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QUANTIFICATION DES RISQUES DE MORTALITÉ LIÉS À L'HABITAT CHEZ DES ESPÈCES DE POISSONS LACUSTRES

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RÉSUMÉ

Les caractéristiques physiques des habitats aquatiques modifient les interactions écologiques ainsi que la distribution spatiale chez les poissons. Nous avons mené des expériences d'attachement (angl. : « tethering experiments ») pour examiner l'effet de la transparence de l'eau et du couvert de macrophytes sur le risque de mortalité chez huit espèces de poissons retrouvées dans le lac Saint-Pierre (Québec, Canada). Le risque de mortalité pour six des huit espèces était influencé par la transparence ou par l'interaction entre la transparence et le couvert de macrophytes. Ces résultats indiquent que les variations dans la transparence pourraient générer une hétérogénéité spatiale de l'abondance des poissons par le biais d'effets directs, tel la réduction du nombre d'individus à l'échelle locale par la prédation, ou d'effets indirects, tel l'évitement des habitats plus risqués.

Mots-clés : analyses de survie, comportement, couvert de végétation, interactions prédateur-proie, mortalité, régression de Cox, transparence.

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AVANT-PROPOS

Ce mémoire comprend deux chapitres. Le premier représente une synthèse en français du projet de maîtrise. Le second est un article en anglais qui sera soumis pour publication dans le *Journal canadien des sciences aquatiques et halieutiques* et qui présente les résultats de mon projet de maîtrise.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

CHAPITRE 1
QUANTIFICATION DES RISQUES DE MORTALITÉ LIÉS À L'HABITAT CHEZ DES ESPÈCES DE POISSONS LACUSTRES

Introduction

Les caractéristiques de l'habitat influencent les interactions écologiques et la distribution spatiale des espèces de poissons (Jackson et al. 2001). La transparence de l'eau (Abrahams et Kattenfeld 1997; Utne-Palm 2002; van de Meutter 2005), le couvert de végétation (Savino et Stein 1989*a*,*b*; Eklöv 1997) ainsi que leur interaction peuvent fortement influencer les risques de prédation et la mortalité. Pour les espèces visuelles, la turbidité élevée peut contraindre les interactions entre les prédateurs et les proies en modifiant la distance de détection et la fréquence de rencontre entre les prédateurs et les proies. La faible visibilité diminue ainsi l'efficacité du comportement d'évitement chez les espèces proies (Abrahams et Kattenfeld 1997; Turesson et Brönmark 2007). Dans ces circonstances, les prédateurs réduisent principalement le nombre de proies de manière directement proportionnelle à la fréquence de rencontre avec celles-ci. En eaux claires, par contre, les proies peuvent détecter les prédateurs à une plus grande distance et ainsi les effets des prédateurs sont principalement indirects, résultant de la modification du comportement de la proie (Abrahams et Kattenfeld 1997; van de Meutter et al. 2005). Le couvert de végétation peut également affecter les interactions entre les proies et les prédateurs. Alors que certains prédateurs tel le brochet (*Esox lucius*), utilisent invariablement un mode de prédation à l'affût, d'autres, tel l'achigan à grande bouche (*Micropterus salmoides*), passent d'un mode de recherche active des proies à un mode de prédation à l'affût lorsque la densité de végétation augmente (Savino et Stein 1989*a*; 1989*b*). Le succès de prédation de certains prédateurs peut aussi être influencé par les modifications comportementales qui affectent l'utilisation du couvert par les proies en fonction de la densité de la végétation. Ainsi, en laboratoire, le succès de capture du brochet et de l'achigan à grande bouche est moins élevé avec le crapet arlequin (*Lepomis macrochirus*), car cette proie utilise davantage le couvert à mesure que la densité de la végétation augmente (Savino et Stein 1989b), contrairement au tête-de-boule (*Pimephales promelas*), qui utilise peu le couvert (Savino et Stein 1989b). De plus, les interactions prédateur-proie peuvent être influencées par les effets interactifs de la transparence de l'eau et du couvert de végétation. Par exemple, la perche eurasienne (*Perca fluviatilis*), une espèce visuelle, évite le couvert de végétation comme refuge à la prédation lorsque exposée à la prédation par le brochet à des transparences élevées (Skov et al. 2007).

L'impact de la transparence de l'eau (Rodríguez et Lewis 1997; Tejerina-Garro et al. 1998; Ostrand et Wilde 2004; Pouilly et Rodríguez 2004) et du couvert de macrophytes (Eklöv 1997; Petry et al. 2003) sur les interactions prédateur-proie jouent également un rôle important dans la structuration des communautés de poissons dans différents écosystèmes d'eau douce mondiaux. Dans la plaine inondée du fleuve Orénoque au Venezuela, les espèces de poissons utilisant davantage la vision étaient numériquement plus abondantes dans les lacs d'eaux claires, alors que les espèces possédant des adaptations sensorielles aux conditions de faible intensité lumineuse étaient prédominantes dans les lacs d'eaux turbides (Rodríguez et Lewis 1997). Ainsi, le résultat des interactions prédateur-proie dépendait des adaptations sensorielles des espèces au milieu optique (Rodríguez et Lewis 1997). La complexité structurelle de l'habitat peut aussi influencer les communautés de poissons en affectant les interactions entre les prédateurs et les proies tel que le brochet et sa proie, la perche eurasienne (Eklöv 1997). Au lac Degersjön, Suède, l'abondance de la perche eurasienne était la plus élevée à une densité de végétation intermédiaire (40-60 tiges · m^{-2}) comparativement aux zones ou la végétation était dense (60-150 tiges · m^{-2}), peu dense (5-40 tiges · m^{-2}) ou absente (0 tiges · m^{-2}), reflétant possiblement un compromis entre la disponibilité des ressources alimentaires (macroinvertébrés en association avec la végétation) et des refuges (Eklöv 1997). De plus, en absence de végétation, la perche eurasienne utilise une stratégie de quête alimentaire en groupe qui semble plus efficace que le mode de prédation à l'affût que le brochet utilise invariablement (Eklöv 1992). Par contre, en présence de végétation, la perche eurasienne s'alimente plutôt en solitaire, alors que le brochet voit son efficacité de prédation augmenter comparativement à la perche eurasienne (Eklöv et Diehl 1994).

Les exemples présentés montrent comment la transparence de l'eau et la végétation peuvent structurer les communautés de poissons de par leurs impacts sur les interactions prédateur-proie. L'objectif de cette étude était d'évaluer les effets de la transparence de l'eau, du couvert de macrophytes et de leur interaction sur le risque de mortalité pour huit espèces de poissons abondantes au lac Saint-Pierre, un lac fluvial du fleuve Saint-Laurent (Québec, Canada). L'hétérogénéité spatiale marquée de la transparence et du couvert de végétation de ce lac en fait un système propice pour examiner le lien entre le risque de mortalité et les caractéristiques de l'habitat. Le risque a été évalué par le biais d'expériences d'attachement (Minello 1993) et d'analyses de survie (Therneau et Grambsch 2000). La plupart des études antérieures ont exprimé le risque de mortalité en fonction de la proportion des individus survivant à la fin d'une expérience (e.g., McIvor et Odum 1988; Clark et al. 2003; Moody et Aronson 2007). Par contre, contrairement aux analyses de survie, cette approche ne permet pas d'extraire de manière optimale toute l'information contenue dans les temps de survie. De plus, les résultats basés sur la proportion d'individus survivant après une période de temps fixe peuvent dépendre sensiblement de la durée de cette période.

Méthodes

Aire d'étude

Le lac Saint-Pierre (Québec, Canada) (46°12' N, 72°50'O) est un lac fluvial qui constitue le dernier élargissement du fleuve Saint-Laurent avant son entrée dans l'estuaire (Figure 2.1). Ce lac est grand (superficie moyenne = 315 km^2 ; 469 km^2 lors des crues printanières) et peu profond (profondeur moyenne = 3.17 m). La zone littorale affiche une grande hétérogénéité spatiale en regard de la transparence (Frenette et al. 2003) et du couvert de macrophytes (Vis et al. 2003). La communauté ichtyenne du lac Saint-Pierre est composée d'environ 50 espèces de poissons résidentes (La Violette et al. 2003).

Expériences d'attachement

Les expériences d'attachement (angl, : « tethering experiments ») ont été conduites dans les zones littorales des rives nord et sud du lac Saint-Pierre (Figure 2.1), entre le 18 juin et le 30 août 2005. Huit espèces étaient considérées dans l'étude : la barbotte brune (*Ameiurus nebulosus*), la laquaiche argentée (*Hiodon tergisus*), le méné émeraude (*Notropis atherinoides*), le méné jaune (*Notropis crysoleucas*), le museau noir (*Notropis heterolepis*), le queue-à-tache-noire (*Notropis hudsonius*), l'omisco (*Percopsis omiscomaycus*) et la perchaude (*Perca flavescens*) (Tableau 2.1). Les sites ont été sélectionnés dans la zone littorale de manière à considérer un large éventail de valeurs de transparence et de couvert de macrophytes. Par contre, l'éventail des valeurs pour chaque espèce pouvait varier en fonction de leur occurrence dans différents habitats (Tableau 2.1). Les poissons utilisés dans les expériences étaient capturés à la seine de rivage (10 m x 2 m) en zone littorale, identifiés et mesurés (longueur à la fourche). Les poissons étaient attachés à un dispositif d'attachement permettant d'enregistrer le temps de survie (Ha 1996; Danilowicz et Sale 1999 ; Figure 2.2). Chaque chronographe comprenait un chronomètre et un système à déclenchement aimanté fixé dans un disque en résine permettant d'être submergé dans l'eau (diamètre : 9 cm) et suspendu à une corde de 50 cm. Un poisson était relié à une plaque de métal par un fil de nylon (longueur ~ 40 cm ; résistance 1 kg) passé dans le muscle sous la nageoire dorsale. Lorsqu'une prédation survenait, la plaque de métal était retirée de l'aimant, déclanchant le chronomètre. Afin d'éviter le déclenchement des dispositifs d'attachement dus aux mouvements normaux de nage des plus grandes proies plutôt que par un événement de prédation, la taille des poissons utilisés dans les expériences correspondait approximativement aux tailles des poissons utilisés par Ha (1996) (Tableau 2.1). Au premier jour, les poissons étaient attachés aux dispositifs préalablement mis en place entre 12h00 et 17h00 et étaient recueillis au deuxième jour entre 8h00 et 1200 (durée médiane des expériences : 20.6 h ; quartiles 25%-75% : 19.6 - 22.2 h) où le temps de survie des individus était noté, le cas échéant. Le temps de survie était déterminé comme étant la durée totale de l'expérience (de la mise à la sortie de l'eau) moins le temps écoulé depuis l'événement de prédation et la sortie de l'eau du dispositif. Un poisson n'ayant pas subi de prédation à la fin de l'expérience (temps de survie = durée de l'expérience) était codé comme un temps de survie tronqué. Puisqu'une proie attachée ne peut s'échapper, les expériences d'attachement peuvent créer des biais dans la détermination des risques de mortalité et surestimer les taux de prédation qui seraient normalement observés sur le terrain (Peterson et Black 1994). Par contre, cette étude ne visait pas à mesurer le risque absolu de mortalité, mais plutôt à comparer le risque relatif de mortalité dans différents habitats pour chaque espèce (Aronson et Heck 1995; Aronson et al. 2001). Nous avons assumé que le biais dû à l'attachement était comparable entre les habitats puisque la même technique d'attachement a été utilisée pour tous les individus (Aronson et Heck 1995; Aronson et al. 2001).

Mesures environnementales

À chaque site, la transparence de l'eau, le pourcentage de macrophytes émergents, la profondeur de l'eau et la taille du substrat étaient mesurés au premier jour de l'expérience. La transparence et la profondeur de l'eau étaient également mesurées au deuxième jour de l'expérience à la sortie de l'eau des dispositifs d'attachement. La transparence de l'eau était mesurée avec un disque de Secchi, un tube transparent (diamètre : 3.5 cm, longueur : 150 cm ; Dahlgren et al. 2004) et un tube de Snell (diamètre : 4.5 cm, longueur : 120 cm ; van de Meutter et al. 2005). Les données fournies par les tubes nous permettaient d'obtenir des mesures de transparence lorsque la transparence du Secchi excédait la profondeur de l'eau ce qui générait une lecture tronquée. Le disque de Secchi est l'instrument le plus couramment utilisé pour mesurer la transparence de l'eau. Par contre, les lectures étaient tronquées à 63% des sites expérimentaux. La relation entre les mesures du tube transparent et du disque de Secchi était linéaire (R^2 = 0.91) et non linéaire entre les mesures du tube transparent et du tube de Snell. Malgré que les mesures du tube de Snell permettaient généralement d'obtenir des mesures de transparence même si les valeurs du tube transparent étaient tronquées, nous avons standardisé toutes les mesures à l'échelle du tube transparent en raison de sa relation linéaire avec le disque de Secchi. Les valeurs tronquées pour le tube transparent ont été imputées par l'équation de la régression mettant en relation les mesures du tube transparent et les mesures du tube de Snell. Les paramètres de la régression ont été estimés par régression tronquée (Gelman et Hill 2007) des mesures du tube transparent (transformation en racine carrée) en relation avec les mesures du disque de Secchi. Pour les sites où la transparence excédait la limite des instruments (données tronquées pour tous les instruments ; 14.9% des sites), les valeurs de transparence ont été estimées à partir de modèles de régressions multiples en utilisant la latitude, la longitude, le jour julien et la profondeur d'eau comme variables prévisionnelles (R^2 = 0.65). Afin d'éviter que les fils de nylon du dispositif ne s'entremêlent aux macrophytes, les dispositifs étaient toujours installés aux abords de la végétation mais jamais à l'intérieur du couvert. Le couvert de macrophytes a été quantifié comme étant le pourcentage de macrophytes émergents sur une superficie de 2 m x 2 m centré sur le dispositif d'attachement. La taille du substrat à été quantifiée visuellement à partir d'échantillons de substrat prélevés à l'aide d'une carotte (diamètre interne : 20 mm) en quatre points également espacés autour du périmètre d'un cercle (rayon = 1 m) centré sur le dispositif d'attachement. La taille des particules de substrat était codée en fonction de l'échelle de Wentworth (1 = argile, 2 = limon, 3 = sable, 4 = gravier, 5 = roches) (Murphy et Willis 1996) et nous avons utilisé la moyenne de ces quatre points.

Analyses quantitatives

Pour chaque espèce, une courbe de Kaplan-Meier (Therneau et Grambsch 2000) a été préalablement utilisée pour examiner la survie en fonction du temps. D'autre part, le modèle de régression de Cox (Therneau et Grambsch 2000) a été utilisé pour évaluer l'effet des variables prévisionnelles sur le risque de mortalité pour chacune des espèces. Le modèle de régression de Cox est une approche semi paramétrique estimant la relation entre des covariables et le temps de survie. Cette approche tient compte de deux particularités statistiques des temps de survie : les temps de survie peuvent être tronqués à droite (un poisson n'ayant pas subi de prédation à la fin de l'expérience) et leur distribution est habituellement non normale (les temps de survie ne peuvent être négatifs) (Therneau et Grambsch 2000). Le modèle de régression de Cox se défini comme suit:

$h\ (t \mid X) = h_0\ (t) \exp\ (\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i)$,

où $h\ (t \mid X)$ est la fonction de risque au temps t pour les covariables $x_1, x_2, \ldots\ x_i$. La fonction de risque comprend deux parties; le risque de base, h_0, qui dépend seulement du temps et une fonction exponentielle des covariables prévisionnelles $x_1, x_2, \ldots, x_n$ et de leurs coefficients $\beta_1, \beta_2, \ldots \beta_n$. Bien que les valeurs des covariables prévisionnelles varient en fonction du temps, les coefficients de régression doivent être constants (on assume que les risques sont « proportionnels »). Pour chaque espèce, sept modèles ont été considérés : un modèle sans variables prévisionnelles; deux modèles incluant soit la transparence ou le couvert de macrophytes comme variable prévisionnelle; un modèle incluant les deux variables prévisionnelles et leur interaction et deux modèles incluant les deux variables prévisionnelles et leur interaction ainsi que la longueur à la fourche des poissons, la profondeur de l'eau ou les deux covariables. La transparence et la profondeur de l'eau étaient d'abord considérées comme variables prévisionnelles fixes dans le temps, et ensuite comme variables prévisionnelles variant en fonction du temps, puisque la transparence et la profondeur de l'eau pouvaient varier substantiellement entre le début et la fin d'une expérience (Therneau et Grambsch 2000). Lorsque les variables prévisionnelles étaient fixes dans le temps, nous avons utilisé la valeur de la variable prévisionnelle mesurée au début de l'expérience, en assumant que sa valeur demeurait constante jusqu'à la fin de l'expérience (Figure 2.3a). Lorsque les variables prévisionnelles variaient en fonction du temps, elles étaient mesurées deux fois, une fois au début et une fois à la fin de l'expérience et des valeurs intermédiaires (horaires) étaient également obtenues par interpolation linéaire (Figure 2.3b) (Therneau et Grambsch 2000). Le modèle avec le critère de sélection d'Akaike corrigé pour la taille de l'échantillon (AICc ; Burnham et Anderson 2002) le plus faible était sélectionné comme étant le meilleur modèle parmi les sept modèles considérés. Les résidus (martingale, scaled-Schoenfeld, Cox-Snell, deviance, dfbeta) ont été examinés graphiquement afin de vérifier la prémisse de la proportionnalité des risques, la présence de cas aberrants et le besoin de transformation pour les variables prévisionnelles (Therneau et Grambsch 2000; Tableman et Kim 2004). Le ratio du risque, $h\ (t \mid X) / h_0$

(*t*), qui représente le risque relatif de mortalité par rapport au risque de base, a été dérivé des résultats des régressions de Cox et examiné graphiquement afin de visualiser l'influence des variables prévisionnelles. Toutes les analyses ont été menées avec le module survival (version 2.3.1) dans l'environnement R (version 2.5.0 ; R Development Core Team 2007).

Résultats

Les courbes de survie de Kaplan-Meier montraient qu'il y avait un déclin abrupte de la survie des espèces dans les premières heures suivant le début des expériences, suivi d'un déclin plus graduel, à l'exception de la barbotte brune (Figure 2.4). La survie finale variait selon trois groupes d'espèces, la survie étant plus élevée pour la barbotte brune (~75%), intermédiaire pour trois espèces (museau noir, perchaude, omisco; ~35%) et faible pour les quatre autres espèces (laquaiche argentée, méné émeraude, méné jaune, queue à tache noire; ~10%).

Le risque de mortalité pour six des huit espèces était influencé par la transparence de l'eau ou par une interaction de la transparence de l'eau et du couvert de macrophytes (Tableau 2.2). Le couvert de macrophytes à lui seul n'aidait pas à prédire le risque de mortalité et était seulement inclus dans le modèle pour le museau noir, en interaction avec la transparence de l'eau. L'influence de la transparence de l'eau dépendait de la densité de végétation ; le risque diminuait considérablement avec une augmentation de la transparence de l'eau lorsque le couvert de macrophytes était présent, mais augmentait peu avec une augmentation de la transparence de l'eau lorsque que le couvert de macrophytes était absent (Figure 2.5a). Le risque de mortalité diminuait avec une augmentation de la transparence de l'eau pour la laquaiche argentée, le méné émeraude, le méné jaune et la perchaude ; pour ces espèces le risque était de 2.7 – 7.5 fois plus élevé en eaux turbides qu'en eaux claires. Le risque de mortalité augmentait avec une augmentation de la transparence de l'eau pour le queue à tache noire (4.9 fois plus élevé en eaux claires qu'en eaux turbides) (Figures 2.5f). Finalement, la transparence de l'eau n'affectait pas le risque de mortalité pour la barbotte brune ni pour l'omisco (Figure 2.5b,g).

Discussion

La vulnérabilité des proies dépend de leurs caractéristiques physiques (ex., comportement, couleur, morphologie) qui affectent leur détection par les prédateurs (Lima et Dill 1990; Fuiman et Magurran 1994; Rowe et Denton 1997; Sass et al. 2006). Les courbes de survie de Kaplan-Meier indiquaient que la survie, indépendamment du type d'habitat, semblait reliée à un gradient en couleur chez les espèces ainsi qu'à la présence d'épines. La survie était plus élevée pour l'espèce ayant une coloration plus foncée (barbotte brune), intermédiaire pour les espèces ayant une coloration plus pâle avec des patrons foncés sur le corps, tels que des bandes ou des taches (museau noir, omisco et perchaude) et faible pour les espèces ayant des colorations plus pâles ou argentées (laquaiche argentée, méné émeraude, méné jaune, queue-à-tache-noire). Certaines couleurs ou propriétés réflectives pourraient donc réduire le risque de mortalité des proies en diminuant leur visibilité face aux prédateurs (Fuiman et Magurran 1994; Johnsen 2001; Carvalho et al. 2006). Les épines peuvent être également de bonnes défenses pour les proies en décourageant les prédateurs de leur consommation (Hoogland et al. 1956; Moody et al. 1983; Sass et al. 2006). La présence d'une importante épine dorsale et d'épines latérales chez la barbotte brune pourrait aussi avoir contribué à sa survie élevée. Deux des trois espèces dans le groupe de survie intermédiaire (omisco et perchaude) possédaient des épines mais les quatre espèces ayant une faible survie en était dépourvues.

Les régressions de Cox indiquent une forte influence de la transparence de l'eau sur les risques de mortalité pour la plupart des espèces. La relation entre la transparence de l'eau et le risque de mortalité était principalement non linéaire et changeait plus rapidement à de faibles transparences. Les changements en transparence de l'eau (et en turbidité) affectent généralement le succès de quête alimentaire en modifiant la distance de réaction des prédateurs et la fréquence de rencontre avec les proies. De manière similaire aux patrons de risques de mortalité observés dans cette étude, la distance de réaction des prédateurs diminue habituellement de manière non linéaire avec une augmentation de la turbidité et change plus rapidement à de faibles turbidités (Utne-Palm 2002). Ce patron est également retrouvé chez des espèces dans des groupes taxonomiques variés tels que chez le saumon chinook (*Oncorhynchus tshawytscha*) (Gregory et Northcote 1993), le crapet arlequin (Miner and Stein 1996), l'omble de fontaine (*Salvelinus fontinalis*) (Sweka et Hartman 2001), l'achigan à petite bouche (Sweka et Hartman 2003), et le *Clinostomus funduloides* (Zamor et Grossman 2007), bien que la réponse peut être parfois linéaire comme chez la truite arc-en-ciel (*Oncorhynchus mykiss*) (Barrett et al. 1992).

La turbidité peut gêner l'habileté des prédateurs et des proies à se détecter mutuellement (Utne-Palm 2002). Puisque les effets de la turbidité sur la détection des proies peuvent être positifs et négatifs, il est difficile de prédire si les changements en turbidité avantageront le prédateur ou la proie. L'augmentation de la turbidité peut avantager le prédateur ou la proie dépendamment des caractéristiques optiques de l'environnement aquatique, de l'utilisation de la vision ou de d'autres mécanismes sensoriels par le prédateur et la proie ou selon l'utilisation de camouflage ou de d'autres mécanismes comportementales compensatoires par la proie (Thetmeyer et Kils 1995; Reid et al. 1999; Utne-Palm 2002). Les prédateurs spécialistes ou occasionnels les plus abondants au lac Saint-Pierre sont l'achigan à petite bouche (*Micropterus dolomieu*), l'achigan à grande bouche, le crapet-soleil (*Lepomis gibbosus*), la perchaude, le brochet, le doré jaune (*Sander vitreum*) et la barbotte brune (M.A. Rodríguez, données non publiées). Trois de ces prédateurs possèdent des adaptations spécifiques leur permettant de s'alimenter avec efficacité dans des conditions de faible intensité lumineuse et de faible transparence. Le brochet a une bonne vision et un système de ligne latérale bien développé et peut se nourrir activement la nuit (Skov et al. 2002). Le doré jaune est plus actif et consomme plus de proies en eaux turbides qu'en eaux claires (Ryder 1977, Vandenbyllaardt 1991). En effet, le doré jaune possède un tapetum lucidum qui améliore la sensibilité de la rétine et un système de macrorécepteurs améliorant l'acuité visuelle dans des conditions où l'intensité lumineuse est faible ; ces adaptations fournissent ainsi un avantage pour le doré jaune en comparaison aux autres prédateurs s'alimentant en eaux turbides (Ryder 1977). Finalement, la barbotte brune possède des senseurs tactiles et chimiques lui permettant de s'alimenter lorsque la visibilité est faible (Hoagland 1933; Sherman et Moore 2001). Les résultats de cette étude indiquent que les risques de mortalité sont généralement plus élevés à de faibles transparences et suggèrent que les adaptations des proies aidant à la détection des prédateurs en eaux claires, telles qu'une meilleure détection visuelle des prédateurs en eaux claires en combinaison avec l'adoption de comportements appropriés par la proie, ne sont pas aussi efficaces en eaux turbides et rendent celles-ci plus vulnérables aux prédateurs présents en eaux turbides. En eaux claires par exemple, les proies attachées ont peut être offert moins de contrastes visuels aux prédateurs, contrairement aux eaux turbides, ou ont pu être capable de détecter visuellement les prédateurs à une distance leur permettant d'orienter leur corps et réduire leurs chances de détection par le prédateur (Thetmeyer and Kils 1995)

Malgré la littérature abondante montrant le rôle de refuge de la végétation pour les poissons (ex., Savino et Stein 1982; Heck et Orth 2006; Sass et al. 2006), le couvert de macrophyte n'a pas semblé influencer le risque de prédation dans notre étude, à l'exception du museau noir, pour lequel l'effet significatif du couvert était en interaction avec la transparence de l'eau. L'absence d'effets du couvert de macrophytes pourrait être reliée au positionnement des dispositifs d'attachement aux abords des couverts de macrophytes. Les habitats aux abords de la végétation semblent souvent caractérisés par une forte intensité des interactions prédateur-proie (Walters et Juanes 1993). Des expériences d'attachement effectuées dans des lacs du Wisconsin et du Michigan ont montré que le risque de mortalité pour le crapet-arlequin, le crapet-soleil, la perchaude et le tête-de-boule, était presque nul à l'intérieur du couvert de végétation. Par contre, le risque de mortalité atteignait un maximum aux abords du couvert de végétation et déclinait graduellement de la zone littorale à la zone pélagique (Sass et al. 2006). Puisque nos sites d'échantillonnage étaient concentrés aux abords des couverts de macrophytes mais jamais l'intérieur ni dans la zone pélagique, l'intensité de la prédation a pu être élevée pour la majorité de nos sites, ce qui ne fournissait pas un contraste suffisamment fort pour détecter l'effet du couvert de végétation sur le risque de mortalité.

Le risque de mortalité semblait plus grand en eaux peu profondes pour le museau noir et la perchaude. Bien que les habitats en eaux peu profondes sont généralement reconnus comme étant des zones de refuge pour les poissons juvéniles en comparaison aux eaux plus profondes (Ruiz et al. 1993; Linehan et al. 2001; Sass et al. 2006), les eaux peu profondes ne semblent pas toujours servir d'habitats de refuge (Sheaves 2001). Les piscivores au delta de la rivière Sacramento-San Joaquin, Californie, sont abondants dans les eaux peu profondes et répondent de manière densité-dépendante aux changements saisonniers de la disponibilité de proies (Nobriga et Feyrer 2007).

Les résultats de cette étude suggèrent que la variation de la transparence de l'eau dans la zone littorale du lac Saint-Pierre pourrait générer une hétérogénéité spatiale de l'abondance des poissons soit par des effets directs, tel la réduction locale de l'abondance de proies par prédation, soit par des effets indirects, tel la modification du comportement des proies qui éviteraient les habitats plus risqués (Abrahams et Kattenfeld 1997 ; van de Meutter et al. 2005).

CHAPITRE 2

QUANTIFYING HABITAT-DEPENDENT MORTALITY RISK IN LACUSTRINE FISHES

Quantifying habitat-dependent mortality risk in lacustrine fishes by means of tethering trials and survival analyses

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Abstract: Habitat features influence the ecological interactions and spatial distribution of fish species. For example, water transparency and macrophyte cover, as well as their interaction, can strongly influence predation risk and mortality. We conducted tethering trials in Lake St. Pierre (Quebec, Canada), to assess the effects of water transparency and macrophyte cover on the mortality risk of eight abundant fish species; brown bullhead (*Ameiurus nebulosus*), mooneye (*Hiodon tergisus*), emerald shiner (*Notropis atherinoides*), golden shiner (*Notropis crysoleucas*), blacknose shiner (*Notropis heterolepis*), spottail shiner (*Notropis hudsonius*), trout-perch (*Percopsis omiscomaycus*), and yellow perch (*Perca flavescens*). Kaplan-Meier survival curves showed that mortality risk varied substantially among three groups of species having high, intermediate, or low survival rates. Cox regression models showed that mortality risk for six of the eight species was influenced by water transparency or by an interaction of transparency with macrophyte cover. These results indicate that variation in water transparency may generate spatial heterogeneity in fish abundance either through direct effects, such as local reduction in prey numbers by predation, or indirect effects, such as behavioural avoidance of risky areas by prey.

Résumé : Les caractéristiques physiques des habitats aquatiques modifient les interactions écologiques ainsi que la distribution spatiale chez les poissons. Nous avons mené des expériences d'attachement (angl. : « tethering experiments ») pour examiner l'effet de la transparence de l'eau et du couvert de macrophytes sur le risque de mortalité chez huit espèces de poissons retrouvées dans le lac Saint-Pierre (Québec, Canada). Le risque de mortalité pour six des huit espèces était influencé par la transparence ou par l'interaction entre la transparence et le couvert de macrophytes. Ces résultats indiquent que les variations dans la transparence pourraient générer une hétérogénéité spatiale de l'abondance des poissons par le biais d'effets directs, tel la réduction du nombre d'individus à l'échelle locale par la prédation, ou d'effets indirects, tel l'évitement des habitats plus risqués.

Key words: Cox regression, predator-prey interactions, mortality, transparency, vegetation cover

Introduction

Habitat features influence the ecological interactions and spatial distribution of freshwater fish species (Jackson et al. 2001). Water transparency and macrophyte cover, as well as their interaction, can strongly influence predation risk and mortality (Savino and Stein 1989*a*,*b*; Abrahams and Kattenfeld 1997; Eklöv 1997; Utne-Palm 2002). For visual species, water turbidity can constrain predator-prey interactions by modifying both detection distance and encounter rate between prey and predator (Abraham and Kattenfeld 1997; Turesson and Brönmark 2007). Reduced visibility in turbid waters leads to a decline in the effectiveness of antipredator behaviours in prey. Therefore, in turbid waters, predators reduce prey numbers in direct proportion to the rate at which they encounter their prey. In contrast, in clear waters prey can detect predators at a greater distance and predators affect prey numbers mostly by indirect effects resulting from behavioural modifications in prey (Abrahams and Kattenfeld 1997; van de Meutter et al. 2005). Vegetation cover may also alter behaviour of predators and prey and their interactions (Savino and Stein 1989*a*; 1989*b*). Although some predators, such as the northern pike (*Esox lucius*), are restricted to an ambushing strategy, others, such as the largemouth bass (*Micropterus salmoides*), may switch from an ambushing to a searching tactic as vegetation density increases (Savino and Stein 1989*a*; 1989*b*). Success of predators at capturing prey can also be influenced by behavioural modifications that affect use of cover by prey as a function of vegetation density. In the laboratory, capture success of largemouth bass and pike was greater on bluegills (*Lepomis macrochirus*), which increase their use of vegetation as a cover at greater vegetation density, than in fathead minnows (*Pimephales promelas*), which make less use of vegetation as cover (Savino and Stein 1989*b*). Additionally, predator-prey interactions can be influenced by interactive effects of water transparency and macrophyte cover. For example, the Eurasian perch (*Perca fluviatilis*), a visual species, reduces its use of vegetation as cover against predation by northern pike at high water transparency (Skov et al. 2007).

The effects of water transparency and macrophyte cover on predator-prey interactions contribute to structuring of fish communities in different freshwater ecosystems of the world (Eklöv 1997; Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998; Petry et al. 2003;Ostrand and Wilde 2004; Pouilly and Rodríguez 2004). In the floodplain of the Orinoco River (Venezuela), fish relying on vision are numerically dominant in clear lakes, whereas those relying on sensory adaptations to low light predominate in turbid lakes (Rodríguez and Lewis 1997). The outcome of foraging interactions in the floodplain lakes depends on responses to water transparency that reflect the sensory adaptations of individual species (Rodríguez and Lewis 1997). Fish community structure can also respond to structural habitat complexity associated with macrophytes as observed for the pike and its prey, the Eurasian perch (Eklöv 1997). In Lake Degersjön, Sweden, young Eurasian perch appeared to be more abundant at intermediate vegetation density (40-60 stems $\cdot$ m^{-2}), comparatively where vegetation was very dense (60-150 stems $\cdot$ m^{-2}), scarce (5-40 stems $\cdot$ m^{-2}), or absent (0 stems $\cdot$ m^{-2}), possibly reflecting a trade-off between the availability of food resources and refuge from predation (Eklöv 1997). In the absence of vegetation, the Eurasian perch foraged in groups and had greater foraging efficiency than pike (Eklöv 1992). However, in the presence of vegetation, the Eurasian perch foraged individually and had lower foraging efficiency than pike (Eklöv and Diehl 1994).

The examples above show that water transparency and macrophyte cover can structure fish populations and communities through their impacts on predator-prey interactions. The objective of this study was to assess the effects of water transparency, macrophyte cover, and their interaction, on the relative mortality risk of eight abundant fish species in Lake Saint Pierre, a fluvial lake of the St. Lawrence River (Québec, Canada). The marked spatial heterogeneity of transparency and vegetation cover of this lake makes it a suitable system for examining the link between mortality risk and habitat characteristics. Mortality risk was assessed by means of tethering trials (Minello 1993) and survival analyses (Therneau et Grambsch 2000). Most previous tethering studies have derived predation risk from the proportion of individuals still alive at the end of a trial (e.g., McIvor and Odum 1988; Clark et al. 2003; Moody and Aronson 2007). However, in contrast with survival analyses, this approach does not efficiently exploit the information contained in survival times; furthermore, results based on the proportion of individuals surviving after a fixed period can depend sensitively on the length of that period.

Materials and methods

Study area

Lake St. Pierre (46°12' N, 72°50'W) is a fluvial lake of the St. Lawrence River (Québec, Canada) (Fig. 2.1). The lake is large (surface area: mean = 315 km^2; 469 km^2 during the spring floods) and shallow (mean water depth = 3.17 m). Lake St. Pierre has distinct water masses along its northern, central, and southern portions, which differ consistently in physical and chemical characteristics because lateral mixing is limited in the lake (Frenette et al. 2003). Macrophyte beds are widespread in the littoral zones. Macrophyte cover is more extensive on the south shore than on the north shore. Approximately 50 resident fish species are found in the lake.

Tethering trials

Tethering trials were conducted in the littoral zone of Lake St. Pierre (Fig. 2.1) between 18 June to 30 August, 2005. Eight species were included in the study: brown bullhead (*Ameiurus nebulosus*), mooneye (*Hiodon tergisus*), emerald shiner (*Notropis atherinoides*), golden shiner (*Notropis crysoleucas*), blacknose shiner (*Notropis heterolepis*), spottail shiner (*Notropis hudsonius*), trout-perch (*Percopsis omiscomaycus*), and yellow perch (*Perca flavescens*) (Table 2.1). Trial sites were chosen along the north and south shores of the lake to encompass a wide range in transparency and macrophyte cover; however, ranges for individual species varied according to the species' patterns of occurrence in different habitats (Table 2.1). Fish used in the trials were collected from the littoral zone of the lake with a seine net, identified, and measured (fork length). Individual fish were then tethered to a chronograph designed to record survival time (Ha 1996, Danilowicz and Sale 1999; Fig. 2.2). Each chronograph comprised a timer and a magnetic switch, embedded in a waterproof resin disk (diameter: 9 cm) suspended from a 50-cm cord. Fish were attached to a small steel plate in the chronograph by a monofilament line (length: ~40 cm) sutured through muscle tissue below the dorsal fin. When a tethered fish was pulled away from the chronograph by a predator, the steel plate was detached from a magnet, which triggered the chronograph. To avoid spurious triggering of the chronograph by the normal swimming motions of larger prey rather than by predator attack, the fish used in the trials were within the range of maximum prey sizes used by Ha (1996) (Table 2.1). Fish were set on the tethering devices on the first day of a trial between 12:00 and 17:00 and retrieved the following day between 8:00 and 12:00 (median duration of trials: 20.6 h; 25%-75% quartiles: 19.5-22.2 h). Survival time was determined as the total duration of the trail (from immersion to retrieval) minus the time elapsed from the capture event to the retrieval of the chronograph. Trials in which no attack had been recorded at the end of the trial (i.e., survival time = trial duration) were coded as "censored". Tethering impedes natural escape behaviours and enhances the rate of attack compared to unattached prey; therefore, tethering trials yield relative, not absolute, rates of predation (Peterson and Black 1994). Because the objective of this study was to compare relative mortality risk among habitats, we used the same tethering technique in all trials and assumed that any bias arising from tethering would be comparable across habitats (Aronson and Heck 1995, Aronson et al. 2001).

Environmental variables

At each trial site, water transparency, macrophyte cover, water depth, and substratum size were measured on the first day of the trial, when the chronograph was deployed. Water transparency and water depth were also measured on the second day of the trial, when the chronograph was recovered. Water transparency was measured with three instruments: a conventional Secchi disk, a clear transparency tube (diameter: 3.5

cm, length: 150 cm; Dahlgren et al. 2004), and a Snell tube (diameter: 4.5 cm, length: 120 cm; van de Meutter et al. 2005). The tubes allowed for measurement of transparency when readings from the Secchi disk were truncated because Secchi transparency exceeded water depth. Secchi transparency is the most commonly used of these transparency measures; however, Secchi readings were truncated at 63% of the trial sites. The transparency tube and Secchi measurements were related linearly to each other (R^2 = 0.91), and nonlinearly to the Snell readings. Although the Snell tube generally allowed for measurement of transparency even when readings from the transparency tube were truncated, we standardized all measurements to the scale of the transparency tube because of its linear relationship with Secchi depth readings. Truncated values for the transparency tube were imputed by means of a regression equation relating transparency tube to Snell readings. The regression parameters were estimated by censored regression (Gelman and Hill 2007) of transparency tube (square-root transformed) on Secchi depth. For sites at which transparency exceeded the range of all instruments (14.9% of all sites), transparency was estimated from multiple regression models using latitude, longitude, Julian day, and water depth as predictors (R^2 = 0.65). To avoid entanglement of the monofilament line with macrophytes near the device, the device could be placed along the edges of a macrophyte bed, but not within the bed. Macrophyte cover was quantified as the percentage of emergent vegetation within a 2 m x 2 m quadrat centred on the tethering device. Substratum size was assessed visually from sediment samples collected with a core sampler (internal diameter = 20 mm) at four points spaced equally along the perimeter of a circle (radius = 1 m) centred on the device. Substratum size was coded as one of five categories (0 =

clay, 1 = silt, 2 = sand, 3 = gravel, 4 = boulder; Murphy and Willis 1996) and averaged over the four points.

Quantitative analyses

For each species, a Kaplan-Meier curve (Therneau and Grambsch 2000) was used to examine survival as a function of time before assessing the effect of habitat predictors on survival. The effect of predictor variables on survival was then quantified by means of Cox regression, a semi-parametric approach that deals effectively with two statistically troublesome characteristics of survival times: non-normality (survival times cannot be negative) and right-censoring (death has not yet occurred when the trial is ended) (Therneau and Grambsch 2000; Tableman and Kim 2004). The Cox regression model can be written as:

$$h\ (t \mid X) = h_0\ (t) \exp\ (\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n),$$

where $h\ (t \mid X)$ is the mortality risk (or "hazard") at time t. The hazard function contains two parts: the baseline mortality risk, h_0, which varies in time, and a time-independent exponential function of predictors $x_1, x_2, \ldots, x_n$ weighed by their regression coefficients $\beta_1, \beta_2, \ldots, \beta_n$. Although the value of the covariates can vary in time, the regression coefficients must be constant (the "proportional hazards" assumption). For each species, a set of seven models including different combinations of predictors was considered initially: a model with no predictors; two models with either water transparency or macrophyte cover as predictors; a model including both predictors and their interaction;

and two models including both predictors and their interaction, as well as fish size, water depth, or both as covariates. Because both water transparency and water depth could vary substantially between the beginning and the end of a trial, each set of seven models was built twice, once for "time-fixed" predictors and the other for "time-varying" predictors (Therneau and Grambsch 2000). In the time-fixed approach, a single value of the predictor, measured at the beginning of the trial, is assumed to remain constant until the end of the trial (Fig. 2.3a). In the time-varying approach, the predictor is measured both at the beginning and at the end of the trial, and intermediate (hourly) values of the predictor are obtained by linear interpolation (Fig. 2.3b) (Therneau and Grambsch 2000). The model with the lowest value for Akaike's information criterion, corrected for sample size (AICc; Burnham and Anderson 2002), was selected as the best model among the fourteen candidates. Diagnostic checks of residuals (martingale, scaled-Schoenfeld, Cox-Snell, deviance, and dfbeta residuals) were performed to verify the proportional hazards assumption, detect potential outliers, and assess the need for transformation of the predictors (Therneau and Grambsch 2000; Tableman and Kim 2004). Risk ratios, $h\ (t \mid X)/\ h_0\ (t)$, which represent mortality risk relative to the baseline risk, were derived from the Cox regression results and examined graphically to visualize the influence of predictors. All analyses were performed using the survival package (version 2.31) in the R environment (version 2.5.0; R Development Core Team 2007).

Results

The Kaplan-Meier survival curves showed a steep decline in survival during the first hours of exposure, followed by more gradual decline, for all species except the brown bullhead (Fig. 2.4). Terminal survival varied markedly among three groups of species: it was highest for brown bullhead (~75%), intermediate for three species (blacknose shiner, trout-perch, and yellow perch; ~35%), and lowest for the four remaining species (emerald shiner, golden shiner, mooneye, and spottail shiner; ~10%).

The Cox regression models showed that mortality risk for six of the eight species was influenced by water transparency or by an interaction of transparency with macrophyte cover (Table 2.2). Macrophyte cover singly was not a useful predictor of mortality risk and only was included in the model for blacknose shiner, in interaction with water transparency. Mortality risk was negatively related to water depth for blacknose shiner and yellow perch, but did not appear to depend on body length for any of the species. The influence of water transparency on mortality risk was contingent on macrophyte cover for the blacknose shiner: risk declined briskly with increase in water transparency when macrophyte cover was abundant, but increased slightly with increase in water transparency when macrophyte cover was absent (Fig. 2.5a). Mortality risk declined markedly with increase in water transparency for emerald shiner, golden shiner, mooneye, and yellow perch; for these species, mortality risk was 2.7-7.5 times greater in turbid than in clear waters (Fig. 2.5c,d,e,h). Mortality risk increased with increase in water transparency for the spottail shiner (4.9 times greater in clear than in turbid waters) (Fig. 2.5f). Neither water transparency nor macrophyte cover appeared to affect mortality risk for brown bullhead or trout-perch (Fig. 2.5b,g).

Discussion

The vulnerability of prey depends on characteristics (e.g., behaviour, colour, morphology) that affect detection by predators (Lima and Dill 1990; Fuiman and Magurran 1994; Rowe and Denton 1997; Sass et al. 2006). The Kaplan-Meier curves indicated that survival, grouped across habitats, appeared to be linked to coloration pattern and the presence of spines. Survival was greatest for the species that had the darkest body coloration (brown bullhead), intermediate for species that have lighter body coloration and spots or striped patterns (trout-perch, blacknose shiner, and yellow perch), and lowest for species that have silvery or light-coloured bodies (emerald shiner, golden shiner, mooneye, and spottail shiner). Mortality risk might be reduced by specific coloration patterns or reflective properties that reduce conspicuousness to predators (Fuiman and Magurran 1994; Johnsen 2001; Carvalho et al. 2006). Spines can also act as effective deterrents against predators (Hoogland et al. 1956; Moody et al. 1983; Sass et al. 2006). The presence of strong dorsal and lateral spines for the brown bullhead may have contributed to its low mortality risk. Two out of three species that had intermediate survival (trout-perch and yellow perch), but none of those that had low survival, have dorsal spines.

The Cox regressions pointed to a strong influence of water transparency on mortality risk for most species. The relationship between water transparency and mortality risk was predominantly nonlinear and tended to change most rapidly at low transparency. Changes in water transparency (and turbidity) generally affect fish foraging success by modifying the reactive distance of predators and encounter rate. Similar to the pattern for mortality risk in the present study, reactive distance of predators usually declines nonlinearly with increasing turbidity and changes most rapidly at low turbidity (Utne-Palm 2002). This pattern that holds across broadly differing taxa: Chinook salmon (*Oncorhynchus tshawytscha*) (Gregory and Northcote 1993), bluegill sunfish (Miner and Stein 1996), brook trout (*Salvelinus fontalis*) (Sweka and Hartman 2001), smallmouth bass (Sweka and Hartman 2003), and rosyside dace (*Clinostomus funduloides*) (Zamor and Grossman 2007), although the response may be linear sometimes (rainbow trout; Barrett et al. 1992).

Turbidity can hinder the ability of both predators and prey to detect each other (Utne-Palm 2002). Predicting whether changes in turbidity will benefit the predator or the prey is difficult because turbidity has both positive and negative effects on prey detection. Increased turbidity can yield the upper hand to either predator or prey, depending on the optical properties of the underwater environment, the reliance on vision and other sensory mechanisms by the predator and prey, and the use of camouflage or compensatory behavioural mechanisms by the prey (Thetmeyer and Kils 1995; Reid et al. 1999; Utne-Palm 2002). The most abundant strict or occasional piscivores in Lake St. Pierre are smallmouth bass (*Micropterus dolomieu*), largemouth bass, pumpkinseed (*Lepomis gibbosus*), yellow perch, northern pike, walleye (*Sander vitreum*), and brown bullhead (M.A. Rodríguez, unpublished data). Three of these piscivores have specific adaptations that enable them to forage effectively under conditions of low light and low transparency. Northern pike have well-developed vision and lateral line systems and can feed actively at night (Skov et al. 2002). Walleye are more active and consume more prey in turbid than in clear waters (Ryder 1977;

Vandenbyllaardt et al. 1991). Walleye have a tapetum lucidum that increases retinal sensitivity, and macroreceptors that increase visual acuity in low light conditions; these adaptations provide a foraging advantage over other predators in turbid conditions (Ryder 1977). Brown bullhead have sensitive tactile and chemical sensors that allow for foraging when visibility is poor (Hoagland 1933; Sherman and Moore 2001). The finding that mortality risk was generally highest at low transparency suggests that prey adaptations that help avoid predators in clear waters, such as early visual detection of predators in clear waters coupled with appropriate behavioural response by the prey, were not as effective in turbid waters, which rendered prey vulnerable to turbid-water predators. For example, tethered fish may have offered less visual contrast to predators in clear than in turbid waters, or may have been able to visually detect predators at a distance in clear waters and orient their bodies so as to reduce the chances of being seen by the predator (Thetmeyer and Kils 1995).

Although many studies have demonstrated the role of vegetation as a potential refuge for prey (e.g., Savino and Stein 1982; Heck and Orth 2006; Sass et al. 2006), macrophyte cover did not appear to influence predation risk in our study, with the exception of blacknose shiner, for which the effect of macrophyte cover was in interaction with water transparency. The apparent absence of macrophyte effects may be related to the positioning of trial sites along the edge of the macrophyte beds. Edge habitats often are the setting for strong predator-prey interactions (Walters and Juanes 1993). In a study that used tethered pumpkinseed, bluegill, yellow perch, and fathead minnow as prey, predation was least intense within macrophyte beds, strongest at the edge of the beds, and declined gradually from the littoral through the pelagic zone (Sass et al. 2006). Because our trial sites were concentrated near the edge of macrophyte beds and were never deep within the macrophyte beds or the pelagic zone, the intensity of predation may have been high at most trial sites, perhaps providing insufficient contrast to detect the effect of vegetation cover on mortality risk.

Mortality risk appeared to be greater in shallow-water habitats for both blacknose shiner and yellow perch. Although shallow-water habitats are usually recognized as safer for juvenile fishes than deeper waters (Ruiz et al. 1993; Linehan et al. 2001; Sass et al. 2006), they do not always provide refuge from predation (Sheaves 2001). Piscivores in the Sacramento-San Joaquin River Delta, California, are abundant in shallow water and show density-dependent responses that allow them to track seasonal change in prey availability in that habitat (Nobriga and Feyrer 2007).

The results of this study suggest that variation in water transparency in the littoral zone of Lake St. Pierre may generate spatial heterogeneity in fish abundances, either through direct effects, such as local reduction in prey numbers by predation, or indirect effects, such as behavioural avoidance of risky areas by prey (Abrahams and Katteenfield 1997; van de Meutter et al. 2005).

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Table 2.1. Abundance of the fish species studied in Lake St. Pierre, with median and quartiles (25% - 75%) for habitat characteristics (water transparency, macrophyte cover, water depth) and fork length of fish used in the tethering trials. The number of trials is also given.

	Abundance in lake		Characteristics of habitat and fish in tethering experiments				
Species	Relative (%)	Rank	Water transparency (cm)	Macrophyte cover (%)	Water depth (cm)	Fork length (mm)	Number of trials
Brown bullhead *Ameiurus nebulosus*	3.2	7	193 (128-222)	5 (0-15)	100 (84-111)	50 (47-53)	55
Mooneye *Hiodon tergisus*	1.0	18	182 (101-209)	0 (0-5)	80 (70-105)	68 (61-80)	25
Emerald shiner *Notropis atherinoides*	8.4	3	57 (34-80)	1 (0-15)	100 (80-174)	60 (56-68)	69
Golden shiner *Notropis crysoleucas*	8.4	4	66 (31-128)	5 (0-90)	98 (80-114)	63 (56-68)	106

Table 2.1 (continued and concluded).

Blacknose shiner *Notropis heterolepis*	1.4	12	76 (38-134)	5 (0-80)	100 (80-150)	44 (43-46)	70
Spottail shiner *Notropis hudsonius*	4.8	5	80 (58-165)	0 (0-50)	99 (75-150)	57 (47-82)	59
Yellow perch *Perca flavescens*	24.5	2	91 (61-161)	5 (0-15)	81 (70-105)	47 (44-53)	100
Trout-perch *Percopsis omiscomaycus*	4.0	6	116 (60-218)	0 (0-20)	92 (82-105)	58 (50-74)	93

Table 2.2 . Coefficient estimates, standard errors, and *P* values for model terms of the Cox regression model, by species.

Species	Model term	Estimate	SE	*P*
Ameiurus nebulosus[a]	Transparency	-0.254	0.255	0.920
Brown bullhead				
Hiodon tergisus[a]	Transparency	-0.422	0.210	0.045
Mooneye				
Notropis atherinoides[a]	Transparency	-0.409	0.136	0.003
Emerald shiner				
Notropis crysoleucas[a]	Transparency	-0.290	0.108	0.008
Golden shiner				
Notropis heterolepis[b]	Transparency	0.086	0.155	0.580
Blacknose shiner	Macrophyte	-0.133	0.166	0.420
	Transparency x Macrophyte	-0.380	0.149	0.011
	Water depth	-0.320	0.158	0.043
Notropis hudsonius[b]	Transparency	0.401	0.142	0.005
Spottail shiner				
Perca flavescens[b]	Transparency	-0.424	0.135	0.002
Yellow perch	Water depth	-0.484	0.136	< 0.001
Percopsis omiscomaycus[a]	Transparency	-0.079	0.123	0.520
Trout-perch				

[a] Time-fixed covariates

[b] Time-varying covariates

Figure captions

Figure 2.1. Map of Lake St. Pierre, Quebec, Canada. Black dots represent the littoral sites where trials were run.

Figure 2.2. Chronographic tethering device used to evaluate the mortality risk of fish species.

Figure 2.3. Use of water transparency and water depth as either constant or time-varying predictors in Cox regressions. In a), a single value of the predictor (c_1), measured at the beginning of the trial (t_{initial}), is assumed to remain constant until the end of the trial (t_{final}). In b), the predictor is measured both at the beginning (c_1) and at the end of the trial (c_2). Intermediate values of the predictor are obtained by linear interpolation between t_{initial} and t_{final} (dotted line).

Figure 2.4. Kaplan-Meier survival curves showing estimated survivorship vs. time, by species.

Figure 2.5. Mortality risk ratio as a function of water transparency for a) blacknose shiner (*Notropis heterolepis*), b) brown bullhead (*Ameiurus nebulosus*), c) mooneye (*Hiodon tergisus*), d) emerald shiner (*Notropis atherinoides*), e) golden shiner (*Notropis crysoleucas*), f) spottail shiner (*Notropis hudsonius*), g) trout-perch (*Percopsis omiscomaycus*), and h) yellow perch (*Perca flavescens*). In a), the mortality risk ratio is shown as a function of water transparency for two different levels of macrophyte cover, to illustrate the interaction between transparency and cover. The dashed horizontal line represents the baseline mortality risk. Note the different scales on the y-axes.

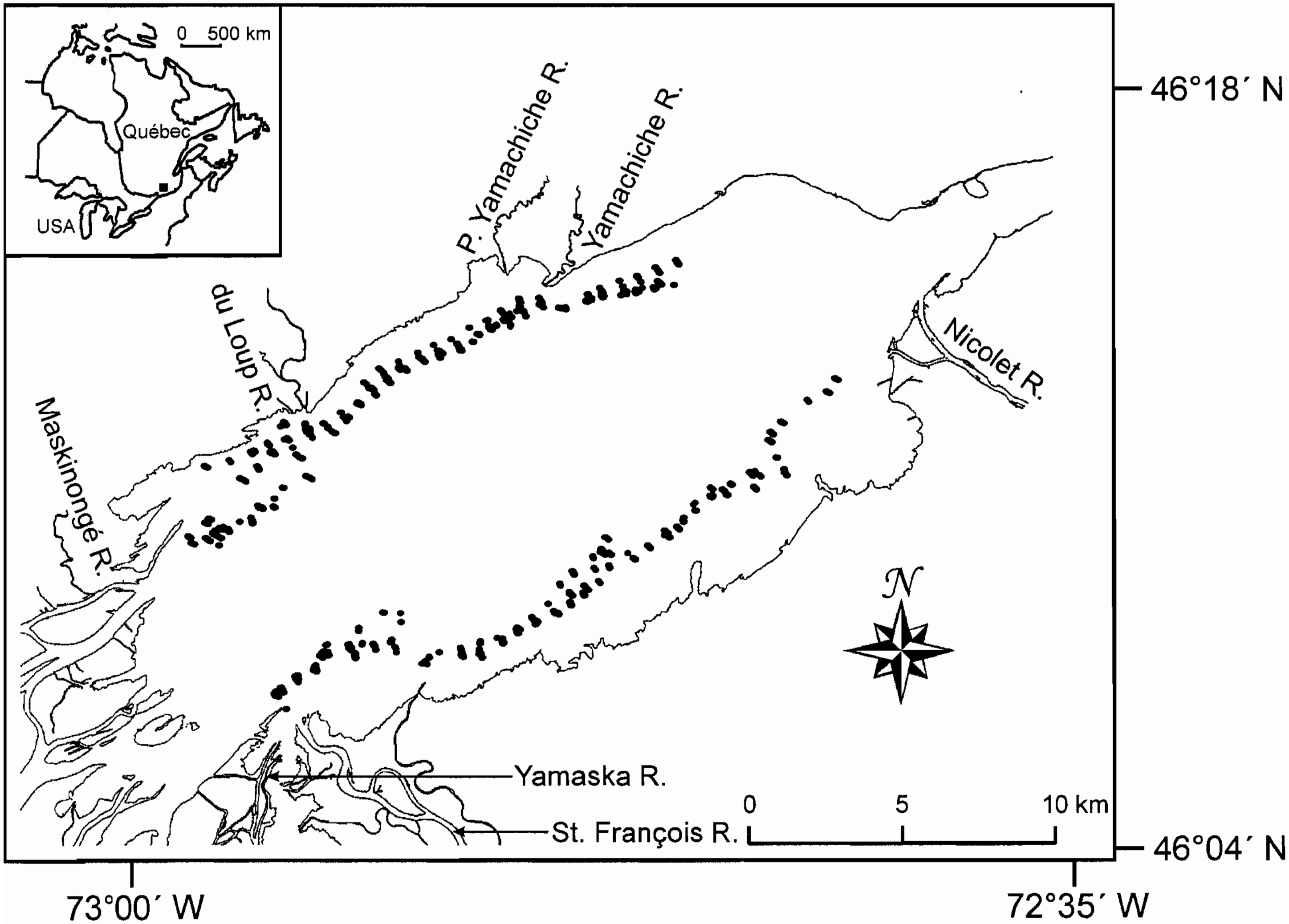

Figure 2.1. Laplante-Albert et al.

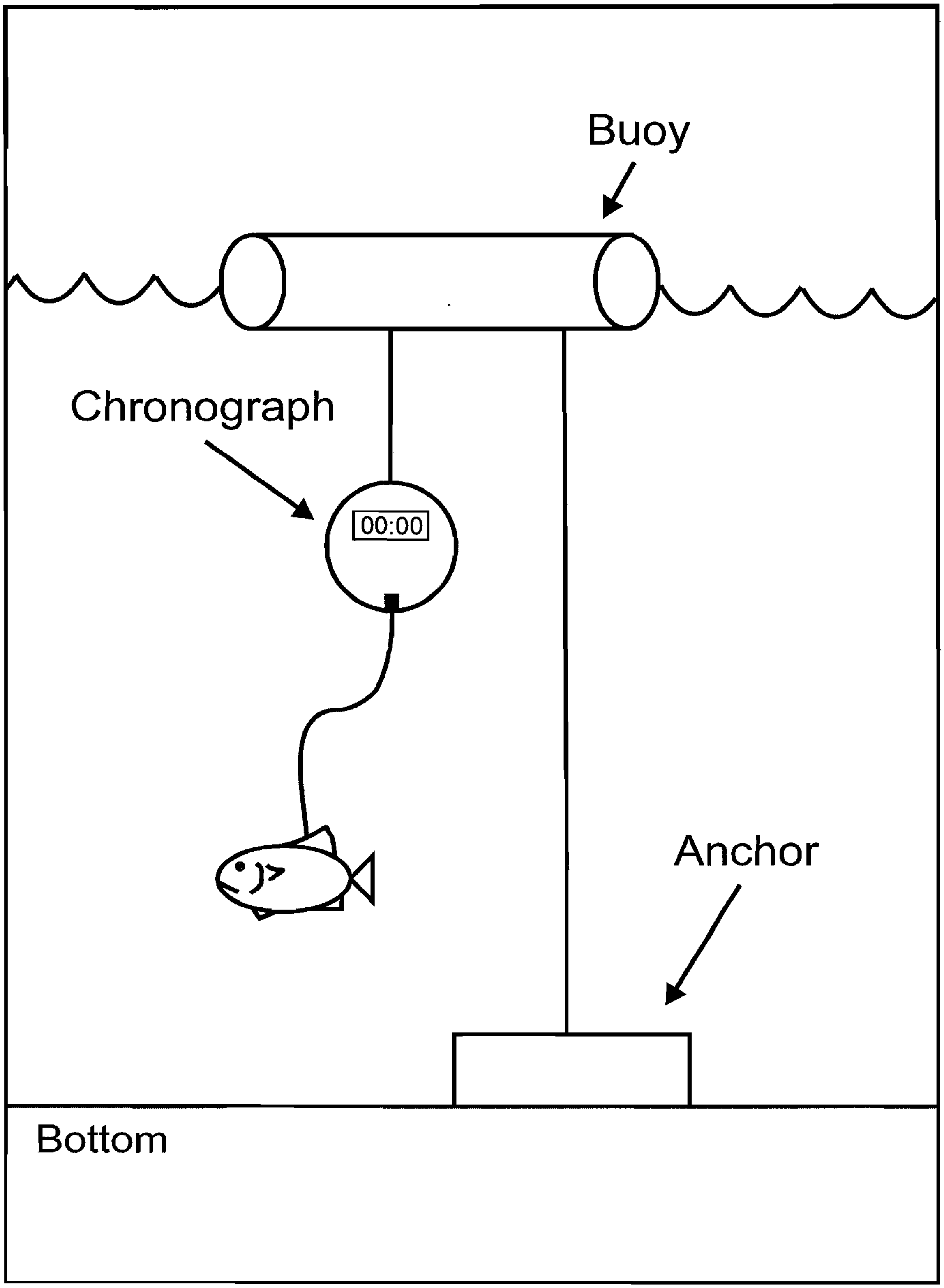

Figure 2.2. Laplante-Albert et al.

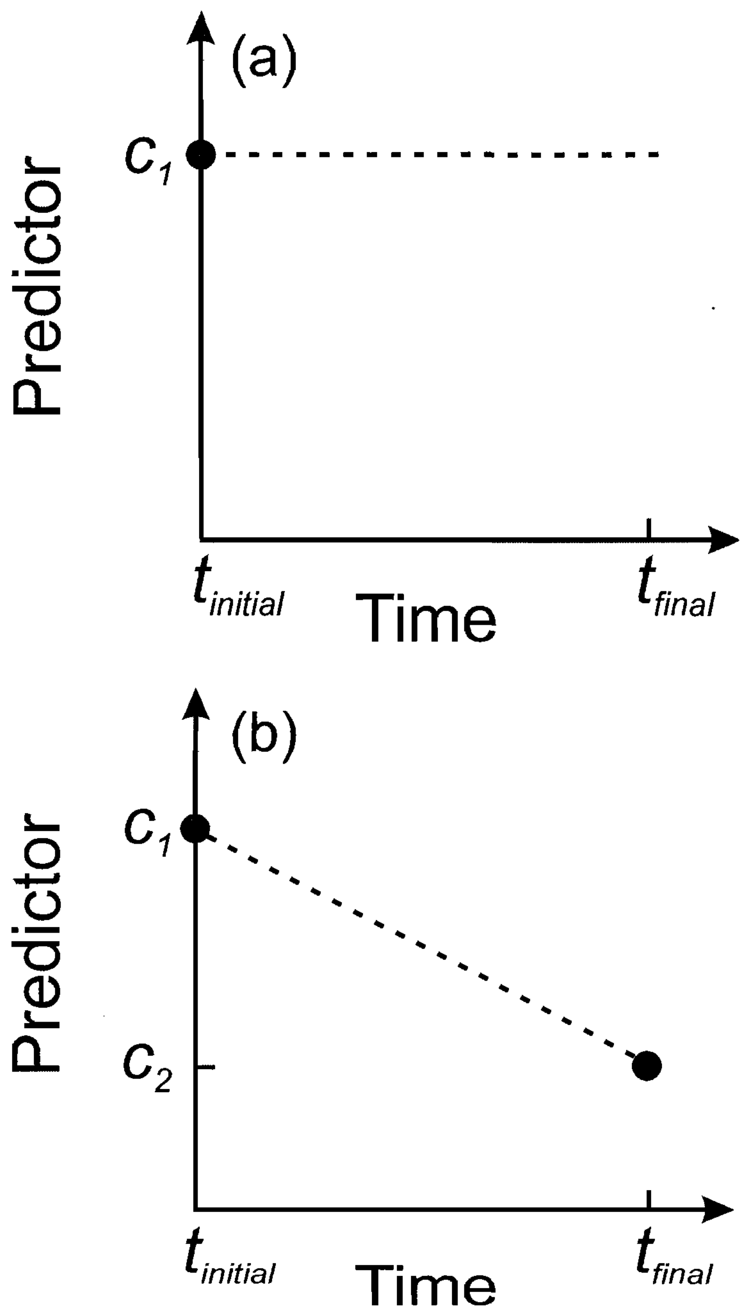

Figure 2.3. Laplante-Albert et al.

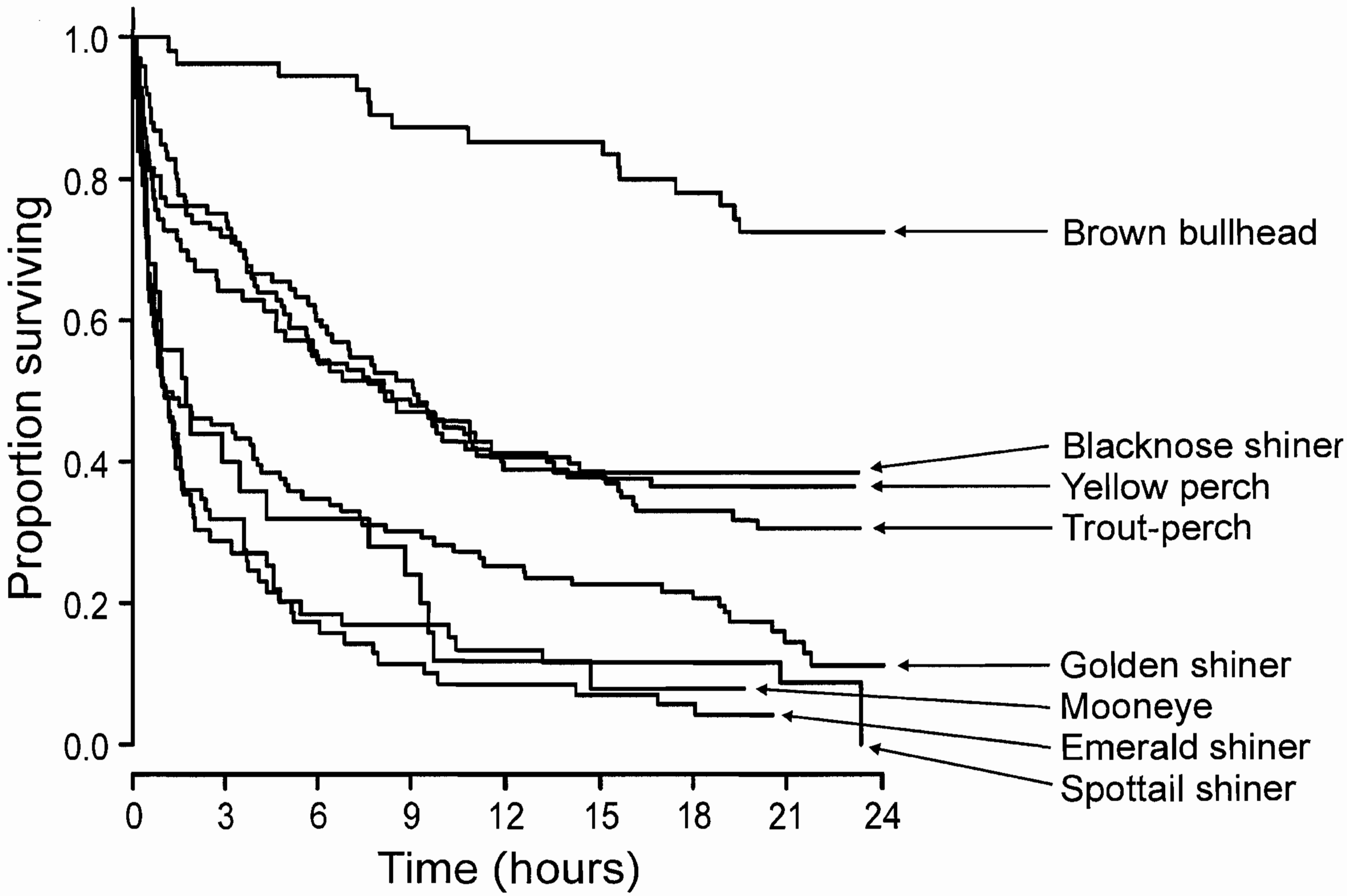

Figure 2.4. Laplante-Albert et al.

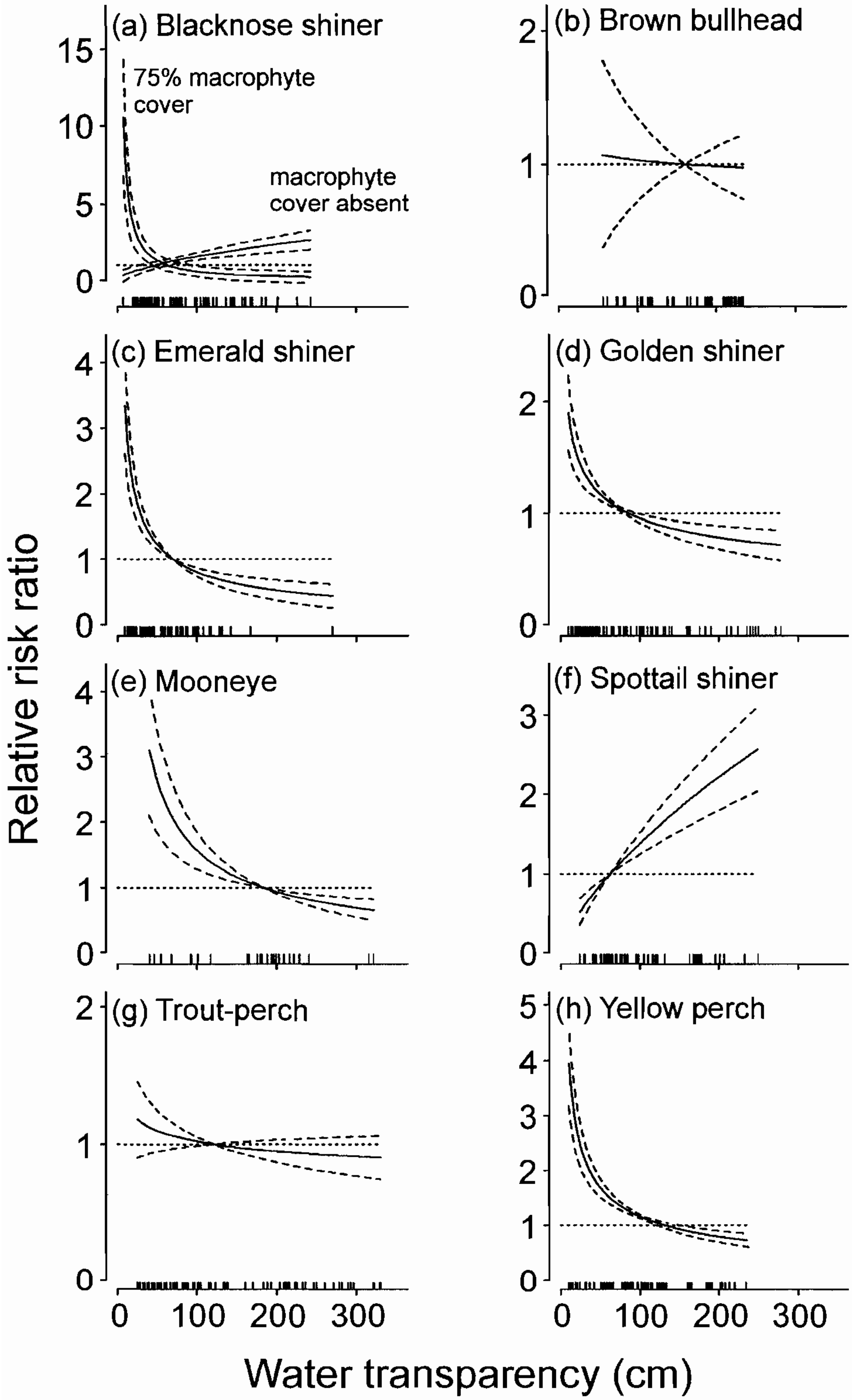

Figure 2.5. Laplante-Albert et al.

ANNEXE

Instructions to authors of the Canadian journal of fisheries and aquatic sciences

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Scope of the Journal and guidelines for papers

The Journal welcomes manuscripts reporting significant new knowledge and understanding of fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results.

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We continue to discourage papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); confirm only previously established principles; or apply standard techniques without breaking new methodological ground. Studies that are clearly preliminary or fragmentary, or whose relevance to broader issues is not demonstrated, and interpretations solely of an unsupported speculative nature will not be entertained.

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- avows that the manuscript is not being considered for publication elsewhere;
- suggests potential referees;
- identifies other manuscripts, including "extended abstracts", containing the same, similar, or related information, from which other manuscripts may be generated;
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- explains any real or perceived conflicts of interest (see Ethics section, Conflict of interest and disclosure).

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If the Editor agrees to consider a submitted manuscript for publication, the Editorial Office will request the return as soon as possible of copyright assignment and (or) license forms signed by all authors. Before a manuscript can be accepted for publication, all authors are required to complete a copyright assignment or license form assigning or licensing rights to NRC. Most authors will sign the assignment form, which transfers all rights to NRC. Employees of the government in Commonwealth countries will sign a license form that allows them to retain Crown copyright, and employees of the US government will sign a form agreeing to publication, since no US copyright exists. Copyright transfer forms are available from the Editor, in the first issue of the volume, or on the Web site of the Journal (pubs.nrc-cnrc.gc.ca/eng/forms/index).

Editorial process

Receipt of manuscripts

Once the Editor has decided to consider the manuscript for publication, the corresponding author of a submitted manuscript will receive a formal acknowledgement letter and will be requested by the Editorial Office to complete necessary forms as soon as possible. If the Editor has decided not to consider it for publication, then the corresponding author will be notified of this decision via e-mail.

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Each manuscript is normally submitted to two referees for appraisal. However, the Editor will return unreviewed those manuscripts that do not fall within the Journal's scope or character, and those that exceed the Journal's guidelines for prior publication as "extended abstracts" (guidelines available from the Editorial Office's Web site at uoguelph.ca/~cjfas/). Papers submitted for inclusion in supplements are treated with the same rigor of review as articles in regular issues.

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Authors resubmitting a manuscript after previous rejection or withdrawal must indicate the manuscript number assigned to the previous submission in their cover letter. These resubmitted manuscripts are treated as new papers. Authors may submit the new manuscript by e-mail or via **OSPR**EY, along with a detailed, point-by-point reply to all issues raised during the previous evaluation.

Publication process

General

The Editorial Office checks all accepted manuscripts for conformation to the *Instructions to Authors* and to ensure that all necessary paperwork is present. Any areas that are identified as problematic will be addressed by the Editorial Office in consultation with the corresponding author. Once the Editorial Office has resolved any problems with the manuscript and the original signed Assignment of Copyright forms have been received from all authors, the manuscript is forwarded to NRC Research Press in Ottawa for publication. The papers are prepared for publication by a professional copy editor responsible for ensuring that the final printed work is consistent in form and style.

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Once the paper has been accepted, all correspondence should be with NRC Research Press, National Research Council of Canada, Ottawa, ON KlA 0R6, Canada (fax: 613-952-7656; e-mail: pubs@nrc-cnrc.gc.ca; URL: pubs.nrc-cnrc.gc.ca). NRC Research Press may make editorial changes as required, but will not make substantive changes in the content of a paper without consultation with the author and the Editor.

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General

The ethical standards expected of authors, referees, and editors are described in the NRC Research Press Publication Policy (published in the January 1996 issue of the *Canadian Journal of Fisheries and Aquatic Sciences*, on the Journal Web site at pubs.nrc-cnrc.gc.ca/eng/policy/index.html, or upon request).

Duplicate and prior publication

It has long been a policy of the *Canadian Journal of Fisheries and Aquatic Sciences* to not publish manuscripts that have been published elsewhere. The Editor considers a paper not eligible for publication if most of the content of the paper (*i*) is under consideration for publication or is published in a journal or book chapter; or (*ii*) is under consideration for publication or is published in a conference proceedings or a government publication, with a substantial circulation (distributed to 100 or more individuals over a wide area). Authors may place a draft of a submitted article on their Web site or their organization's server, provided that the draft is not amended once accepted for publication. We encourage authors to insert hyperlinks from preprints to the final published version on the NRC Research Press Web site (pubs.nrc-cnrc.gc.ca). Abstracts or extended abstracts related to conferences do not constitute prior publication. Extended abstracts are usually under 1000 words and do not include presentation of detailed tables and graphics of the results of the study. Further guidelines on extended abstracts are available from the Editorial Office's Web site (uoguelph.ca/~cjfas/).

Assurance of authorship

In the cover letter, the corresponding author must affirm that all of the authors have contributed substantially to the manuscript and approved the final submission.

Suggesting reviewers

Authors may suggest names of referees that may or may not be used, but the selection of the referees is at the discretion of the Editor. When suggesting referees, please provide full addresses, telephone and fax numbers, and e-mail if available.

Conflict of interest and disclosure

The Editor recognizes that authors and peer reviewers may have real or perceived conflicts of interest arising from intellectual, personal, or financial circumstances of their research. Submitted manuscripts should include full disclosure of funding sources for the research and the letter of transmission should include an explanation of any real or perceived conflicts of interest that may arise during the peer review process. Failure to disclose such conflicts may lead to refusal of a submitted manuscript.

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The manuscript should be **double-spaced**, including references, tables, and figure captions, and formatted for 21.5 × 28 cm (8.5 × 11 in.) or ISO A4 paper. Each page should be numbered, beginning with the title page. Continuous line numbers should also be included for the text. For material that is to be set in italics, use an italic font; do not underline. Use capital letters only when the letters or words should appear in capitals.

Organize the manuscript on the basis of the purpose or scope of the study as stated in the Introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in the presentation of manuscripts.

Assure that everything in each section is relevant to the heading and that everything in each paragraph is relevant to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

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Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (*i*) it allows the reader to judge whether the article is of potential interest and (*ii*) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximum amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g., X-ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to …" or "Investigations on …" Good titles greatly assist scientists and librarians in using scientific literature and aid indexers in preparing titles for keyword indexes. Series titles should be avoided.

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The title page should contain the following. (*i*) The full title of the paper. (*ii*) Authors listed in the order in which they are to appear at the head of the printed article. (*iii*) Affiliation and address (including e-mail address) for each author. This should reflect the affiliation and address at the time of the study. Indicate current affiliations and addresses (including e-mail addresses) that differ from those in the by-line in a footnote. (*iv*) Name, address, telephone number, fax number, and e-mail address of the author responsible for correspondence.

Authors' names

The Editor urges all authors to use full forenames rather than initials and (or) one forename.

Abstract

An abstract is required for every contribution and should contain accurate descriptive words that will draw the reader to the content. This is particularly important because contemporary alerting services and search engines will search this text. It should not be more than 175 words and should appear on a separate page. The concise abstract should present the paper content accurately and should supplement, not duplicate, the title in this respect. Authors able to submit abstracts in both fluent English and French are encouraged to do so. Abstracts submitted in one language will be translated into the other official language by the Journal translator. References should not be cited in the abstract unless they are absolutely essential, in which case full bibliographic information must be provided.

Like the title, the abstract enables readers to determine the paper's content and decide whether they need to read the entire paper. Begin the abstract with the main conclusion from the study and support it with the relevant findings. Limit details of methods to those needed in understanding what was done and work them into statements of findings. Avoid using phrases such as "… is discussed" or "… was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37**: 268–282).

Introduction

Limit the Introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and methods

Materials and methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine … we …". If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work and condense them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made so as to avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the captions. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text (see Supplementary material section).

Discussion

Limit the Discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the Discussion with a short summary of the significance of the work and conclusions drawn. If the Discussion is brief and straightforward, it can be combined with the Results section.

Acknowledgements

Acknowledgements should be written in the third person. We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

Footnotes

Footnotes to material in the text should not be used unless they are unavoidable, but their use is encouraged in tables. Where used in the text, footnotes should be cited in the manuscript by superscript Arabic numbers (except in the tables, see below) and should be numbered serially beginning with any that appear on the title page. Each footnote should be typed on the manuscript page upon which the reference is made; **footnotes should not be included in the list of references.**

Equations and list of symbols

Equations should be clearly typed; triple-spacing should be used if superscripts and (or) subscripts are involved. Superscripts and subscripts should be legible and carefully placed. Distinguish between lowercase *l* and the numeral *one*, and between capital *O* and the numeral *zero*. A letter or symbol should represent only one entity and be used consistently throughout the paper. Each variable must be defined in the text or in a **List of symbols** to appear after the reference list. Variables representing vectors, matrices, vector matrices, and tensors must be clearly identified. Numbers identifying equations must be in parentheses and placed flush with the **left margin**. In numbering, no distinction is made between mathematical and chemical equations.

References

General form

The author is responsible for verifying each reference against the original article. Each reference must be cited in the text using the surnames of the authors and the year, for example, (Walpole 1985) or Green and Brown (1990). Depending on the sentence construction, the names may or may not be in parentheses, but the year always is. If there are three or more authors, the citation should give the name of the first author followed by et al. (e.g., Green et al. 1991). If references occur that are not uniquely identified by the authors' names and year, use *a*, *b*, *c*, etc., after the year, for example, Green 1983*a*, 1983*b*; Green and Brown 1988*a*, 1988*b*, for the text citation and in the reference list.

Uniform reference locators (URLs) or digital object identifiers (DOIs) are useful in locating references on the Web, and authors are encouraged to include these; they should be added to the reference in the reference list (see example below).

Unpublished reports, private communications, and in-press references

References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings are not cited in the reference list but may be included in parentheses in the text, giving all authors' names and initials. For a private communication, year of communication should also be given (e.g., J.S. Jones (personal communication, 1999)). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. If an unpublished book or article has been **accepted for publication**, include it in the reference list followed by the notation "In press". Do not include volume and page number in an in-press reference, as these are subject to change before publication.

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The **reference list** must be double-spaced and placed at the end of the text. References must be listed in alphabetical order according to the name of the first author and not numbered. References with the same first author are listed in the following order. (*i*) Papers with **one author only** are listed first in chronological order, beginning with the earliest paper. (*ii*) Papers with **dual authorship** follow and are listed in alphabetical order by the last name of the second author. (*iii*) Papers with **three or more authors** appear after the dual-authored papers and are arranged chronologically.

General guidelines on references

References should be selected judiciously and be largely restricted to significant, published literature. References should follow the form used in current issues of the Journal. The names of serials are abbreviated in the form given in *Chemical Abstracts Service Source Index* (*CASSI*) (Chemical Abstracts Service, 2540 Olentangy River Road, P.O. Box 3012, Columbus, OH 43210-0012, USA). In doubtful cases, authors should write the name of the serial in full. The Journal encourages the inclusion of issue numbers, which should be placed in parentheses after the volume number. The following bibliographic citations illustrate the punctuation, style, and abbreviations for references.

Examples of references types, including electronic references

Journal article with DOI:

Newbury, M.G., and Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. doi:10.1139/F04-113.

Journal article with URL:

Newbury, M.G., and Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. Available from pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f04-113_61_ns_nf [accessed 28 October 2005].

Journal article available online only (with DOI):

van der Sanden, J.J., and Hoekman, D.H. 2005. Review of relationships between grey-tone co-occurrence, semivariance, and autocorrelation based image texture analysis approaches [online]. Can. J. Remote Sens. **31**(3): 207–213. doi:10.1139/rs03-011.

Entire issue of journal:

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Report:

Sanders, W.W., Jr., and Elleby, H.A. 1970. Distribution of wheel loads in highway bridges. National Cooperative Highway Research Program Report 83, Transportation Research Board, National Research Council, Washington, D.C.

Book:

Williams, R.A. 1987. Communication systems analysis and design. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Book in a series:

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Part of book:

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. McNeil and D.C. Himsworth. Oregon State University Press, Corvallis, Oreg. pp. 203–229.

Paper in conference proceedings:

Kemp, A.L.W. 1969. Organic matter in the sediments of Lakes Ontario and Erie. *In* Proceedings of the 12th Conference on Great Lakes Research, Ann Arbor, Mich., 5–7 May 1969. International Association for Great Lakes Research, Ann Arbor, Mich. pp. 237–249.

Institutional publications and pamphlets:

Dzikowski, P.A., Kirby, G., Read, G., and Richards, W.G. 1984. The climate for agriculture in Atlantic Canada. Available from the Atlantic Advisory Committee on Agrometeorology, Halifax, N.S. Publ. ACA 84-2-500. Agdex No. 070.

Corporate author:

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, D.C.

Thesis:

Keller, C.P. 1987. The role of polysaccharidases in acid wall loosening of epidermal tissue from young *Phaseolus vulgaris* L. hypocotyls. M.Sc. thesis, Department of Botany, The University of British Columbia, Vancouver, B.C.

Web site citation:

Quinion, M.B. 1998. Citing online sources: advice on online citation formats [online]. Available from worldwidewords.org/articles/citation.htm [accessed 20 October 2005].

Translation:

Koike, A., and Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. [Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Tables

Tables must be typed on separate pages, placed after the list of references, and numbered with Arabic numerals in the order cited in the text. The title of the table should be a concise description of the content, no longer than one sentence, that allows the table to be understood without detailed reference to the text. Column headings should be brief, but may be amplified by footnotes. Vertical rules should not be used. A copy of the Journal should be consulted to see how tables are set up and where the lines in them are placed. Footnotes in tables should be designated by symbols (in the order *, †, ‡, §, ||, ¶, #) or superscript lowercase italic letters. Descriptive material not designated by a footnote may be placed under a table as a **Note.** Numerous small tables should be avoided, and the number of tables should be kept to a minimum.

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Figure captions should be listed on a **separate page** and placed after the tables. The caption should informatively describe the content of the figure, without need for detailed reference to the text. Experimental conditions should not be included, but should be adequately covered in the Methods. For graphs, captions should not repeat axis labels, but should describe what the data show. A single caption can be provided for multipart (composite) figures, with necessary details on the separate parts, identified by their individual labels. If the separate parts require enough information to warrant separate captions, then the composite should be separated into individual figures.

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An appendix should be able to stand alone, as a separate, self-contained document. Figures and tables used in an appendix should be numbered sequentially but separately from those used in the main body of the paper, for example, Fig. A1, Table A1, etc. If references are cited in an appendix, they must be listed in an appendix reference list, separate from the reference list for the article. If there is more than one appendix, label as follows: Appendix A, Appendix B, etc.

Supplementary material

Supplementary material (or data) consists of extra tables, figures (maps), detailed calculations, and data sets produced by the authors as part of their research, but not essential for understanding or evaluating the paper, and not published with the article in the print edition of the Journal. Depending on the policy of the Journal, such material may or may not be peer reviewed with the article. Supplementary material should be submitted with the article. During Web submission (**OSPREY**), relevant files should be attached under "Supplementary data". The National Research Council of Canada maintains a depository in which supplementary material may be placed, either at the request of the author or at the suggestion of the Editor. In addition, supplementary material can be made available at no charge in its native file format on the Journal Web site. It will be linked from the Web page of the associated article. Tables and figures should be numbered in sequence separate from those published with the paper (e.g., Fig. S1, Table S1). The supplementary material should be referred to in the printed article by footnotes. Printed copies of material in the depository may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Computer programs

It is not the policy of the Journal to publish detailed printouts of computer program statements. Where the availability of these details enhances the usefulness of the paper, the author should submit the program information electronically as Supplementary material (see section above).

Illustrations

General

Each figure or group of figures should be planned to fit, after appropriate reduction, into the area of either one or two columns of text. The maximum finished size of a one-column illustration is 8.6 × 23.7 cm (3.4 × 9.3 in.) and that of a two-column illustration is 18.2 × 23.7 cm (7.2 × 9.3 in.). The figures (including halftones) must be numbered consecutively in Arabic numerals, and each one must be referred to in the text and must be self-explanatory. All terms, abbreviations, and symbols must correspond with those in the text. Only essential labelling should be used, with detailed information given in the caption. Submission of noncontinuous (screened) photographs and scanned illustrations printed out on laser printers is not recommended, as moirés develop; a moiré is a noticeable, unwanted pattern generated by rescanning or rescreening an illustration that already contains a dot pattern.

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All lines must be sufficiently thick (0.5 points minimum) to reproduce well, and all symbols, superscripts, subscripts, and decimal points must be in good proportion to the rest of the drawing and large enough to allow for any necessary reduction without loss of detail. Avoid small open symbols; these tend to fill in upon reproduction. **Lettering produced by dot matrix printers or typewriters, or by hand, is not acceptable**. The same font style and lettering sizes should be used for all figures of similar size in any one paper. Original recorder tracings of **NMR**, **IR**, **ESR spectra**, etc., are not acceptable for reproduction; they must be redrawn.

Maps

Maps must have very **clear, bold patterns** and must show longitudes and latitudes (or UTM coordinates) and a scale to ensure proper identification of study locations. On **maps of Quebec**, the official name of municipalities must be used (e.g., Québec, Montréal, Clarke City) and physical features must be in French (e.g., Lac Bienville) except for those that are considered of pan-Canadian significance. Areas of pan-Canadian significance have an official form in English and French (e.g., Atlantic Ocean and Océan Atlantique) and should appear in the language of the paper. Quebec (the province) must also appear in the language of the paper. For a complete list of names of areas of pan-Canadian significance, see pp. 236–237 of *Le guide du rédacteur* (2nd ed., 1996), published by Public Works and Government Services Canada, Ottawa, ON K1A 0S5.

Photographs

Photographs should be continuous tone, of high quality, and with strong contrast. Only essential features should be shown. A photograph, or group of them, should be planned to fit into the area of either one or two columns of text **with no further reduction**. Electron micrographs or photomicrographs should include a scale bar directly on the print. The best results will be obtained if the authors match the contrast and density of all figures arranged as a single plate.

Colour illustrations

Colour illustrations will be at the author's expense. Further details on prices are available from Cecily Pearson, Managing Editor of the Journal (613-993-9099; fax: 613-952-7656; e-mail: cecily.pearson@nrc-cnrc.gc.ca).

Preparation of electronic graphic files

The preferred graphic application of NRC Research Press is CorelDraw! For other applications that can be used, see the electronic graphics list at pubs.nrc-cnrc.gc.ca/eng/journals/graphics.

PC or Macintosh versions of True Type or Type 1 fonts should be used. **Do not use bitmap or nonstandard fonts.**

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Remember that the more complex your artwork becomes, the greater the possibility for problems at output time. Avoid complicated textures and shadings, especially in vector illustration programs; this increases the chance for a poor-quality final product.

Bitmap (raster) files are image files produced using a grid format in which each square (or pixel) is set to one level of black, colour, or grey. A bitmap (rasterized) file is broken down into the number of pixels or picture elements per inch (ppi). Pixels per inch is sometimes referred to as dots per inch (dpi). The higher the resolution of an image, the larger the number of pixels contained within the rectangular grid. The proper resolution should be used when submitting bitmap artwork. The minimum requirements for resolution are 600 dpi for line art, 1200 dpi for finelines (line art with fine lines or shading), 300 dpi for halftones and colour, and 600 dpi for combinations (halftones with lettering outside the photo area).

All **colour** files submitted must be as CMYK (cyan, magenta, yellow, and black). These colours are used in full-colour commercial printing. RGB graphics (red, green, and blue; colours specifically used to produce an image on a monitor) will not print correctly.

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Bitmaps can be imported into vector/draw applications only for the purpose of adding and overlaying information, lines, text, etc. Bitmaps should not be resized, cropped, rotated, or otherwise manipulated after importing.

Multimedia formats — Audio and video clips in the major multimedia formats are now accepted for NRC Research Press journals published in full-text HTML. For accepted formats, see the Electronic graphic list published on the Journal Web site.

Manuscript guidelines

Style guides

As a general guide for biological terms, *The CSE Manual for Authors, Editors, and Publishers: Scientific Style and Format* (7th ed., 2006) published by the Council of Science Editors, Reston, VA 20190, USA, is recommended.

Spelling

Spelling should follow *Webster's Third New International Dictionary* or the *Oxford English Dictionary*. Authors are responsible for consistency in spelling.

Nomenclature, abbreviations, and acronyms

Nomenclature and abbreviations should follow the rules recommended by the International Union of Biochemistry (IUB) Committee of Editors of Biochemical Journals with support of IUPAC. As a general guide for biological terms, *The CSE Manual for Authors, Editors, and Publishers: Scientific Style Format* (7th ed., 2006), published by the Council of Biology Editors, Reston, VA 20190, USA, is recommended. For enzyme nomenclature, *Enzyme Nomenclature (1992): Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology* (Academic Press, San Diego, Calif.) should be followed.

Abbreviations and acronyms that are standard in the discipline need not be defined. All others must be defined when they are first mentioned in the text and those with more than one meaning should be avoided.

Units of measurement

SI units (Système international d'unités) should be used or SI equivalents should be given. Avoid ambiguous forms such as g $C/m^2/day$; use g $C{\cdot}m^{-2}{\cdot}day^{-1}$. This system is explained and other useful information is given in the *Metric Practice Guide* (2000) published by CSA International (178 Rexdale Blvd., Toronto, ON M9W 1R3, Canada). For practical reasons, some exceptions to SI units are allowed. Units such as kilocalorie, reciprocal centimetre (wave number), and atmosphere may be used for the foreseeable future.

Statistical analyses

The assumptions and (or) the model underlying any statistical analysis should be clearly stated. Symbols such as * and **, denoting levels of significance, should not be used except in conjunction with the actual values of the associated test statistic; actual p values are preferred.

Fish

The Journal follows the names and spelling for fishes recommended in *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (6th ed., Spec. Publ. No. 29, American Fisheries Society, 2004) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (Trans. Am. Fish. Soc. **119**: 2–15, 1990).

Writing numbers

In writing long numbers, the digits should be separated into groups of three, counted from the decimal marker to the left and right. The separator should be a space and not a comma, period, or any other mark, for example, 25 562 987 and not 25,562,987. In English text, the decimal marker should be a point, for example, 0.1 mL and not 0,1 mL. The decimal point in all numbers between 1 and −1, except 0, must be preceded by a 0. The sign × should be used to indicate multiplication, e.g., 3×10^6 and not $3 \cdot 10^6$.

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