaient un refuge ou non. Durant les expériences de respirométrie, les taux métaboliques étaient estimés en présence et en absence de refuge. Avec ce design, il était possible de quantifier si l'effet de la présence de refuge serait similaire avant et après l'expérience sociale. Nous avons posé l'hypothèse que la présence de refuge diminuerait les taux métaboliques des vairons mais que cet effet serait de moins grande ampleur après l'expérience sociale. Cette hypothèse a été partiellement supportée par les résultats. Les taux métaboliques estimés en présence de refuge étaient plus bas que ceux estimés en absence de refuge durant les deux expériences de respirométrie mais la taille de l'effet n'a pas été influencée par l'expérience sociale. Ce design a également permis de déterminer si l'expérience sociale pouvait influencer les dépenses énergétiques futures. Nous avons posé l'hypothèse que SMR serait influencé par la taille des groupes sociaux et par la présence de refuge ou non dans les aquariums. Encore une fois, l'hypothèse a été partiellement supportée. Le SMR a augmenté après l'expérience sociale, et ce, de manière deux fois plus importante pour les poissons gardés en groupes de 4 que pour les poissons gardés en groupe de 8. Cependant, la présence de refuge dans les aquariums durant l'expérience sociale n'a pas eu d'effet sur les taux métaboliques. Les résultats démontrent que la taille des groupes peut influencer les dépenses énergétiques futures des individus, même lorsqu'ils se retrouvent seuls.

La principale contribution du **Chapitre 3** était d'investiguer les effets de la taille des groupes sociaux sur les taux métaboliques des poissons. L'environnement social peut influencer les comportements, les niveaux de stress et les dépenses énergétiques des individus (Gilmour et al. 2005, Webster and Ward 2011). Or, il y a peu d'études sur les effets de l'environnement social sur les réponses physiologiques. Cela s'explique en partie par le fait qu'il y a peu de recherches qui intègrent la physiologie et le comportement, les deux disciplines étant le plus souvent séparées (Cooke et al. 2014a). Cela s'explique également du fait que le paradigme dominant en physiologie comparée est que les processus physiologiques influencent les comportements individuels qui influencent ensuite les réponses populationnelles (Gilmour et al. 2005). Les études ayant considéré l'effet des dynamiques sociales sur les réponses physiologiques se sont surtout intéressées aux effets de la position hiérarchique (Sloman et al. 2000, Killen et al. 2014, Metcalfe et al. 2016), de la personnalité (Redpath et al. 2010) ou de l'isolation sociale (Nadler et al. 2016, Huang et al. 2020) sur le métabolisme. Les travaux du **Chapitre 3** se distinguent par la comparaison des effets de la taille des groupes sociaux sur le métabolisme. Les résultats démontrent d'ailleurs que la taille des groupes sociaux peut influencer les taux métaboliques. Dans le cas des vairons, le stress individuel semblait diminuer avec la taille des groupes sociaux.

La prochaine étape serait d'investiguer les dynamiques sociales dans les groupes de différentes tailles afin de mieux comprendre ce qui explique les différences observées dans les taux métaboliques. Les mouvements d'agression peuvent augmenter les taux d'activité et augmenter les demandes énergétiques (Marchand and Boisclair 1998, Killen et al. 2016b). En outre, les taux métaboliques peuvent être influencés par le niveau hiérarchique des individus. Ils peuvent être corrélés à la dominance (Metcalfe et al. 2016) ou au stress chronique chez les individus soumis (Sloman et al. 2000). Il pourrait également être intéressant de reproduire les travaux du **Chapitre 3** avec des groupes de tailles différentes. On pourrait s'attendre à des différences dans l'intensité de la compétition selon la taille des groupes, ce qui pourrait influencer la stabilité des structures hiérarchiques (Pottinger and Pickering 1992, Sloman and Armstrong 2002). Une diminution de la vigilance individuelle dans des groupes de taille plus grande pourrait aussi diminuer les dépenses énergétiques (Nadler et al. 2016, Culbert et al. 2019). Comprendre les effets de l'environnement social sur les dépenses énergétiques pourrait amener des modifications de protocoles de recherche impliquant des poissons sociaux. Plus encore, ce type de recherche pourrait permettre d'estimer la proportion de la variabilité inter-individuelle observée dans les réponses physiologiques à des gradients environnementaux qui serait attribuable à la sociabilité.

Perspectives

La variable refuge a occupé une place centrale dans cette thèse étant donné l'espèce modèle utilisée pour le **Chapitre 1**. En effet, les conditions environnementales identifiées au **Chapitre 1** comme étant les plus importantes pour la sélection des habitats de l'espèce modèle devaient être utilisées dans un contexte expérimental pour le **Chapitre 2** afin d'étudier les conséquences physiologiques de la sélection des habitats. Les travaux des **Chapitres 2** et **3** ont montré que la présence de refuge pouvait avoir un effet différent sur les taux métaboliques selon l'espèce étudiée. Chose certaine, la présence de refuge est une composante importante de la sélection des habitats (Fukui 2001, Michaels and Preziosi 2015) qui peut influencer la croissance et les taux de survie des animaux (Hughes and Ward 1993, Tufto et al. 1996, Moreno et al. 1996).

Les travaux de cette thèse ont contribué à l'avancement des connaissances sur les conséquences physiologiques de la sélection des habitats, en particulier celles liées à l'utilisation de refuge et à la taille des groupes sociaux. Les conséquences physiologiques d'autres conditions environnementales liées à la sélection des habitats devraient également faire l'objet de recherche futures, en particulier les régimes d'écoulement dans les rivières. Les poissons d'eaux vives sont naturellement exposés à des fluctuations variables de vitesses de courant et de température de l'eau, et celles-ci devraient être accentuées avec les changements climatiques (van Vliet et al. 2013). Inversement, les perturbations anthropiques, telles les barrages hydro-électriques, diminuent généralement les crues maximales et affectent la variabilité temporelle des régimes d'écoulement (Macnaughton et al. 2015). L'étude des effets de ce genre d'altérations sur les poissons d'eaux vives est nécessaire afin de mieux prédire leur capacité à faire face aux facteurs de stress environnementaux associés aux changements climatiques (Cooke et al. 2013c, Horodysky et al. 2015).

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Annexe I.

Bande dessinée « Jouer à la cachette : une question de personnalité »


Jouer à la cachette:
Une question de personnalité
MartinPM
Emmanuelle Chrétien
Vous l'ignorez peut-être, les poissons ont des personnalités.
As-tu le résultat du test?
Attends. Dernière question.
Bienvenue Bar rayé
Carpe d'Aujourd'hui
Quiz personnalité
15. Vos vacances idéales:
A) La ville: égouts de Montréal
B) Un lac au bord d'un chalet
C) La mer morte: tourisme extrême
Clic!
Pis?!
Type «anguille»: votre personnalité est insaisissable!
Haha!
Un sujet fascinant. Emmanuelle Chrétien n'y pensait pourtant pas au début de son doctorat en biologie.
Elle a d'abord confirmé l'importance des cachettes pour l'Achigan à petite bouche, un poisson des rivières du Québec.
Mais pourquoi c'est si important pour l'achigan de se cacher?
Métro-boulot-dodo, les factures, les enfants...
Des fois j'ai besoin d'être dans ma bulle!
Pas une si petite bouche que ça!
Est-ce qu'un poisson stressé se calme plus rapidement dans une cachette?
Je le vérifie en comparant leur consommation d'oxygène...
Expérience en cours
Avec cachette
Sans cachette
Mesure d'oxygène


Emmanuelle a répété cette expérience à l'Université de Montréal avec plusieurs achigans.
Analyses en cours
Résultatooo
PAS GRAND CHOSE!
Comme souvent en science, son expérience n'a pas montré de résultats significatifs.
BANG!
Les achigans se calment au même rythme, dans les bassins avec ou sans cachette.
DRAMATISATION
Découragée, la chercheure sombre dans une période intense de procrastination.
Les chats qui se plantent!
Top5 niaiseux
Scrolle! Scrolle!
Jusqu'à ce qu'elle pense à la notion de «personnalité»
Carpe ou crapet?
Test de personnalité
Tellement!
Chez une espèce animale, tout les individus n'ont pas les mêmes traits de comportement.
T'es toujours agressif!
T'es toujours mou! Tu M'ÉNARVES!
Chez l'achigan, les individus de type «dominants/agressifs» bénificieraient davantage des cachettes. Ils sont toujours tellement énervés après leurs voisins et leurs proies qu'ils ont besoin d'une cachette pour se calmer.
J'haïs tout le monde!
Cachez-moi!
SPA grave
Venez relaxer
Bain tourbillon
Tellllement relaxe!
En tenant compte de la personnalité, on voit les résultats d'Emmanuelle différemment.
Personnalité
Sans cachette
Temps de retour au calme
Cachette
Relaxe@vite
agressif
Très énervé
Relaxe
soumis
Correct
Toujours correct
D'où l'importance de regarder chaque recherche sous différents angles.
Tu sauras que chaque personnalité permet de mieux comprendre notre monde!
MartinPM