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Modélisation des effets des ensemencements et du couvert nuageux sur les patrons d'utilisation d'habitats des juvéniles de saumons de l'Atlantique

par

Philippe Girard

Département des sciences biologiques
Faculté des arts et des sciences

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Ce mémoire intitulé :

Modélisation des effets des ensemencements et du couvert nuageux sur les patrons d'utilisation d'habitats des juvéniles de saumons de l'Atlantique.

présenté par :
Philippe Girard

a été évalué par un jury composé des personnes suivantes :

Bernard Angers..............président-rapporteur
Daniel Boisclair.............directeur de recherche
Michel Leclerc...............codirecteur
Michel Lapointe.............membre du jury

Mémoire accepté le ....

Sommaire

L'Indice Probabiliste d'Habitat (IPH) est un modèle développé dans le but de prédire la distribution des poissons dans un milieu riparien et d'en inférer la qualité des microhabitats. Ce modèle a donné des résultats intéressants dans le cas des juvéniles de saumons de l'Atlantique (*Salmo salar;* Guay *et al.* 2000*)*. La présente recherche a tenté, dans un premier temps, d'utiliser les qualités prédictives de ce modèle afin de dissiper des incertitudes reliées aux ensemencements de juvéniles de saumons de l'Atlantique élevés en pisciculture. Dans un deuxième temps, un approfondissement de l'approche IPH est réalisé afin de mettre en relief les facteurs environnementaux affectant le comportement des juvéniles de saumons de l'Atlantique et la qualité des modèles développés sur le terrain.

Le premier chapitre porte sur une étude au cours de laquelle 250 tacons de pisciculture ont été ensemencés dans une section de 200m de rivière. Nous avons ainsi tenté i) de déterminer le taux d'installation ainsi que le choix d'habitat des juvéniles ensemencés et ii) d'évaluer l'impact de l'ensemencement sur la distribution spatiale des juvéniles sauvages. La quantification de la qualité des habitats disponibles a été réalisée grâce à un IPH développé sur la rivière. Les résultats ont montré que seulement 6% des poissons ensemencés ont été retrouvés dans la section. Par contre, ceux-ci ont été observés dans les meilleurs habitats disponibles. Aucun changement dans la distribution spatiale des juvéniles sauvages n'a été détecté. Ces travaux suggèrent que les tacons de pisciculture éprouvent beaucoup de difficultés à s'installer à proximité de l'endroit où ils sont ensemencés mais que ceux qui restent sont capables de détecter les meilleurs habitats et d'y établir un territoire alimentaire.

Le deuxième chapitre porte sur un aspect comportemental méconnu des juvéniles de saumons de l'Atlantique : la variabilité journalière de la stratégie alimentaire estivale. Des plongées successives ont montré que l'abondance de tacons sauvages pouvait varier d'un facteur de 700% d'un jour à l'autre et que le couvert nuageux expliquait 77% de cette variabilité. Nous avons aussi montré l'impact de cette variabilité sur le développement d'IPH. Nos résultats suggèrent qu'un indice développé en conditions ensoleillées prédit mieux la qualité des habitats. Nous concluons que le couvert nuageux doit être pris en compte lors d'études portant sur l'habitat des juvéniles de saumons de l'Atlantique.

Mots clés: distribution spatiale, ensemencement, habitat, juvéniles, modélisation, pisciculture, rivière, saumon Atlantique.

Summary

The Habitat Probabilistic Index (HPI) is a model developed in order to predict fish distribution in a riparian habitat and to infer about microhabitat quality. This model gave interesting results in the case of Atlantic salmon juveniles (*Salmo salar*; Guay *et al.* 2000). The first part of this present work aimed to use the predictive qualities of the HPI to answer some questions linked to the stocking of hatchery-reared juveniles of Atlantic salmon. The second part of this work aimed to bring out the environmental factors that influence the behaviour of Atlantic salmon juveniles and the quality of the HPI developed on field.

In the first chapter of this work, we aimed to i) determine the capacity to adopt a territory and the choice of habitats performed by the hatchery fish and ii) evaluate the impact of stocking on the spatial distribution of wild juveniles, after a stocking of 250 hatchery-reared fish in a 200m river section. The quantification of the habitats quality was obtained with a HPI developed for the river. Results have shown that only 6% of hatchery fish remained in the section where stocking was performed. However, those that have been observed after stocking were found in the best habitats available according to the prediction of the HPI. Furthermore, no change into the spatial distribution of wild juveniles have been detected. Our work suggest that hatchery fish have great difficulties to adopt a territory close to the location where they have been stocked but those that remained in the section seemed able to chose a profitable habitat.

The subject of the second chapter is a misunderstood behavioural aspect of Atlantic salmon juveniles: the day-to-day variability of the summer foraging strategy. Successive diving have shown that the abundance of wild parrs could vary within 700%

from a day to another. The cloud cover explain 77% of that variability. We showed the effect of that variability on the development of HPI. Our results suggested that an index that was developed under cloudless conditions give better predictions of the habitat quality. We conclude that the cloud cover must be take into consideration when one aims to study the habitat of salmon parrs.

Key words: Atlantic salmon, habitat, hatchery, juveniles, modelling, river, spatial distribution, stocking.

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Liste des sigles et des abréviations

95% C.I.: intervalle de confiance à 95%.

CIRSA : Centre Interuniversitaire de Recherche sur le Saumon Atlantique.

D50 : diamètre médian des grains.

F : statistique de Fisher-Snedecor.

F1 : première génération suivant un croisement.

HPI (IPH) : Indice Probabiliste d'Habitat.

λ (lambda): variable complexe de l'IPH.

n : effectif.

NHM (MNH) : Modèle Numérique d'Habitat.

NNE : Nord-Nord-Est.

p : probabilité.

P_n: paramètres de l'équation correspondant à la variable λ.

r : coefficient de corrélation linéaire de Pearson.

R^2 : coefficient de régression.

S : substrat.

SD : écart-type (Standard Deviation).

t : statistique de Student.

V : vitesse moyenne du courant.

Z : profondeur.

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à mon grand-père, Raymond Girard
et à Kim.

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Introduction

La répartition géographique naturelle du saumon de l'Atlantique (*Salmo salar*) s'étend de l'est de l'Amérique du Nord à la Grande-Bretagne, le Portugal et la Scandinavie (Scott et Crossman 1974). On retrouve donc des rivières fréquentées par des saumons de l'Atlantique dans différents types de paysages présentant des caractéristiques très diversifiées quant à leur géomorphologie ainsi qu'à leur climat qui influencent de nombreuses variables biologiques et physiques des rivières. Au niveau de la géomorphologie et de la géologie, les rivières à saumons présentent aussi bien un substrat composé de roches granitiques que volcaniques ou glaciaires (Elliot *et al.* 1998), lequel déterminera une vaste gamme de caractéristiques écologiques telle la chimie de l'eau (Liu *et al.* 2000; McKee *et al.* 2001) ainsi que la morphologie du bassin versant (Décamps et Naiman 1989; Peterson *et al.* 1995; Elliot *et al.* 1998). Les caractéristiques climatiques influenceront pour leur part, le régime de crue et l'hydrologie des bassins versants (Magillian et Graber 1996) ainsi que la température de l'eau (Peterson *et al.* 2001) qui s'étendra sur toute la plage de résistance thermique du saumon soit de 0°C au niveau des latitudes les plus nordiques de la distribution de l'espèce (Peterson *et al.* 1995) à 25°C en été en Europe de l'Ouest et en Amérique du Nord (Elliot et *al.* 1998; Girard, données non publiées).

Bien que montrant une diversité importante au niveau de leurs caractéristiques écologiques, les écosystèmes ripariens de ces régions ont tous montré des baisses importantes des montaisons de saumons sauvages depuis les cent dernières années (Kennedy 1988; Heggberget *et al.* 1993; Gross 1998). Pour la plupart des scientifiques, ce déclin est attribuable aux activités humaines; car si les rivières de ces régions diffèrent par leurs caractéristiques physiques et biologiques, elles montrent des ressemblances frappantes quant aux perturbations anthropiques de leur bassin versant (Elliot *et al.* 1998). La déforestation des bassins versants et des rives des rivières à saumons provoque une diminution de la capacité d'infiltration des sols et augmente le ruissellement de surface provoquant des modifications du régime des crues (Miller 1990), une augmentation de la température de l'eau ainsi que de l'apport de nutriments (Likens *et al.* 1970). L'utilisation des bassins versants pour des fins agricoles provoque une augmentation de l'apport de contaminants (pesticides, nutriments, etc.) dans les rivières (Frank *et al.* 1982; Miller *et al.* 1982). Les développements industriels et hydroélectriques ont pour leur part provoqué dans un cas, une augmentation importante de la pollution de l'eau et dans l'autre, occasionné l'aménagement de nombreux barrages, détournant les rivières, inondant les terres et bloquant par le fait même la route aux saumons adultes vers les frayères (Peterson *et al.* 1995; Elliot *et al.* 1998). Sans oublier l'urbanisation qui, à elle seule, combine tous les effets décrits ci-haut (Elliot *et al.* 1998). À la fin du 20ième siècle, seules les rivières les plus nordiques conservaient un bassin versant intact ainsi que des conditions physiques et biologiques relativement inaltérées. Par contre ces régions sont les plus susceptibles d'être affectées par les changements climatiques (Minns *et al.* 1992) et par le transport à grande échelle des polluants atmosphériques (Wania and Mackay 1993). Ainsi, en relativement peu de temps, l'humain a profondément altéré la plupart des caractéristiques physiques et biologiques des rivières sur la base desquelles le saumon de l'Atlantique avait pris près de 10 000 ans à s'adapter. Depuis 2001, le saumon de l'Atlantique est considéré par le gouvernement canadien comme une espèce en danger dans certaines régions comme la baie de Fundy.

Certaines solutions ont été proposées afin de palier au problème du déclin des populations de saumons de l'Atlantique. L'interdiction complète de la pêche commerciale en mer dans certains pays dont le Canada et les États-Unis, l'établissement de quotas de pêche sportive dans les rivières (quand elle n'est pas complètement interdite), le relâchement des captures, l'aménagement de passes migratoires et le nettoyage des frayères en sont quelques exemples. Dans le cadre de la première partie de ce mémoire, nous nous concentrerons sur une solution précise : l'ensemencement de juvéniles de saumons élevés en pisciculture.

Bien qu'efficace dans certains cas (Côté 1976), les solutions décrites ci-haut deviennent bien insuffisantes dans les cas les plus extrêmes où les populations de saumons de l'Atlantique ont été complètement décimées. En parallèle, les procédures de pisciculture des salmonidés ont été considérablement améliorées depuis leurs débuts il y a environs un siècle surtout en ce qui a trait à la fertilisation artificielle, l'incubation des œufs ainsi que l'élevage des juvéniles en bassin (Krueger et May 1991). Ces améliorations importantes ont élevé le taux de survie de l'œuf au stade de tacons (1-2 ans) à près de 90% (Locke 1998), un taux de survie considérablement plus élevé que celui retrouvé chez les populations naturelles (1,5% selon Côté 1976). Dans ces conditions, plusieurs millions de poissons de pisciculture peuvent être produits chaque année (Krueger et May 1991). Cette situation explique pourquoi l'introduction de juvéniles de saumons de pisciculture est considérée depuis plusieurs décennies comme la solution la plus rapide, facile et profitable pour la restructuration partielle ou complète des populations naturelles de saumons de l'Atlantique (Moring *et al.* 1995). L'ensemencement de poissons de pisciculture est d'ailleurs la solution privilégiée par de nombreux aménagistes de rivières (Kennedy 1988; Gross 1998) et des résultats satisfaisants semblent avoir été obtenus au niveau de l'amélioration du statut de certaines populations de poissons reliées à la pêche sportive (Lange *et al.* 1995) et aux pêcheries commerciales (Krueger et May 1991). Cependant, plusieurs questions concernant les impacts sur les populations naturelles et la survie des juvéniles de saumons ensemencés restent sans réponse, et le débat sur l'utilisation des spécimens de pisciculture pour des fins de restauration reste ouvert (Bowles 1995, Lange *et al.* 1995, McGurin *et al.* 1995, Radonsky and Loftus 1995).

L'ensemencement de saumons de pisciculture pourrait selon certains affecter la dynamique ainsi que la génétique des populations naturelles de saumons de l'Atlantique. La dynamique des populations serait influencée via l'augmentation de la compétition pour l'espace et pour l'accès à la nourriture provoquée par une augmentation de l'effectif de la population (Chapman 1966). Selon Heggberget *et al.* (1993) la compétition accrue provoquée par un ensemencement affecterait la croissance des individus, la production de saumoneaux ainsi que le potentiel reproducteur des populations naturelles. La diversité génétique des populations serait entre autre affectée par l'introduction de nouveaux allèles, sélectionnés en pisciculture (Busack et Currens 1995). En effet, la composition génétique des populations naturelles (induite par la sélection naturelle) diffère de celle des populations provenant des piscicultures (induite par la sélection artificielle). Ces différences peuvent se traduire par des variations importantes tant morphologiques que comportementales pouvant affecter le *fitness* des individus en nature (Krueger et May 1991; Leary *et al.* 1995), la productivité et le maintien des populations à long terme (Busack et Currens 1995). Conséquemment, selon Gross (1998), les ensemencements de poissons de pisciculture auraient causé beaucoup plus de tort que de bien aux populations naturelles. Toujours selon Gross (1998), près de 94% de l'ensemble de l'effectif mondial du saumon de l'Atlantique (effectifs en nature et en pisciculture combinés) serait composé, de nos jours, d'individus issus des piscicultures.

Par contre, toutes ces hypothèses sur l'impact négatif des ensemencements sont sous-jacentes à la capacité des saumons ensemencés à adopter des comportements dit «naturels» (alimentation, évitement des prédateurs, etc.) après l'ensemencement, ce qui favorisera leur survie en rivière (Maynard *et al.* 1995). Or, la propension des poissons issus des piscicultures à adopter de tels comportements est mise en doute par plusieurs auteurs (Dickson et MacCrimmon 1982; Johnson et Abraham 1991; Maynard *et al.* 1995; Locke 1998). Selon ces auteurs, les conditions d'élevage dans les bassins de pisciculture (grandes densités de poissons, alimentation mécanique, faible courant d'eau, etc.) provoqueraient la production de poissons incapables de combattre le fort courant des rivières ou d'adopter un comportement alimentaire naturel en plus de montrer des réponses inappropriées à la prédation.

Les incertitudes sont donc nombreuses quant aux impacts et succès réels des ensemencements. Le premier chapitre de ce mémoire tentera d'amener une contribution au débat en examinant le taux d'installation en rivière de juvéniles issus de pisciculture, leur choix d'habitats alimentaires et les effets de cet ensemencement sur les patrons de répartition des individus sauvages en utilisant les qualités prédictives de l'IPH et de la modélisation numérique bidimensionnelle des microhabitats.

L'IPH est un modèle développé dans le but de prédire la répartition des poissons dans un milieu riparien et d'en inférer la qualité des microhabitats. Ce modèle a donné des résultats intéressants dans le cas des juvéniles de saumons de l'Atlantique (*Salmo salar;* Guay *et al.* 2000*)*. Cependant certaines considérations pouvant influencer la qualité de cet indice et des études qui en découlent doivent être mises et relief. Le développement de l'IPH (ainsi que plusieurs autres indices de qualité d'habitat) nécessite l'évaluation des conditions utilisées et évitées par les poissons via un échantillonnage visuel en apnée (Guay *et al.* 2000). Cependant, il existe une variabilité journalière caractérisant le comportement alimentaire des juvéniles naturels de saumons durant la période estivale. Cette variabilité temporelle naturelle se traduit par des variations importantes du nombre de juvéniles qui s'alimentent dans la colonne d'eau d'une journée à l'autre : les densités pouvant varier de 1,5 poissons/100m² à 4 poissons/100m² dans certains bons habitats dans des conditions hydrologiques similaires (Girard, données non publiées). Or, si des efforts importants ont été mis en œuvre afin de développer des indices puissants permettant de prédire l'hétérogénéité spatiale de la qualité des habitats de poissons en rivières tout en tenant compte du dynamisme caractérisant ces systèmes (Bovee et Milhous 1978,1982; Souchon 1989; Heggenes 1996; Guisan et Zimmerman 1999; Guay *et al.* 2000), il en va autrement pour ce qui est de cette variabilité temporelle dont l'importance semble être resté insoupçonnée.

Le deuxième chapitre de ce mémoire traitera de cette variabilité journalière du comportement alimentaire des juvéniles de saumons de l'Atlantique. Un modèle prédictif du nombre de poissons s'alimentant dans la colonne d'eau sera développé en faisant l'hypothèse que le contrôle de ce comportement est sous l'influence de certaines variables environnementales. De plus, nous décrirons l'effet de cette variabilité du comportement alimentaire des juvéniles sur le développement des IPH.

Chapitre 1

Spatial interactions between hatchery-reared and wild juveniles of Atlantic salmon (*Salmo salar*) after stocking in a river.

Summary

A stocking of 250 hatchery parrs of Atlantic salmon have been performed in a 200 m long reach of the Escoumins river. Following this stocking, we aimed to i) quantify the adoption of a territory and the choice of habitat by the stocked parrs and ii) evaluate the impacts of the stocking on the spatial distribution of the wild parrs. The quantification of the quality of the habitats available over the reach under study have been performed with a habitat probabilistic index (HPI). The results show that 3 and 7 days after stocking, only 6% of the stocked fish remain in the 200 m reach. However, those that remained have been observed in the best habitats available according to the habitat index predictions. Furthermore, no change in the spatial distribution of wild fish have been detected. Our work suggest that hatchery parrs stocked in river have great difficulties to survive or to remain close to the stocking point. However, the observation of those that stay close to the stocking point suggest that hatchery parrs are able to detect favourable habitats and to adopt a foraging territory.

Résumé

Nous avons ensemencé 250 tacons de saumon de l'Atlantique de pisciculture dans une section de 200m de la rivière des Escoumins. Suite à cet ensemencement, nous avons i) déterminé le taux d'établissement ainsi que le choix d'habitat des juvéniles ensemencés et ii) évalué l'impact de l'ensemencement sur la distribution spatiale des juvéniles sauvages. La quantification de la qualité des habitats disponibles a été réalisée grâce à un indice probabiliste d'habitat (IPH). Les résultats ont montré que 3 et 7 jours après l'ensemencement, seulement 6% des poissons ensemencés ont été retrouvés dans la section de rivière de 200m. Par contre, ceux-ci ont été observés dans les meilleurs habitats disponibles prédits par l'indice probabiliste. De plus, aucun changement dans la distribution spatiale des juvéniles sauvages de saumons de l'Atlantique n'a été détecté. Nos travaux suggèrent que les tacons ensemencés ont beaucoup de difficultés à survivre ou à s'installer à proximité de l'endroit où ils sont ensemencés. Par contre, l'observation de ceux qui sont restés près du point d'ensemencement suggère qu'ils sont capables de détecter les meilleurs habitats et d'y établir un territoire alimentaire.

Introduction

The stocking of hatchery juveniles is a procedure widely used to support and restore natural populations of Atlantic salmon (*Salmo salar*; Kennedy 1988, Heggberget 1993, Moring et al. 1995, Gross 1998). The short term (days, months) success of stocking may be defined by the ability of hatchery fish to mimic the behaviour of wild fish (Maynard et al. 1995). During the summer, wild juveniles of Atlantic salmon (parrs) generally adopt a territorial behaviour. They hold a 'sit-and-wait' position over a 'home rock' that serves as a shelter against the flow and they perform frequent movements of few decimetres to capture invertebrates drifting in the current (Kalleberg 1958, Fausch 1984). Recent studies suggest that the surface area of the summer habitat used by a single juvenile of Atlantic salmon may be composed of a mosaic of interconnected territories overlapping with territories used by adjacent fish (Armstrong et al. 1999) and that a portion of the parr population may explore their environment (Rodriguez 2002). Notwithstanding the spatial scale employed to describe individual feeding habitats, adoption of a territorial behaviour is expected to determine the success of parrs via its effect on their net energy gain (Fausch 1984). It is also expected that the benefits and the costs associated with territories may vary between habitats at the scale of reaches and river segments (Fausch and White 1981). Hence, the ability of hatchery fish to adopt and maintain a territory in a profitable habitat may indicate the short term success of stocking.

Few studies documented the ability of parrs to establish a territory when stocked in unfamiliar habitats. Saunders and Gee (1964) observed that wild parrs that were moved as far as 200 m from their point of capture did not adopt a territory in their new habitat and returned to their original territories within 40 days. In contrast, Armstrong et al.

(1997) observed that wild parrs transplanted from one area of a stream into an enclosed section of this same stream adopted a territory within three days of stocking in their new habitat. These fish selected a territory within 30m of their point of stocking and did not accumulate near the barriers delimiting the experimental stream section. Hence, they did not display any well defined homing behaviour towards their original territories. While the study of Saunders and Gee (1964) illustrates the capacity of parrs to display a homing behaviour and their difficulty to establish a territory in an unfamiliar area, that of Armstrong et al. (1997) indicates that parrs do not display a homing behaviour, that they can easily adopt a new territory when stocked in unfamiliar areas, and that a territory can be established close to the point of stocking. Since both studies were performed using wild fish, neither allows to anticipate the behaviour of hatchery parrs stocked in a natural environment.

The short term effects of hatchery fish on wild fish is also a source of controversy. Some studies suggest that hatchery fish are more subjected to predation and that they should suffer higher mortality rates than their wild counterparts (Noakes 1978; Donnelly and Whoriskey 1993; Jonsson et al. 1993). Hatchery fish has also been presumed to be less efficient than wild fish at exploiting their environments (Dickson and MacCrimmon 1982). However, hatchery fish have been argued to be more aggressive and more competitive than wild parrs (Youngson and Verspoor 1998; Rhodes and Quinn 1998; Rhodes and Quinn 1999). Hence, it is presently difficult to predict the effects of the stocking of hatchery fish on habitat utilisation pattern of wild parrs in rivers.

The objectives of our work were 1) to quantify the ability of hatchery-reared parrs to locate favourable habitats and to adopt a foraging territory, and 2) to evaluate the effect of the stocking of hatchery fish on the distribution of wild parrs.

Material and methods

The general experimental strategy used to attain our objectives combined underwater observations of parrs in a reach and the development of a numerical habitat model (NHM) for that reach. Snorkelling observations were used to map fish distribution before and after stocking of hatchery-reared parrs. The NHM permitted the development of a map of the spatial heterogeneity of habitats quality. Overlapping these maps allowed us to evaluate the choice of habitats made by hatchery parrs and the potential differences in the habitats used by wild parrs before and after stocking.

Study site and species

Sampling was conducted in the Escoumins River in the Haute-Côte-Nord of Quebec at approximately 500 km NNE of Montréal (Fig.1). The watershed of the Escoumins river cover an area of 979.7 km^2. The flow rate of this river is controlled by a group of dams constructed on its source and on its main tributaries. The average discharge during summer 2000 according to the gauging station of the Ministère de l'Environnement du Québec (# 070204) situated at 9 km of the junction between Escoumins River and St. Lawrence River was 7.17 m^3/s. The study site was located at about 20 km from this junction. It consisted in a 300 m reach comprising a 100 m

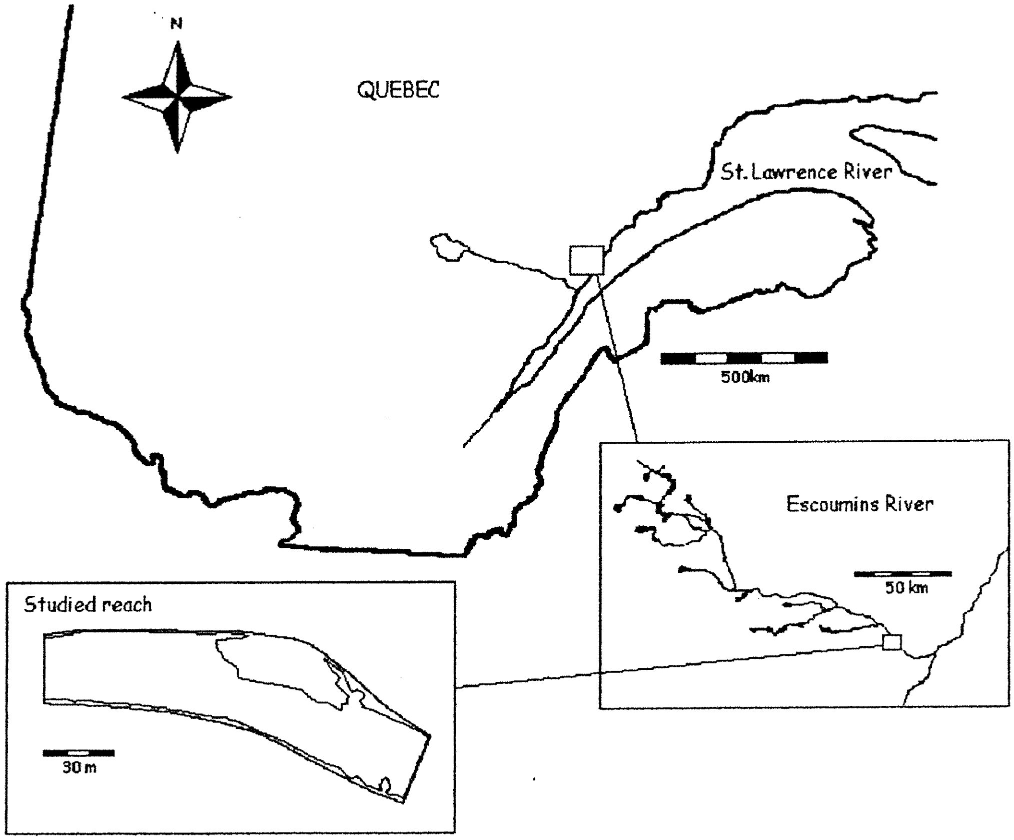

Figure 1. Map of the study site situated on the northern shore of the St. Lawrence river

calibration section (upstream part of the study site) and a 200 m experimental section. The calibration section was used to determine the physical conditions used and avoided by parrs. These data were then used to parametrize the biological component of the NHM. The experimental section was used to stock hatchery fish and to map the fish distribution before and after the stocking operation. The NHM was applied to this section and allowed us to predict habitat quality and its spatial heterogeneity. The wetted surface of the experimental section under a $6.8 m^3/s$ flow rate was $8531 m^2$. The width of the reach under studied ranged from 21.7m to 47.5 m. The study reach is composed of a series of pools (maximum depth of 1.4 m) and riffles. The average slope of the reach is 0.2%. The substrate size of the riverbed ranges from sand ($5 \times 10^{-6} - 4 \times 10^{-5}$ m diameter) to metric boulders (over 1 m diameter). The reach does not contain areas covered by wood debris or a canopy.

The species selected for this study is the Atlantic salmon because of its economical importance in Quebec (sports fishing activities). Furthermore, Atlantic salmon was designated by the Canadian government as an endangered species in some regions of Canada (Fundy Bay) since 2001. Our study focusses on the 1+ to 3+ parrs of Atlantic salmon. Atlantic salmon is the dominant fish species in the reach sampled (97% of the fish observed in the reach). Brook char (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), Longnose sucker (*Catostomus catostomus*), and Sea lamprey (*Petromyzon marinus*) were also observed in the reach studied.

Structure of the numerical habitat model

The NHM is a combination of a hydrodynamic model and of a biological model (Leclerc et al. 1995). The hydrodynamic model (HYDROSYM) is a St-Venant two dimensional (2D vertically integrated) finite element tool with drying-wetting capabilities that predicts the variation of depth and current velocity over the wetted area of a reach at a given flow discharge (Heniche et al. 2000a, b, 2001, Leclerc 1990). Combined with a MODELER, a river-dedicated Geographical Information System (GIS) entirely coupled with HYDROSYM (Secretan et al. 1998), this model uses a topographic description of the riverbed and a map of substrate grain size as inputs (Secretan et al. 2001, Secretan and Leclerc 1998). These measures, combined with physical and numerical coefficients (turbulent viscosity and friction factor) and assumptions about fluid dynamics and equilibrium (conservation mass and momentum), allow under proper boundary and initial conditions to predict and map current velocity and water depth over the reach modeled, and this, for any specified flow.

The biological model is the Habitat Probabilistic Index (HPI; Guay et al. 2000). This model is based on a multivariate logistic regression designed to distinguish the physical (abiotic) conditions used and avoided by fish. It uses, as independent variables, water depth (m), current velocity (m/s), and substrate diameter (m). The predictions of the biological model vary between 0 (poor habitats) and 1 (best habitats), and have been argued to correspond to the probability to find a fish under given combinations of the three physical variables (Guay et al. 2000). This model is based on the assumption that if fish makes a preferential use of a specific range of water depth, current velocity, and substrate grain size, this range corresponds to a habitat of higher quality for fish.

The final operation of the numerical modeling is to combine the (x,y) distributed predictions of the hydrodynamic model for a given flow rate and the equation of the biological model. Depth and current velocity maps produced by the hydrodynamic model combined with the map of substrate grain size are used as inputs for the HPI model to predict and map the spatial heterogeneity of habitat quality over the entire surface of the experimental section. Maps of fish habitat quality are represented using ten categories of habitat patches assigned HPI values ranging from 0 to 1 with increments of 0.1 (0-0.1; 0.1-0.2 etc).

Sampling

Hydrodynamic model

The development of the hydraulic model requires the topographic description of a reach to be modelled and the mapping of substrate grain size over the riverbed of this reach. A topographic map of the experimental section was obtained by taking the latitude, longitude, and the altitude for 2589 sampling points irregularly distributed over the river bed, the shores, and above the high water level of this reach. The rational for selecting their location aims to represent as much as possible the morphological variability and local bed features. Each sampling point was georeferenced with a total station (an electronic theodolite combined with an electronic distance measurement system, SOKKIA SET3B) and an electronic data logger (SOKKIA SDR33). We estimated substrate grain size at each topographic sampling point through values of D50 (median size). Given that the volume of a stone is determined by three axes (A being the longest and C the shortest axis), D50 is defined as the length (in m) of the B-axis of the median stone within a 1 m^2 area (Wolman 1954). D50 was visually estimated after a proper training and calibration against stone count samples.

Biological model

The development of HPI necessitates the description of the conditions used (presence) and avoided (absence) by natural parrs. Therefor, these data were taken in the calibration section before stocking. Snorkelling was performed to locate parrs that held a territory. Parrs were considered to be holding a territory when they were in a 'sit-and-wait' position or when they were performing movements from what could be identified as their 'home rock' to capture drifting preys. Divers swam upstream to avoid fish disturbance (Cunjak et al. 1988) and followed a series of transects perpendicular to water current such that the entire surface area of the calibration section was scanned visually. For each parr holding a territory, the home-rock was marked with a numbered and coloured rock. Parrs were chased downstream after the observation to avoid recording the same fish twice. Measures of water depth (m), current velocity (m/s), and substrate grain size (m) were taken on the sixty locations where fish was observed (fish presence). These same variables were also estimated at an equal number of locations selected at random and for which no fish were observed within a 2 m radius (fish absence). Water depth was measured with a measuring rod (± 1 cm). Average current velocity was estimated during 30 sec using a Price or Pygmy current meter installed at 40% of the water column at a given sampling location (*e.g.* 40 cm from the bottom in 1 m of water). Substrate grain size (D50) was estimated visually in an area of 1 m^2 centred on the home rock (fish presence) or the location of the measurement of water depth (fish absence). This sampling was completed within three consecutive cloudless days (August 16th to 18th 2000) under similar hydraulic conditions (flow ranging between 5.5 and 6.1 m^3/s).

Fish distribution

A snorkelling procedure similar to that used to develop HPI was used to quantify fish distribution in the experimental section (upstream diving; 100% of the surface area of the section). Each territory occupied by a fish was marked with a coloured rock and georeferenced with a total station. This procedure was used to obtain precise maps of natural parrs distribution within the experimental section 10 and 4 days before stocking (July 18th and 25th 2000), and of natural and hatchery-reared parrs distribution 3 and 8 days after (August 1st and 6th 2000) the stocking (July 29th 2000). Flow rate was noted before and after each sampling day at a gauging station located 11 km downstream of the reach studied. No important tributary enters the Escoumins River between the study reach and the gauging station (#070204, Ministère de l'Environnement of Quebec). This strategy was used to insure that hydrodynamic simulations (and hence the NHM simulations of habitat quality) would be performed under flow conditions that adequately represents flow rates that prevailed during the mapping of fish distribution.

Stocking procedure

Hatchery parrs (F1) were carried from the Pisciculture of Tadoussac (operated by the Ministère de l'Environnement of Quebec at 50 km from study site) to the study reach in oxygenated bags. Each of the 250 parrs stocked in the reach were marked by fin clipping (the adiposous fin was cut). The stocking was performed from the upstream limit of the calibration section to the downstream limit of the experimental section to minimise the potential effects of the flushing of introduced parrs. Releases were spaced by approximately 12 m over the complete length of the reach. Fish were released in the river in groups of ten in areas of slow current velocity and near the shore. Parrs selected for stocking in the experimental section averaged 9.2 cm (SD = 0.99 cm; n = 30). This size was chosen because it corresponded to the average size of wild parrs in Escoumins River captured by electrofishing in the period of late July to early August (average = 9.33cm ; SD = 1.09 cm; n =30). This strategy was employed to avoid a potential size effect on the outcome of the stocking operation and on ensuing interactions (i.e. that hatchery fish would be advantaged or disadvantaged by their size).

Computations

The HPI was developed by constructing a matrix containing the data of the presence or absence of fish (respectively noted 1 or 0: column 1 of the matrix) and the values of the three physical conditions (water depth; current velocity; D50: columns 2-4 of the matrix) used or avoided by parrs in the calibration section. The following Gaussian multivariate logistic regression (Guay et al. 2000) was used to predict the probability of finding a fish under different combinations of water depth, current velocity, and substrate grain size;

$$\text{HPI} = 1/(1 + e^{-\lambda}) \qquad (1)$$

where $\lambda = P_0 + P_1Z + P_2V + P_3S + P_4Z^2 + P_5V^2 + P_6S^2 + \ldots$

P_i are the parameters of the Gaussian regression, Z is the depth (m), V is the mean current velocity (m/s), and S is the substrate size (D50; m). The HPI model was developed by raising all independent variables to a power ranging from 1 to 4 and then by performing a stepwise backward regression procedure.

The NHM used in this work partitions (discretises) the surface area of the reach modeled into a series of triangular element each composed of six nodes. NHM thereby represents the reach modelled as a mosaic network of triangular tiles (triangular irregular network: TIN). Quality indices were calculated for the six nodes (for which a simulated water depth, current velocity and substrate value have been obtained by the hydrodynamic model) delimiting each tile. These points are located at the intersection and in the middle of the edges of each of the triangular element making up the grid used to perform our calculation. Maps of areas of the reach having similar habitat quality indices (further referred to as habitat patches) were delineated using these distributions.

Statistical analyses

The ability of the hydrodynamic model to adequately estimate depth and current velocity have been recently discussed (Guay et al. 2001). To evaluate the quality of the estimations performed by the hydrodynamic model, we compared its estimations of depth and current velocity to real measures on comparable flow rate (4.5 m^3/s) for 30 locations randomly selected over the reach. The thirty sampling points were georeferenced in the field such that comparisons with predictions of water depth and current velocity could be made at the same locations. The evaluation of the simulation quality was attained following the procedure proposed by Mesplé et al. (1996). Estimated and measured depths (and velocities) were compared with a major axis. The 95% confidence interval of the slope and of the intercept of this major axis were evaluated. The estimations of the hydrodynamic model were considered as realistic if the 95% C.I. of slope and intercept include 1 and 0 respectively. Mean and variance of estimated and measured depths (and velocities) were also compared with t and F statistics.

The overlapping of the maps of i) predicted habitat quality (HPI) and ii) real fish distribution 10 and 4 days before and 3 and 8 days after the stocking of hatchery fish, served three purposes. First, it allowed us to assess the relationship between predicted habitat quality and the real distribution of wild parrs 10 and 4 days before the stocking of hatchery fish. Second, it permitted us to describe habitat selection by hatchery fish 3 and 8 days after stocking. Third, it provided us with information about changes in wild fish distribution 3 and 8 days after stocking. These objectives were achieved by assessing the existence of a relationship between wild fish densities before stocking and the predictions of habitat quality obtained using NHM, and by comparing the relationships obtained before the stocking of hatchery fish to those after stocking.

We tested the existence of relationships between fish distribution and NHM predictions using four steps. First, the surface area (m^2) of the experimental section represented by each of the ten categories of HPI (ranging from 0 to 1 by increments of 0.1) was calculated. Second, the total number of fish found in areas assigned each of the ten categories of HPI values was calculated. Third, fish density in areas assigned each of the ten categories of HPI values was calculated (number of fish / 100 m^2). Fourth, a polynomial regression was used to test the existence of a relationship between fish density and HPI categories (stepwise regression using HPI, HPI^2, HPI^3 as independent variables). We tested the existence of a relationship between fish density and HPI using fish distribution patterns and predictions of NHM obtained 10 and 4 days before stocking and 3 and 8 days after stocking.

The spatial interaction between wild and hatchery fish was examined using two strategies. The first strategy involved the analysis of the order of the independent variables that significantly contributed to polynomial regressions between fish densities and HPI values. This strategy is based on the possibility that the shape of the relationship between fish density and HPI before stocking could differ from that after stocking hatchery fish. The second strategy consisted in testing the effect of HPI and of a dummy variable representing pre-stocking (0) and post-stocking (1) conditions on wild fish densities. The coefficients of the multiple regression model represent the influence of one of the variable on fish density when the other variable is kept constant (Jolicoeur, 1998). Partial regression coefficients associated to the dummy variable were used to assess the statistical significance of pre- and post-stocking conditions. The partial regression coefficients were quantified with a program for multiple linear regression with permutation test to avoid normality distribution condition linked with usual parametrical test (Anderson and Legendre 1999).

Results

Evaluation of the quality of the simulation performed by the hydrodynamic model

The slope of the major axis calculated between measured and estimated depth under a 4.5 m^3/s flow rate was not significantly different than 1 (95% I.C. [0.821, 1.176], n = 30). In addition, the intercept of this axis was not significantly different than 0 (95%

I.C. [-0.00052, 0.14392], n = 30). The slope of the major axis calculated between measured and estimated current velocity under the same flow rate was also not significantly different than 1 (95% I.C. [-0.088, 0.131], n = 30) and the intercept was not significantly different than 0 (95% I.C. [0.712, 1.217], n = 30). Thus, hydrodynamic model was able to adequately estimate local depth and current velocity in our reach. Furthermore, the mean (depth: $t = -1.22$, $p = 0.15$; current velocity: $t = 0.28$, $p = 0.90$) and the variance (depth: $F = 1.18$, $p = 0.59$; current velocity: $F = 1.59$, $p = 0.83$) of the estimations performed by the hydrodynamic model were not significantly different from the mean and the variance of the measures performed on field on a comparable flow. Hence, the precision of the hydrodynamic model was judge sufficient.

Conditions used and avoided by wild parrs in the calibration section

The flow estimated during the three sampling days required to assess the physical conditions used and avoided by parrs averaged 5.8 m^3/s (ranging from 5.5 to 6.1 m^3/s). These conditions were defined using measurements of environmental conditions in 60 locations where parrs were observed and in 60 locations where parrs were absent. Parrs were found at depths ranging from 0.15 to 0.85 m with a maximum occurrence (24% of fish observed) under depths of 0.5 - 0.6 m (Figure 2a). Current velocities used by these fish ranged from 0.35 to 1.55 m/s. Parrs were most common (17 % of fish observed) under current velocities of 0.6-0.8 m/s (Figure 2b). Averaged substrate composition (D50) over 1m^2 patch used by parrs ranged from 0.005 to 0.4 m. The presence of parrs was highest (25% of fish observed) in locations where D50 was 0.1 to 0.15 m (Figure 2c).

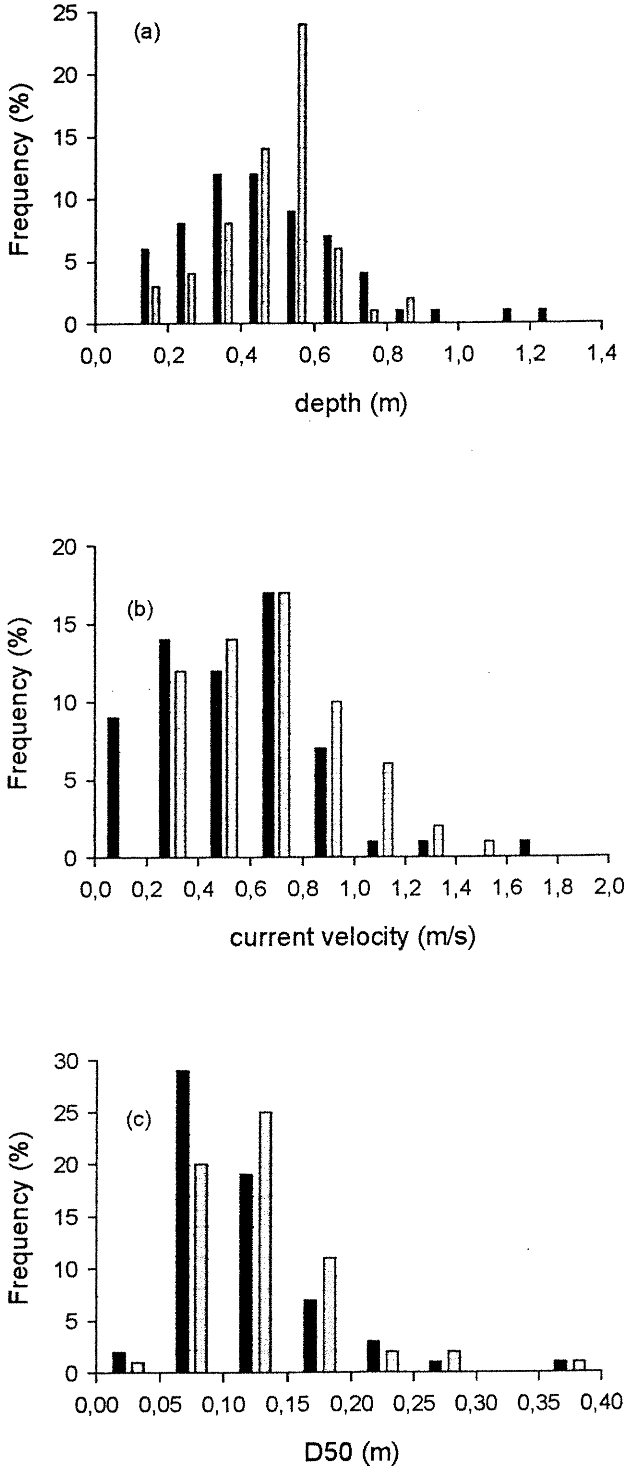

Figure 2. Frequency of depth (a), current speed (b) and substrate (c) used (gray bars) and avoided (dark bars) by 1+ and 2+ parrs.

Sites shallower than 0.4 m and deeper than 0.7 m comprised 27% of the sites where no fish was found (Figure 2a). Low velocities (<0.2 m/s) were clearly avoided by parrs (Figure 2b). One third of the locations where no fish was observed were characterised by small grain size (D50 < 0.1 m; Figure 2c).

The HPI equation developed with the physical characteristics at sites used and avoided by parrs was:

$$\text{HPI} = 1/(1 + e^{-\lambda}) \qquad (2)$$

$$\text{where} : \lambda = -3{,}528 + 9{,}879D + 1{,}413V + 3{,}553S - 9{,}772D^2$$

The absence of terms in V^2 and S^2 could be explain by the absence of high velocities (> 1.7 m/s) and substrate grain sizes (> 0.4 m) in the sample.

Maps of habitat quality predicted by the numerical habitat model

NHM was applied by running the hydrodynamic model with a flow of 6.8 m^3/s. This flow was selected for our habitat simulations because it represented the average flow (SD = 1.34 m^3/s; n = 4) estimated during the mapping of fish in the experimental section. The maps of predicted depth and modulus of current velocities vectors over the experimental section under this flow are presented in figure 2-B. The map of substrate grain size (D50) that compose the riverbed of the experimental section is also show in this figure. The best habitats predicted by the NHM at this flow were assigned HPI values ranging from 0.6 to 0.7 (Figure 3). These best sites represented 2.4 % of the surface area of the experimental section. The worst habitats (HPI from 0 to.0.1) were located close to the shores and covered 5.8 % of the experimental section (Figure 3). The

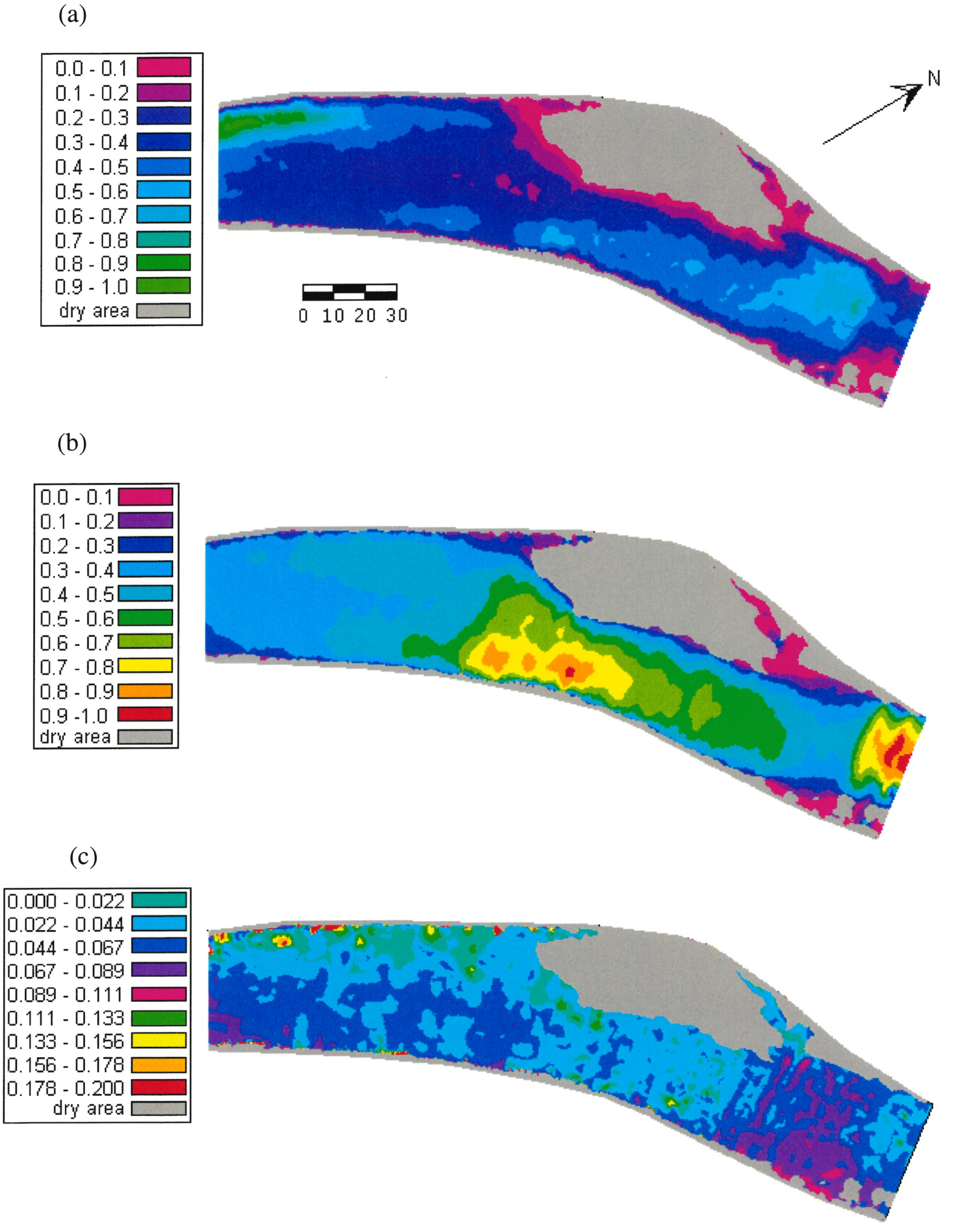

Figure 2-B: Maps of predicted depth (m; a), modulus of the current velocities (m/s; b) and substrate grain size (m; c) in the experimental section.

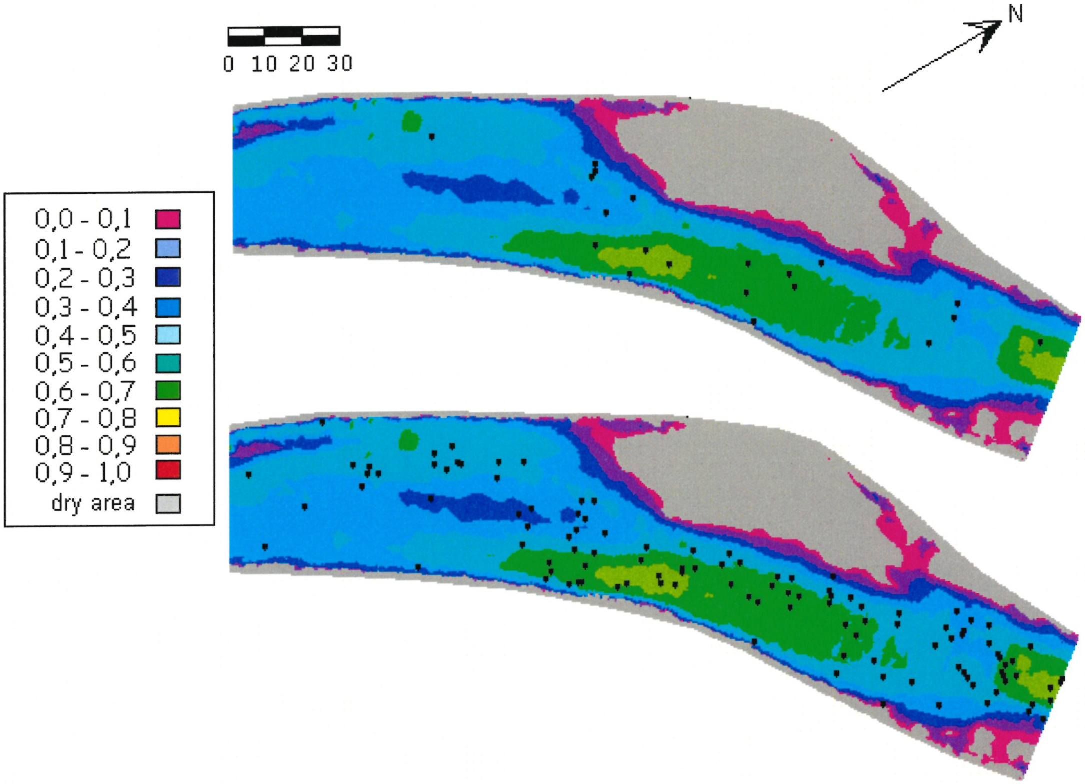

Figure 3. Fish distribution (dots) 11 days (upper map) and 4 days (lower map) before stocking overlaid by the habitats quality predict by the NHM.

habitats assigned HPI values ranging from 0.3 to 0.5 represented 59.7 % of the surface area of this section.

Fish distribution

The number of parrs observed during the two mappings of the distribution pattern of wild fish in the experimental section before the stocking of hatchery fish ranged from 20 (July 16th ; flow = 5.9m^3/s) to 112 (July 25th; flow = 7.2m^3/s). Average parr densities over the entire experimental section before the stocking of hatchery reared fish ranged from 0.23 to 1.31 parrs/100 m^2. However, when we accidentally moved rocks during the snorkelling procedure designed to map fish distribution the July 16th (the day of the lowest fish abundance according to our visual surveys), we noted that many wild parrs were hidden in the interstices of the substrate. Mappings of fish distribution performed after stocking did not show a similar degree of variation in the abundance of wild fish. The abundance of wild fish after stocking ranged from 40 (August 6th ; flow = 8.6m^3/s) to 51 (August 1st ; flow = 5.7m^3/s) and wild fish densities during these dates ranged from 0.47 parrs/100 m^2 to 0.60 parrs/100 m^2. These densities represented respectively 35% and 45% of the density observed four days before stocking, on July 25th. The maps of fish distribution after stocking clearly indicated that few hatchery-reared parrs adopted a territory in the experimental section. Five hatchery fish were observed in the experimental section three days after stocking and nine were found after eight days. It is impossible to know if the hatchery reared parrs observed in the experimental section were originally stocked in the calibration or experimental sections. The efficiency of hatchery-reared parrs to adopt a territory may therefore be expressed either as a percentage of the total number of parrs stocked (2-3.6 % of 250 parrs) or as a percentage of the number of parrs stocked in the experimental section only (3-6 % of 160 parrs).

Relationship between habitats distribution and fish distribution before and after stocking

We found statistically significant relationships between the densities of wild parrs before the stocking of hatchery reared fish and HPI values (Figure 4). HPI explained from 93% (July 16th ; $p<0.005$) to 99% (July 25th ; $p<0.0005$) of the within-section variability in wild fish densities. Fish densities always increased with HPI values predicted by NHM. Mapping of fish distribution after the stocking indicated that the few hatchery reared parrs that remained in the experimental section selected the best habitats available according to the predictions of NHM (Figure 5, HPI = 0.6-07). These observations are confirmed by a significant positive relationships between the density of hatchery-reared parrs and HPI values (Figure 6). This relationship, however, should be treated with caution because of our low sample size.

No difference is found between the order of the polynomial variables used in predicting fish density from HPI before the stocking and that of the models obtained after the stocking of hatchery reared parrs. For three mappings over the four that were performed, the only parameter that remained significant is HPI^2 ($0.001<p<0.00001$). But, for the first mapping before stocking, only HPI^3 was significant with $p<0.001$. However, the low densities observed during this particular mapping could possibly explain this apparent change in the shape of the relationship. Thus, we cannot conclude that the shape of the relationships between wild fish densities and HPI differ after stocking (Figures 4-

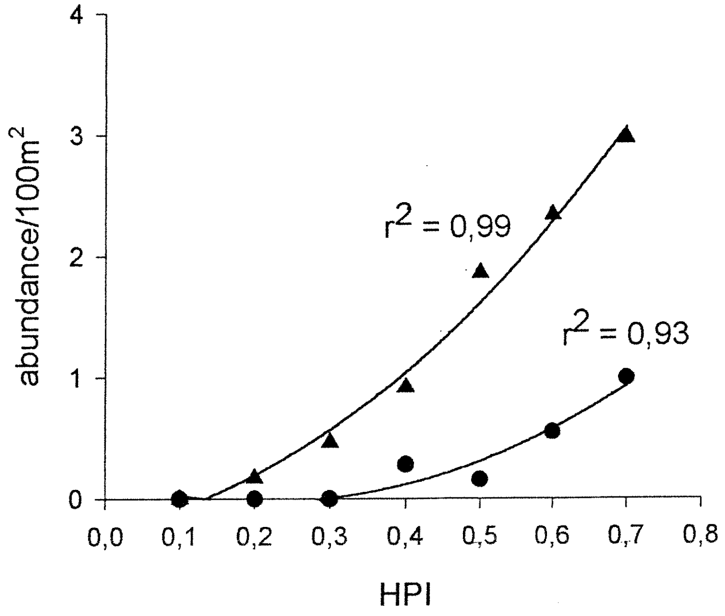

Figure 4. Polynomial regressions between fish densities and HPI values 11 days (circles) and 4 days (triangles) before stocking

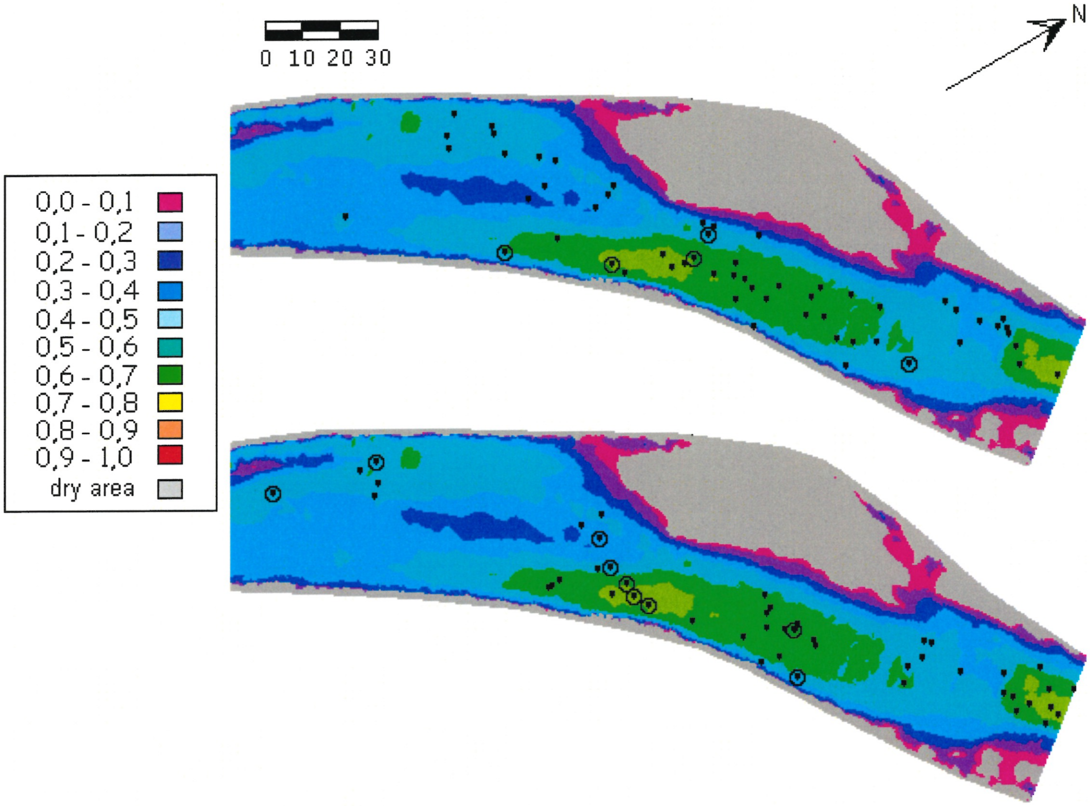

Figure 5. Wild fish (dots) and hatchery-reared fish (circled dots) distributions 3 (upper map) and 8 (lower map) days after stocking.

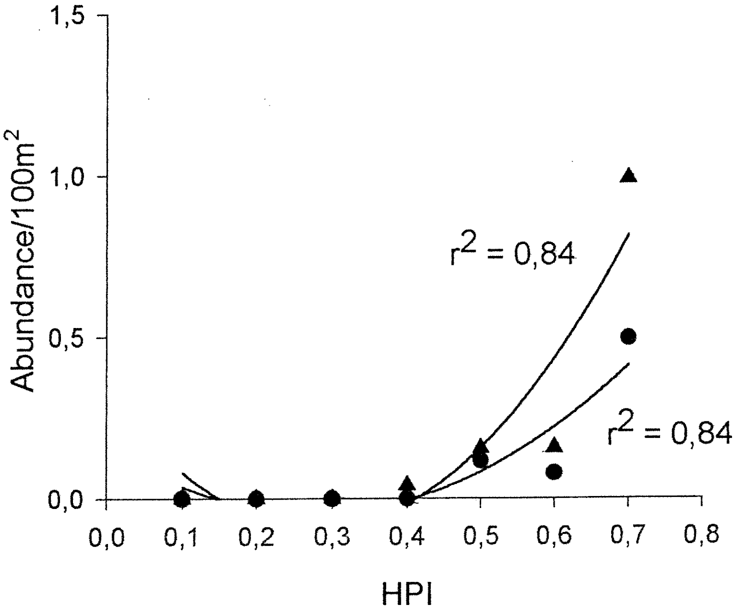

Figure 6. Polynomial regressions between hatchery-reared fish densities and HPI values 3 days (circles) and 8 days (triangles) after stocking

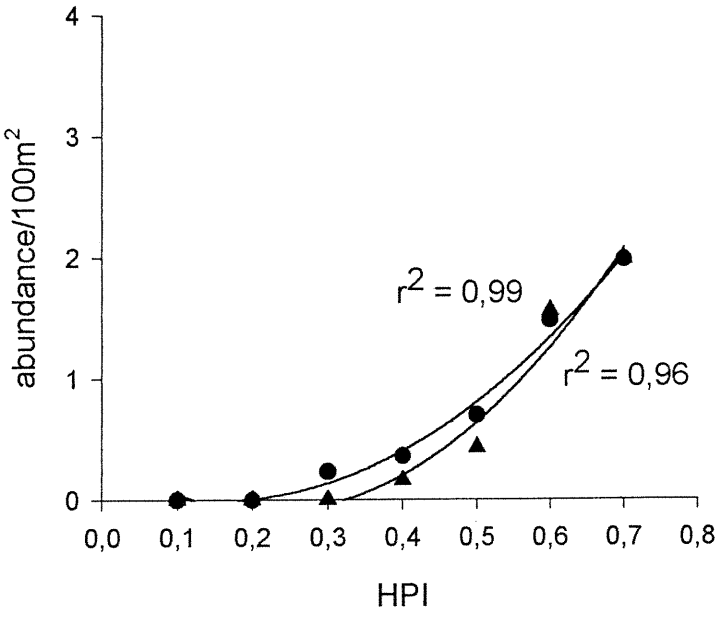

Figure 7. Polynomial regressions between wild fish densities and HPI values 3 days (circles) and 7 days (triangles) after stocking

7). These results are consistent with the multiple linear regression in which the partial regression coefficient associated to HPI is significant ($p<0.001$) but not the partial regression coefficient of the dummy variable representing conditions found before and after the stocking of hatchery reared fish ($p=0.38$). Hence, the density of wild fish before and after stocking of hatchery fish did not differ significantly for given HPI values. These results suggest that stocking hatchery fish had no significant effect on habitat utilisation patterns of wild parrs.

Discussion

Our results suggest that most of the hatchery-reared parrs did not adopt a territory into the section where they have been released. However, the few stocked fish that adopted a foraging territory in that section, chose favourable habitats. The wild fish distribution did not appear to be influenced by the stocking.

Our results contrast with those by Armstrong et al. (1997) who observed that wild parrs adopted a territory within 3 days after their introduction in an enclosed section of 30 m. In our work, 94% of the fish stocked were unable to adopt a territory within a comparable time period despite the fact that our survey was performed on a spatial scale seven times larger than that used by Armstrong et al. (1997). Two reasons could explain these differences. First, Armstrong et al. (1997) worked in an area enclosed with barriers that could induce the adoption of a territory by stocked fish while our experimental section was opened. Second, the study of Armstrong et al. (1997) was conducted on wild parrs captured in areas downstream of their enclosed section while our study was performed using hatchery parrs. This may indicate that wild parrs have a greater ability to adopt a territory in unfamiliar areas than hatchery parrs.

Downstream movements within kilometres from the released point by hatchery salmonids after stocking have already been observed (Smirnov et al. 1983; Richard and Cernera 1989). However, in these two studies, stocking was performed by introducing thousands (46 000 to 100 000) of hatchery juveniles in one point. It has been argued that this stocking procedure favours schooling behaviour by hatchery parrs near the point of release and a mass movement downstream induced by imitation (Smirnov et al. 1983). To avoid massive downstream movements and to favour scattering in our sections, we stocked fish in little groups regularly spaced over the entire length of our sections. Our study indicates that the method we employed to stock fish is not sufficient to permit the adoption of a territory by a large fraction of the hatchery fish. The rearing conditions found in hatchery could be an explanation of the inability of most hatchery fish to remain within meters from the stocking point. In hatchery, rearing conditions contrast with the natural stream conditions. The densities in hatchery tank can be as large as 800 fish/m^2 compared to 0.013 fish/m^2 observed in our experimental section. Fish in hatchery are confronted to water velocities that are less variable than the ones found in rivers. Finally, in hatchery, fish are fed automatically with commercial pellets while in rivers, fish must feed on invertebrates drifting in current. However, we cannot clearly partition the effects of fish origin (wild vs hatchery) and experimental setup (enclosed vs opened section of river) on the difference between the results we obtained and those of Armstrong et al. (1997) regarding the ability of fish to establish a territory in unfamiliar areas. In addition, it is impossible to clearly partition the roles of the rearing conditions from the stress induce by the stocking procedure for the poor settlement of hatchery parrs in the experimental section. For instance, it could be argue that the inability of hatchery fish to adopt a foraging territory is not cause by their origin but by the stress induced by the transportation from the pisciculture to the river and then by the stocking procedure itself. Hence, wild fish that would be stocked following the same procedure should not be able to remain close to the stocking point and adopt a foraging territory. However, our study indicates that it may be prudent to study the interactions between wild and hatchery fish on a temporal scale longer than 8 days and on a spatial scale larger than few hundreds of meters of river.

The few hatchery-reared fish that adopted a territory in the experimental section used the best habitats available. This situation did not appear to affect the spatial distribution of wild fish. However, the number of wild parrs observed in the experimental section after stocking decreased from 0.0077 fish/m^2 (average before stocking) to 0.0053 fish/m^2 (average after stocking). This decrease could be caused by a downstream (or upstream) displacement of wild fish in response to the introduction of hatchery parrs. Two arguments are inconsistent with a displacement of wild parrs after the introduction of hatchery fish. First, many wild fish have been observed hiding in substrate interstices during the mappings performed after stocking. Second, the lowest abundance of fish have been observed during the first mapping (before stocking). Hence, the variations of wild parrs abundance observed in this work (including those between the pre- and post-stocking periods) may only represent the natural day-to-day variation in the number of parrs adopting an actively foraging behaviour. Girard and Boisclair (unpublished results) have demonstrated that the number of parrs hiding in riverbed interstices increases as the cloud cover become more important. They showed that the number of fish observed, on the same river section as the present study, could vary 700% between consecutive days in which the percent cloudiness varied from 0 to 100%. Unfortunately, no cloud cover data were taken during the present study. Hence, the true effect of cloud cover on our data, and particularly on the difference in wild fish abundance before and after the stocking of hatchery fish, cannot be evaluated. However, the variation of the abundance of wild fish between the days before and after the stocking of hatchery fish (<55%) is within the variation that may be expected purely on the basis of the effect of variations in cloud cover.

The potential effect of cloud cover on the number of fish that adopt an active foraging behaviour may affect the interpretation of the results obtained about wild and hatchery fish as well. If hatchery parrs are affected by cloud cover in a manner similar to that of wild parrs, one can expect that the magnitude of the day-to-day variation observed in the number of wild parrs may be applicable to our data on hatchery parrs. The largest variation of wild parr abundance we observed after stocking corresponded to a 65% decrease in wild fish abundance (between our second mapping before stocking and the second mapping after stocking). If we assume that during the second mapping after stocking, 65 % of the hatchery fish were, like the wild fish, hiding in substrate interstices, there may have been twenty-five hatchery parrs in our experimental section during this sampling instead of the nine hatchery fish we observed. Hence, in the best case, 10% of the total number of hatchery parrs stocked (or 16% of the hatchery parrs stocked in the experimental section) may have remained in this section eight days after stocking.

Our work represents the first attempt to use a NHM to evaluate the interactions between hatchery and wild parrs. However, the applicability of NHM depends on the ability of hydraulic models to adequately predict water depth and current velocity. The validation procedure use to evaluate the quality of the simulation performed by the hydrodynamic model show that the means and the variance of its predictions did not differed significantly from the means and variances calculated from the measures performed on field under a comparable flow rate. In addition, the model was able to adequately predict local depth and current velocity for 30 locations over the experimental section. The precision of the hydrodynamic model was judged sufficient. Hence, the applicability of the NHM is justified.

NHM are developed with the expectation that they may allow to estimate and visualise the quantity, the relative quality, and the distribution of habitats available to fish. The strength of the relationships we found between HPI predicted by the NHM and *in situ* fish densities confirms the findings of Guay et al. (2000) that NHM are able to predict biologically meaningful information on local variations of fish habitats. In our study, this characteristic of NHM is particularly useful to assess the possibility that hatchery fish could not adopt a territory in our experimental section because no suitable habitat was available (that this section was already saturated with wild fish). The maps produced by NHM suggests that 34% of the surface area that have a HPI value higher than 0.5 (for a total of 500 m^2) was not occupied by wild fish before stocking of hatchery fish. According to our relationships between HPI and fish densities, densities between 0.5 fish/100m^2 and 2.2 fish/100m^2 are predicted for habitats that have HPI values > 0.5. Thus, we should observe fish abundance between 2.5 and 11 fish in an area of 500 m^2 of habitat with a HPI above 0.5. After stocking, the surface of unused favourable habitats was $400m^2$ or 27% of the surface area of the experimental reach. This area could support 2 to 9 fish. This may indicate that hatchery fish did not move downstream (or upstream) because of the absence of favourable habitats. Our observations and analyses lead us to speculate that the best explanation for the poor efficiency of hatchery fish to adopt a territory near the point of stocking may be their poor ability to adapt to natural conditions.

Chapitre 2

The effect of cloud cover on the diurnal foraging activity of juveniles of Atlantic salmon (*Salmo salar*) and the development of habitat quality indices.

Summary

The day-to-day variation of the diurnal foraging strategy used by Atlantic salmon (*Salmo salar*) parrs during summer is a misunderstood phenomenon which can have great implications for field measurements. Our objectives were i) to assess the relative importance of water temperature and light intensity on the diurnal foraging strategy of parrs, and ii) to evaluate the effect of these variables on predictions of the quantity and quality of summer habitat obtained using a habitat probabilistic index (HPI). Repeated mappings of parrs distribution in a 200m long alluvial reach show that the number of parrs actively foraging in the water column varied 700% between consecutive days. Cloud cover explained a greater part (77%) of the day-to-day variation than water temperature (1.3%). HPI were developed under low, intermediate, and high cloud cover. Two-dimensional numerical habitat models (NHM) were created with these HPI and predictions of the quantity and the quality of the habitats over the study reach were obtained for each of these models. These predictions were compared to the fish distribution observed under low and high cloud cover with regressions of the second order. The results showed a good match between the predictions performed by the models developed under low and intermediate cloud cover and the real fish distribution observed under either low ($0.94 < R^2 < 0.98$) and high cloud cover ($0.79 < R^2 < 0.88$). The performance of the model developed under high cloud cover was lower either under low ($R^2 = 0.82$) and high cloud cover ($R^2 = 0.40$). Our work suggests that HPI must be developed under cloud cover as low as possible.

Résumé

Les variations journalières de la stratégie alimentaire diurne adoptée par les tacons de saumons de l'Atlantique (*Salmo salar*) pendant l'été est un phénomène méconnu qui peut avoir des implications importantes sur les résultats provenant de l'échantillonnage sur le terrain. Les objectifs de ce travail étaient i) d'évaluer l'importance relative de la température de l'eau et de l'intensité lumineuse par rapport à la stratégie alimentaire diurne des tacons et ii) d'évaluer les effets de ces variables sur les prédictions de la quantité et de la qualité des habitats obtenues à l'aide d'indices probabilistes d'habitat (IPH). Des cartographies répetées de la distribution des tacons dans une section de rivière ont montré que l'abondance de tacons s'alimentant dans la colonne d'eau pouvait varier jusqu'à 700% entre deux jours consécutifs. Le couvert nuageux expliquait une plus grande part de cette variabilité (77%) que la température de l'eau (1.3%). Des IPH ont été développés sous des couverts nuageux faible, intermédiaire et élevé. Des modèles numériques bidimensionnels d'habitat ont été créés à partir de ces IPH ce qui a permis de prédire la quantité et de la qualité des habitats pour la section de rivière étudiée pour chacun de ces modèles. Ces prédictions ont été comparées à la distribution réelle des tacons observée sous des couverts nuageux faible et élevé avec des régressions polynomiales du second ordre. Les résultats ont montré une bonne correspondance entre les prédictions des modèles développés sous couverts nuageux faible et intermédiaire et la distribution des tacons observée autant sous un couvert nuageux faible ($0.94 < R^2 < 0.98$) qu'élevé ($0.79 < R^2 < 0.88$). Les performances du modèle développé sous un couvert nuageux élevé étaient plus faibles autant sous un couvert nuageux faible ($R^2 = 0.82$) qu'élevé ($R^2 = 0.40$). Ce travail suggère qu'un IPH doit être développé sous un couvert nuageux le plus faible possible.

Introduction

The diurnal foraging behaviour of juveniles of Atlantic salmon (*Salmo salar*) in the summer consists of holding a position on or above the substrate (most often a rock referred to as 'home-rock') and performing frequent movements in the water column or towards the surface to capture drifting invertebrates (Kalleberg 1958, Fausch 1984). Numerous studies indicate that during the fall and the winter seasons, juveniles of Atlantic salmon (parrs) shift to a cryptic behaviour during the day and emerge from the substrate interstices during the night (Rimmer 1983; Cunjak 1988; Bremset 2000). However, the diurnal cryptic behaviour of parrs does not appear to be a strictly seasonal event. Fraser et al. (1995) observed that parrs that lived in a river draining a glacial catchment (water temperature of 7.7 – 8.4°C) displayed a cryptic behaviour during the day and emerged from the substrate during the night even in the summer. Manipulations of water temperature under laboratory conditions showed that parrs could be induced to adopt a diurnal cryptic behaviour when temperature is dropped below 15°C while they continued to express a diurnal foraging strategy pattern at temperatures above 16°C (Fraser et al. 1995). Adoption of a diurnal cryptic behaviour at water temperatures below 10-15 °C has been hypothesised to be a consequence of a reduced swimming performance at low temperatures (Webb, 1978; Rimmer et al. 1984). This lower swimming capability as been argued to impede on the ability of fish to avoid or escape endothermic predators (Heggenes et al. 1993; Fraser et al. 1995). Recent *in situ* observations performed by Gries et al. (1997) and Gries and Juanes (1998) during late and mid summer show that parrs could display a cryptic behaviour during daylight even at temperature greater than 16°C. These findings suggest that, in the natural environment, other variables than water temperature may affect the daily pattern of fish foraging strategy. Light intensity may affect whether or not these fish adopt a foraging or a cryptic behaviour during the day. It has been demonstrated that the reactive distance (Benfield and Minello, 1996) and the foraging efficiency (Fraser and Metcalfe, 1997) of visual feeders are related to the light intensity. Yet, the effect of light intensity on the decision made by parrs to adopt an active or cryptic behaviour during the day is not known.

Interactions between fish diurnal behaviour and environmental conditions determine the quantity and the quality of opportunities fish have to feed. These interactions may also affect the prediction of biological models about the quality of habitats for parrs. Most biological models are based on a description of the environmental conditions used, available, or avoided by fish (deGraff and Bain 1986, Morantz et al. 1987, Guay et al. 2000). Evaluation of the conditions used or avoided by fish is based on the recording of variables where fish are present or absent. The data are obtained by performing visual surveys. Environmental conditions affecting whether or not fish adopt an active or cryptic behaviour, and hence, or whether or not fish are visible to observers, may also affect the predictions of biological models and the predictions made by habitat models about the quantity, quality, and the spatial distribution of suitable habitats.

The objectives of our work were 1) to assess the relative importance of water temperature and light intensity on the diurnal foraging behaviour of parrs of Atlantic salmon during the summer, and 2) to evaluate the effect of water temperature and light intensity on predictions of the quantity and quality of summer habitats obtained using biological models developed under different environmental conditions.

Material and methods

The general approach used to attain our objectives combined four operations: 1) the observation of the diurnal foraging strategy of parrs to define the number and the location of parrs actively foraging under different water temperature and light intensity conditions in the field, 2) the development of a hydraulic model that allowed to define the physical conditions used and avoided by parrs, 3) the development and the comparison of biological models for different water temperature and light conditions, and 4) the comparison between the real fish distribution and the distribution pattern predicted using biological models developed under different water temperature and light conditions.

Study site and species

Sampling was conducted in the Escoumins River in the Haute-Côte-Nord of Quebec at approximately 500 km NNE of Montréal (Fig.1). The watershed of the Escoumins river cover an area of 979.7 km^2. The flow rate of this river is controlled by a group of dams constructed on its source and on its main tributaries. The average discharge during summer 2001 according to the gauging station of the Ministère de l'Environnement du Québec (# 070204) situated at 9 km of the junction between Escoumins River and St. Lawrence River was 12.14 m^3/s. The study site was 250m long and was located at about 20 km from this junction. The wetted surface of the study reach under a 6.8m^3/s flow rate was 10691 m^2. The width of the reach under studied ranged from 21.7m to 47.5 m. The study reach is composed of a series of pools (maximum depth of 1.4 m) and riffles. The average slope of the reach is 0.2%. The substrate size of the

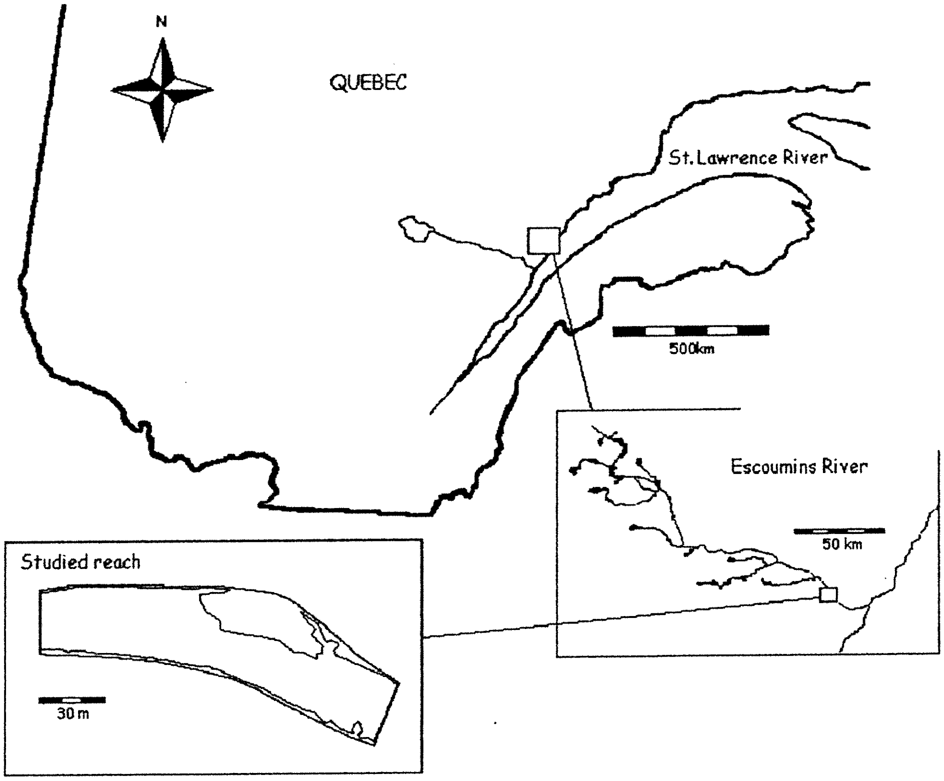

Figure 1. Map of the studied site situated on the northern shore of the St-Lawrence River

riverbed ranges from sand ($5 \times 10^{-6} - 4 \times 10^{-5}$ m diameter) to metric boulders (over 1 m diameter). The reach does not contain areas covered by wood debris or a canopy.

Our study focusses on the 1+ and 2+ juveniles of Atlantic salmon (*Salmo salar*). Atlantic salmon was selected for our study because of the economical importance of this species for Québec's sport fishery. Furthermore, Atlantic salmon was designated as an endangered species in some regions of Canada (Fundy Bay; Amiro and Jefferson 1998) and United States (Gulf of Maine; Colligan and Nickerson 1999). It is expected that studies aimed at expanding our knowledge of the behaviour of these fish and at increasing the validity of models of habitat quality assessment may improve our ability to adopt management decisions to protect and enhance the status of this species. In our study, 1+ (7.5-10 cm fork length FL) and 2+ (9-11.5 cm FL) fish were treated indistinguishably because of their size overlap that did not allow their discrimination during our visual observations. Parrs were the dominant fish at our sampling site (97% of the fish observed over the reach). The other fish species observed were the Brook charr (*Salvelinus fontinalis*), the American eel (*Anguilla rostrata*), the Longnose sucker (*Catostomus catostomus*), and the Sea lamprey (*Petromyzon marinus*).

Numerical habitat modelling

We compared the fish distribution observed in the field to that predicted using biological models developed under different water temperatures and cloud cover using a numerical habitat model (NHM). The NHM is a combination of a hydrodynamic model and of a biological model (Leclerc et al. 1995). The hydrodynamic model (HYDROSYM) is a St-Venant two dimensional (2D vertically integrated) finite element tool with drying-wetting capabilities that predicts the variation of depth and current velocity over the wetted area of a reach at a given flow discharge (Heniche et al. 2000a, b, 2001, Leclerc 1990). Combined with a MODELER, a river-dedicated Geographical Information System (GIS) entirely coupled with HYDROSYM (Secretan et al. 1998), this model uses a topographic description of the riverbed and a map of substrate grain size as inputs (Secretan et al. 2001, Secretan and Leclerc 1998). These measures, combined with physical and numerical coefficients (turbulent viscosity and friction factor) and assumptions about fluid dynamics and equilibrium (conservation mass and momentum), allow under proper boundary and initial conditions to predict and map current velocity and water depth over the reach modeled, and this, for any specified flow.

The biological model is the Habitat Probabilistic Index (HPI; Guay et al. 2000). This model is based on a multivariate logistic regression designed to distinguish the physical (abiotic) conditions used and avoided by fish. It uses, as independent variables, water depth (m), current velocity (m/s), and substrate diameter (m). The predictions of the biological model vary between 0 (poor habitats) and 1 (best habitats), and have been argued to correspond to the probability to find a fish under given combinations of the three physical variables (Guay et al. 2000). This model is based on the assumption that if fish makes a preferential use of a specific range of water depth, current velocity, and substrate grain size, this range corresponds to a habitat of higher quality for fish.

The final operation of the numerical modeling is to combine the (x,y) distributed predictions of the hydrodynamic model for a given flow rate and the equation of the biological model. Depth and current velocity maps produced by the hydrodynamic model combined with the map of substrate grain size are used as inputs for the HPI model to predict and map the spatial heterogeneity of habitat quality over the entire surface of the experimental section. Maps of fish habitat quality are represented using ten categories of habitat patches assigned HPI values ranging from 0 to 1 with increments of 0.1 (0-0.1; 0.1-0.2 etc).

Sampling

Visual observation of the diurnal foraging strategy of parrs under different water temperature and light intensity conditions.

The purpose of this activity was to assess the number and the location of parrs actively foraging over the entire surface area of the reach studied, and this, under different water temperature and light intensity conditions. Parrs were considered to be actively foraging when they were observed holding a position on or above the substrate or when they were performing feeding motions (irrespective of the amplitude of these movements). The number and location of parrs actively foraging was estimated by snorkelling the complete surface area of our study site during a total of thirteen surveys (three surveys from June 29th to 1st July 2001; five surveys from July 5th to 10th; five surveys from August 1st to 5th 2001). One survey began at noon and was completed within two to four hours. During each survey, observers snorkelled upstream following transects nearly perpendicular to the water current to avoid fish disturbance (Cunjak et al. 1988). Each parr defined as actively foraging was recorded by marking its home-rock with a coloured stone. Parrs were chased downstream after the observation to avoid a second recording. When the reach was entirely scanned, the coloured stones were georeferenced with a total station (an electronic theodolite combined with an electronic distance measurement system, Sokkia SET3B) and an electronic data logger (Sokkia SDR33). The percent cloudiness was estimated visually on a 0-100% scale at the beginning, at the mid-period, and at the end of each survey. These informations were taken as measures of the light intensity during each survey. Water temperature in the talweg was simultaneously taken with a hand thermometer. Our surveys allowed not only to count but also to obtain a precise map of fish distribution under contrasting light intensity and water temperature conditions. Flow rate was noted at the beginning and at the end of each sampling day from a gauging station located 11 km downstream from the reach under study (#070204, Ministère de l'Environnement of Quebec). No tributaries enter the Escoumins River between the study reach and the gauging station. Flow was estimated i) to insure that each survey would be performed under a similar flow and ii) to insure that the hydrodynamic simulations would be performed under flow condition similar to that prevailing during the mappings of fish distribution.

Development of a hydraulic model

The development of the biological model used (HPI) requires the description of the depth, current velocity, and substrate size used and avoided by fish. These data were obtained using the hydraulic model and the map of substrate composition covering the reach under study. The hydraulic model was developed using the topography and the map of substrate composition of the reach modeled. These data were obtained by quantifying the latitude, the longitude, and the altitude of 2589 sampling points irregularly distributed over the river bed, shores and above the high water level of the reach studied. These coordinates were georeferenced with the total station. For each point sampled, substrate grain size was estimated using the concept of D50. Given that the volume of a stone is determined by three axes (A being the longest and C the shortest axis), D50 is defined as the length (in m) of the B-axis of the median stone within an area of 1 m^2 centred on the sampling point (Wolman 1954). D50 can be visually estimated after a proper training and calibration against stone count samples. The hydrodynamic model produces maps of water depth and current velocity in this reach under any given flow. The evaluation of the quality of the hydrodynamic simulation was aimed by measuring depth and current velocity (with a Pygmy current meter) on 30 georeferenced locations regularly distributed over our reach. Before and after this procedure, flow was noted at the gauging station.

Computation

Development of biological models

The thirteen surveys were classified according to three categories of cloud cover: low (0% to 33.3%), intermediate (33.3% to 66.7%), and high (66.7% à 100%). Six surveys were performed under low cloud cover, one under intermediate cloud cover, and six were realised under a high cloud cover. HPI were developed using three of the thirteen surveys (one for each of the categories of cloud cover). The surveys used to develop HPI under low and high cloud cover were selected according to a random stratified procedure. The selected surveys were July 5th (flow 6.1m^3/s; 5% cloud cover; number of fish = 141), July 7th (flow 6.3 m^3/s; 50% cloud cover; number of fish = 105), and June 29th (flow 8m^3/s; 100% cloud cover; number of fish = 32).

HPI for these surveys were developed by overlaying the maps of fish distribution and the maps of the physical variables (i.e. depth, current velocity, and substrate) produced by the hydrodynamic model or resulting from our field surveys. The conditions used by parrs were obtained by noting depth, current velocity and substrate grain size associated to each location where a fish have been observed during each of these surveys. The conditions avoided by fish were obtained by noting the environmental conditions over every locations where no fish has been observed within a circle of 2 m radius for each survey. The development of HPI necessitate an equal number of locations used and avoided by fish (further referred as to presences or absences respectively). For each survey, an equal number (i.e. 141, 105 and 32) of absences were randomly selected over the reach. Hence, for each of the three surveys selected, depth, current velocities, and substrate grain size were described for every presence observed on field and for an equal number of absences.

The HPI were developed by constructing matrices containing physical conditions used and avoided by parrs. One matrix was constructed for each of the three clouds conditions selected. The matrices had four columns corresponding to presences or absences (respectively noted 1 or 0; column 1 of the matrices) and the associated local water depth, current velocity and D50 (column 2-4 of the matrices). The following Gaussian multivariate logistic regression (Guay et al. 2000) was used to predict the probability of finding a fish under different combinations of water depth, current velocity, and substrate grain size:

$$\text{(1)} \qquad \text{HPI} = 1/(1 + e^{-\lambda})$$

$$\text{where } \lambda = P_0 + P_1Z + P_2V + P_3S + P_4Z^2 + P_5V^2 + P_6S^2 + \ldots$$

P_i are the parameters of the Gaussian regression, Z is the depth (m), V is the mean current velocity (m/s), and S is the substrate composition (D50 in m). The HPI was developed by raising all independent variables to a power ranging from 1 to 4 and by performing a stepwise backward regression procedure.

The NHM used in this work partitions (discretises) the surface area of the reach modeled into a series of triangular element each composed of six nodes. NHM thereby represents the reach modelled as a mosaic network of triangular tiles (triangular irregular network: TIN). Quality indices were calculated for the six nodes (for which a simulated water depth, current velocity and substrate value have been obtained by the hydrodynamic model) delimiting each tile. These points are located at the intersection and in the middle of the edges of each of the triangular element making up the grid used to perform our calculation. Maps of areas of the reach having similar habitat quality indices (further referred to as habitat patches) were delineated using these distributions. Following this procedure, three habitat maps were created, one associated to each HPI developed under different cloud cover.

Prediction comparisons performed by HPI developed under different water temperatures and cloud cover

The three biological models developed under different conditions of cloud cover and water temperatures could predict different HPI values for given combination of depth, current velocity, and substrate grain size. Hence, we evaluated in which condition of depth, current velocity, or substrate grain size the differences between the predictions produced by the three HPI models were most similar or most different. This objective was attained by estimating HPI values predicted by the three HPI models for the 14 828 points that defined the simulation grid of our NHM model at 6.8 m^3/s (the points of all the triangular tiles that composed the reach modelled). This flow rate was selected because it corresponded to the average flow rate noted during the surveys used to compare real fish distribution to predictions of the spatial distribution of habitats according to NHM (see Statistical analyses, Comparison between the real fish distribution and the distribution pattern of habitats). For each HPI model, we estimated the mean HPI value predicted for seven classes of depth (0 to 1.4 m by interval of 0.2), six classes of current velocity (0 to 1.2 m/s by intervals of 0.2 m/s), and five classes of substrate grain size (5×10^{-6} to 0.032 m, 0.032 to 0.064 m, 0.064 to 2.5 m, 2.5 to 1 m, and over 1 m of diameter). This allowed us to evaluate how the average HPI values differed from one HPI model to another by classes of depth, current velocity, and substrate grain size.

Statistical analysis

Foraging strategy in relation to cloud cover and water temperature

The relationship between the number of parrs actively foraging during the day, cloud cover, and water temperature was evaluated with a multiple regression. This analysis was performed using the average cloud cover and the average water temperature noted at the beginning, in the middle, and at the end of our surveys as independent variables. Average cloud cover was always within 10% of the cloud cover observed in the middle of our surveys except for July 7th and August 1st (Table 1). The relationship between the number of parrs actively foraging during the day, water temperature, and cloud cover was evaluated using either the average cloud cover or, for July 7th and August 1st, the cloud cover observed in the middle of the survey.

Table 1 : Cloud cover (%) measured before, during, and after snorkelling and average water temperature (°C) for each survey. The darker surveys are those that average was not representative of the cloud cover conditions encountered during survey. Gray surveys are those used to develop HPI.

surveys	Cloud cover (%)				Water Temperature (°C)
	before	during	after	average	
June 29th	100	100	100	100,0	16
June 30th	90	90	100	93,3	18
July 1st	100	100	100	100,0	16
July 5th	10	5	0	5,0	20
July 7th	**70**	**50**	**100**	**73,3**	19
July 8th	75	70	60	68,3	18
July 9th	20	30	40	30,0	20
July 10th	70	85	100	85,0	19
August 1st	**15**	**70**	**15**	**33,3**	20
August 2nd	50	100	100	83,3	21
August 3rd	5	10	20	11,7	21
August 4th	50	20	0	23,3	21
August 5th	10	20	40	23,3	20

The coefficients of the multiple regression represent the influence of one of the environmental variable on fish abundance when the other variable is kept constant (partial regression coefficients; Jolicoeur, 1998). The partial regression coefficients were quantified with a program for multiple linear regression with permutation test to avoid normality distribution condition linked with usual parametrical test. Details about these permutations methods are given in Anderson and Legendre (1999).

Evaluation of the quality of the simulation performed by the hydrodynamic model

The ability of the hydrodynamic model to adequately estimate depth and current velocity have been recently discussed (Guay et al. 2001). To evaluate the quality of the estimations performed by the hydrodynamic model, we compared its estimations of depth and current velocity to real measures on comparable flow rate over 30 locations regularly distributed over the reach. The evaluation of the simulation quality was attained following the procedure proposed by Mesplé et al. (1996). Estimated and measured depths (and velocities) were compared with a major axis. The 95% confidence interval of the slope and of the intercept of this major axis were evaluated. The estimations of the hydrodynamic model were considered as realistic if the 95% C.I. of slope and intercept include 1 and 0 respectively. Mean and variance of estimated and measured depths (and velocities) were also compared with t and F statistics.

Comparison between the real fish distribution and the distribution pattern predicted using habitat quality indices developed under different water temperatures and cloud cover.

To perform the comparison between real fish distribution and the habitat quality predictions using the three HPI, new surveys from the 10 remaining were again selected according to the cloud cover that prevailed during these surveys. The selection of these surveys followed the same procedure as described above for the selection of the three surveys used to develop HPI. After removing the three previous surveys, 5 surveys remained in either the low cloud cover and high cloud cover categories but no survey remained in the intermediate cloud cover category. In each category, a survey was selected randomly. Surveys performed on July 1st and 9th were used respectively because of their high (100%) and low (30%) cloud cover conditions. These surveys were used to compare the real fish distribution under two opposite cloud cover conditions with the habitat quality pattern predicted by the habitat quality indices. The procedure used to make this comparison follows five steps. First, we overlay the map of habitat quality and the map of real fish distribution. Second, the surface area of each of the ten classes of HPI was calculated over the river section. Third, the number of fish in each class of habitat was counted. Fourth, the average fish density in each habitat interval was calculated (fish/100m^2, number of fish found within each class of habitat divided by the total surface associated with each class of habitat). Fifth, a polynomial regression was performed to test the existence of a significant positive relationship between fish density and habitat classes. This procedure was repeated six times: 3 HPI (low, intermediate and high cloud cover) x 2 surveys (low and high cloud cover). We are aware that these procedures cannot be interpreted as validation procedures of our indices since the development and the comparison have been done in the same river section and hence possibly with the same fish (spatial autocorrelation). However, these procedures could be used to invalidate an index. We presume that if an index that has been developed over a river section cannot predict adequately the real fish distribution of that same section (where the spatial autocorrelation should facilitate the good match), it should be considered as invalid.

Results

Foraging strategy in relation to cloud cover and water temperature

The number of fish observed during one survey ranged from 12 (August 5th) to 118 (July 5th and August 4th; Figure 2) and averaged of 57 fish. Cloud cover ranged from 5% to 100% and water temperature ranged from 16.5°C to 21.7°C. Multiple regression analysis showed that average cloud cover explained 44% of the variability ($p = 0.001$) of the number of fish actively foraging during our surveys. Water temperature had no statistically significant effect ($p = 0.48$) on the number of fish observed. A similar analysis using cloud cover in the middle of our surveys of July 7th and August 1st suggested that cloud cover explained 58% ($p = 0.001$) of the variability of the number of fish observed. The number of fish actively foraging decreased with cloud cover (Figure 3) and was unaffected by water temperature (Figure 4). The last sampling point of the summer (August 5th) was characterised by a very low number of fish observed ($n = 12$) despite the low cloud cover (25%; Figure 3) and the warm water temperature (20°C; Figure 4). Elimination of the last sampling point of the summer from our analysis had no effect on our interpretation other than increasing the percentage of the variance of the

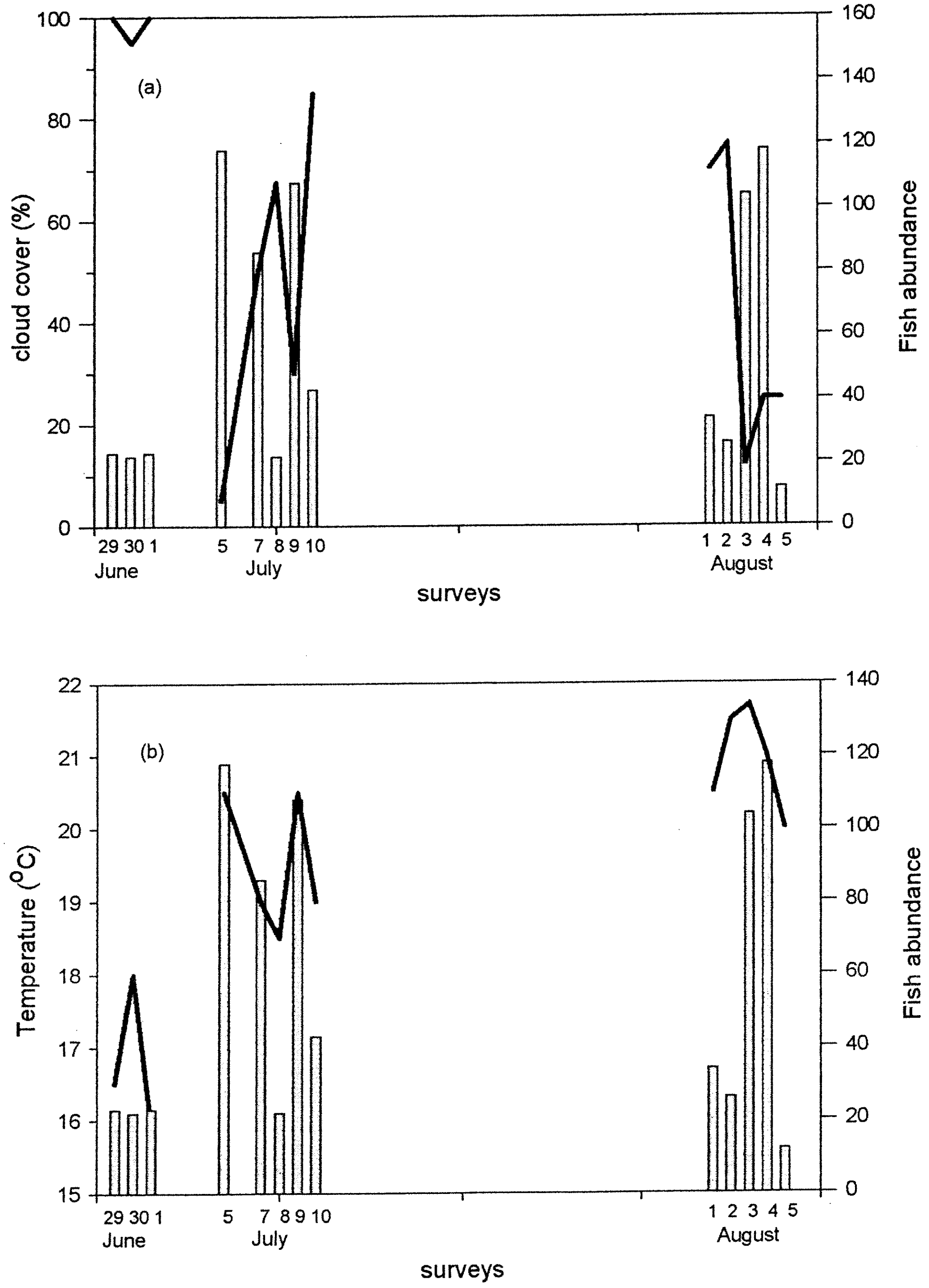

Figure 2. Variations into the abundance of fish (gray bars), the cloud cover (a), and the water temperature (b) during sampling days. Absence of bars means no survey.

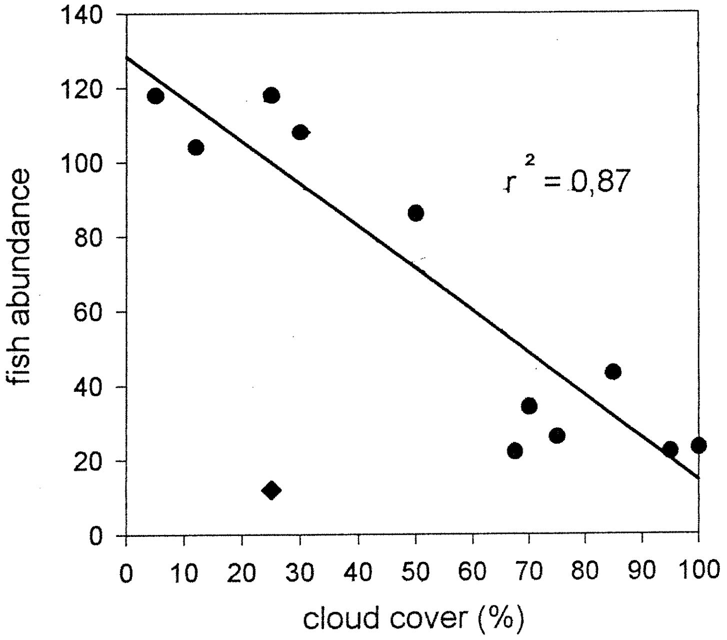

Figure 3. Relation between cloud cover and feeding parrs abundance. Sampling that occured on August 5th is represented by a diamond symbol. The regression line was calculated without including this sample.

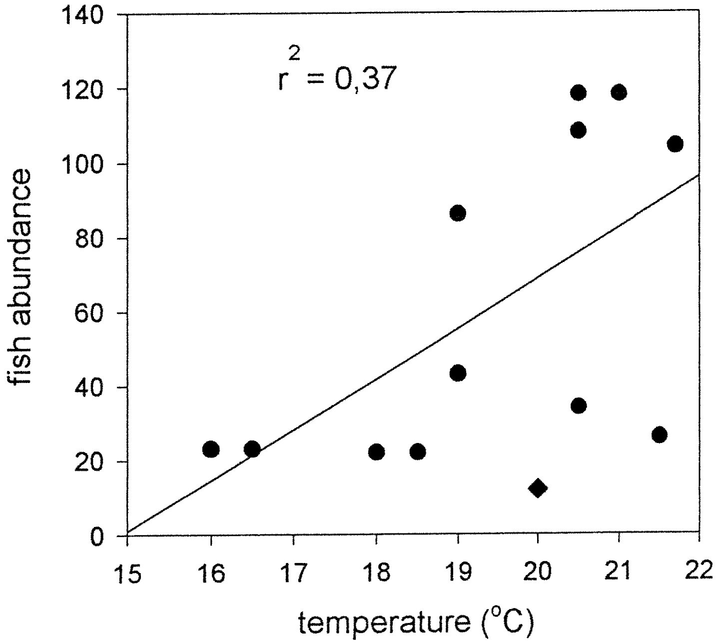

Figure 4. Relation between water temperature and feeding parrs abundance. Sampling that occured on August 5th is represented by a diamond symbol. The regression line was calculated without including this sample.

number of fish observed explained by average cloud cover (middle of survey values used for July 7th and August 1st) to 88%. There was a statistically significant relationship between average cloud cover (middle of survey values used for July 7th and August 1st) and water temperature ($p<0.05$ tested by permutations). Water temperature tended to increase as cloud cover decreased ($r= -0.64$).

Evaluation of the quality of the simulation performed by the hydrodynamic model

The slope of the major axis calculated between measured and estimated depth was not significantly different than 1 (95% I.C. [0.821, 1.176], $n = 30$). In addition, the intercept of this axis was not significantly different than 0 (95% I.C. [-0.00052, 0.14392], $n = 30$). The slope of the major axis calculated between measured and estimated current velocity was also not significantly different than 1 (95% I.C. [-0.088, 0.131], $n = 30$) and the intercept was not significantly different than 0 (95% I.C. [0.712, 1.217], $n = 30$). Thus, hydrodynamic model was able to adequately estimate local depth and current velocity in our reach. Furthermore, the mean (depth: $t = -1.22$, $p = 0.15$; current velocity: $t = 0.28$, $p = 0.90$) and the variance (depth: $F = 1.18$, $p = 0.59$; current velocity: $F = 1.59$, $p = 0.83$) of the estimations performed by the hydrodynamic model were not significantly different from the mean and the variance of the measures performed on field on a comparable flow. Hence, the precision of the hydrodynamic model was judged sufficient.

Development of biological models and comparison of their predictions

Three habitat probabilistic indices were developed. Each one represented a particular level of cloud cover since each one was developed using conditions used and avoided by fish under particular cloud cover conditions. Following equations were found:

$$\mathrm{HPI} = 1/(1 + e^{-\lambda})$$

$$(1) \qquad \lambda = -2.39 + 5.73D + 3.03V + 0.52S - 6.29D^2$$

$$(2) \qquad \lambda = -3.06 + 9.88D + 3.31V - 4.13S - 9.68D^2$$

$$(3) \qquad \lambda = -11.25 + 27.65D + 4.21V + 61.34S - 31.43D^2$$

Equations 1, 2 and, 3 represent respectively the index developed under low, intermediate and high cloud cover. Refer to chapter one (figure 2-A) for the maps of predicted depth and velocities, and for the map of substrate grain size over the study reach. The habitat quality maps show that some predictions performed by the three indices were similar and some others were different (Figure. 5). We observed that either HPI developed under low, intermediate or high cloud cover predicted generally poor habitat (0-0.1) near the shoreline. Furthermore, the habitat quality predictions have common spatial distribution especially between indices developed under low and intermediate cloud cover. We noticed that higher habitat quality (0.6-0.7 to 0.9-1.0 depending on the index) is predicted for habitat located at the south east of the island in the middle of the reach for the three indices. Similarly, poor habitat (0-0.1) is predicted over the upstream limit of the section. However, different patterns can be detected especially between the predictions performed by the index developed under high cloud cover and the two others. We observe that the surface represented by best habitats (0.9-1) predicted by this index is high (15% of the section area). However, this class of habitat is not predicted by the indices developed

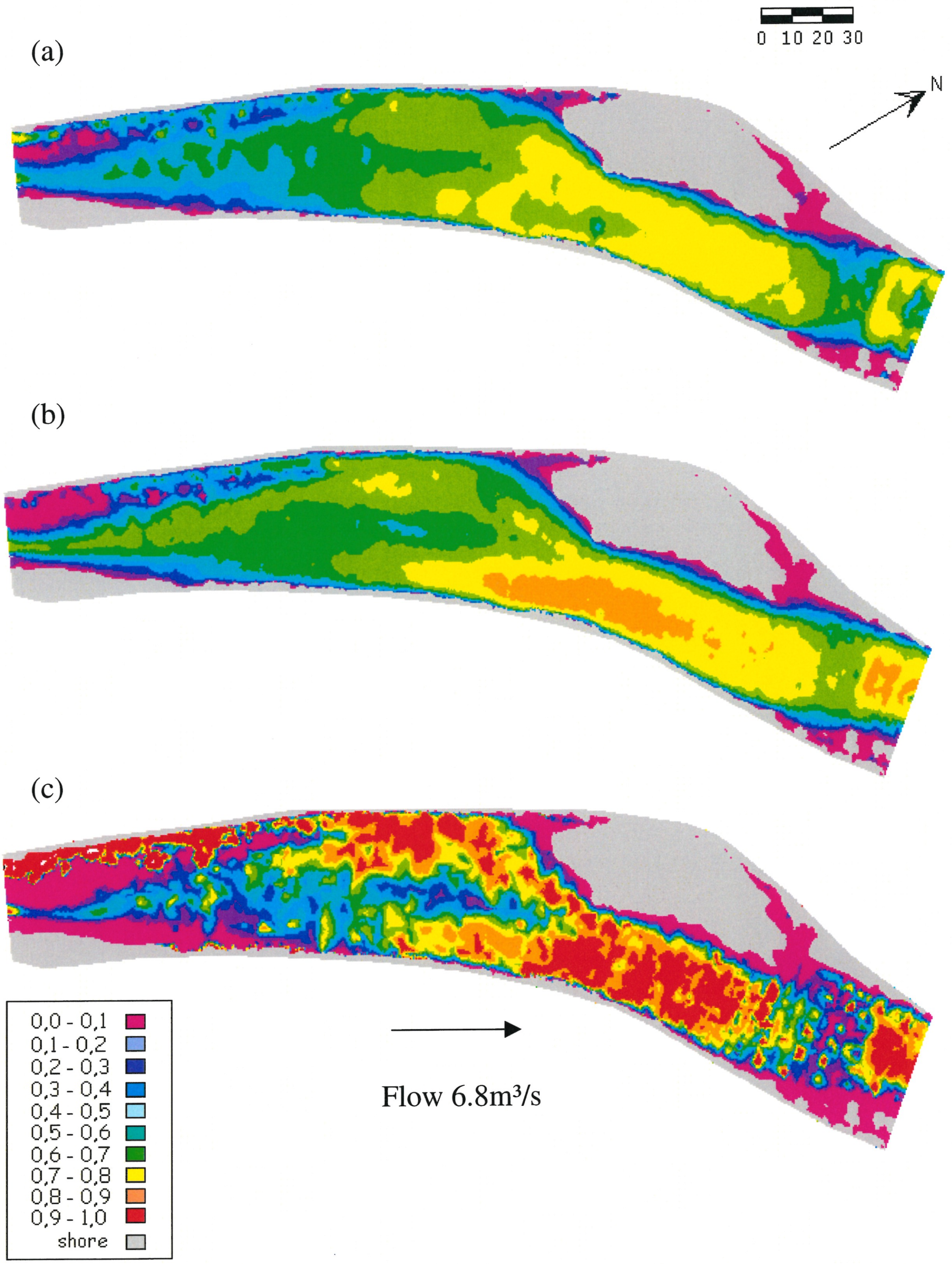

Figure 5. Maps of habitat quality predicted by HPI developed under low (a) intermediate (b) and high (c) cloud cover.

under low and intermediate cloud cover. Other difference in the predictions of the index developed under high cloud cover were situated near the upstream north shore of the section where best habitats (0.9-1) are predicted. But, near the same shore, the two other indices predicted habitat quality that range between 0–0.1 to 0.4-0.5. Despite these differences, the average quality of the entire reach predicted by the three indices are very similar (0.51, 0.54 and, 0.51 for indices developed under low, intermediate and high cloud cover respectively).

We evaluated the differences and the similarities into the predictions of the indices in relation to depth, current velocity, and substrate types. The depth conditions available over the study reach range from 0 to 1.4 m. The three indices predicted greater habitat quality (average between 0.62 and 0.68 depending on the indices) for depth ranging from 0.4 to 0.6 m (Figure 6a). The habitat quality predictions decreased regularly for depth below 0.5 m and over 0.6 m. However, the predictions of HPI developed under high cloud cover increased for depths ranging from 1.2 m and 1.4 m (Figure 6a). This result contrasts with the predictions of the HPI developed under low and intermediate cloud cover that, under this range of depth, predicted their lowest habitat quality (<0.05).

The current velocities available over the reach under a flow of 6.8 m^3/s range from 0 m/s to 1.2 m/s. The three indices predicted greater habitat quality with a current velocity increase (Figure 6b). Hence, the worst habitat quality (0.13 to 0.20 depending on the index) are predicted under current velocity that range from 0 m/s to 0.2 m/s. Conversely, the best habitat quality (0.89 to 0.98 depending on the index) are predicted under current velocity that range from 1.0 m/s to 1.2 m/s. These results suggest that the physical variables involve in the construction of the model must have a large range of

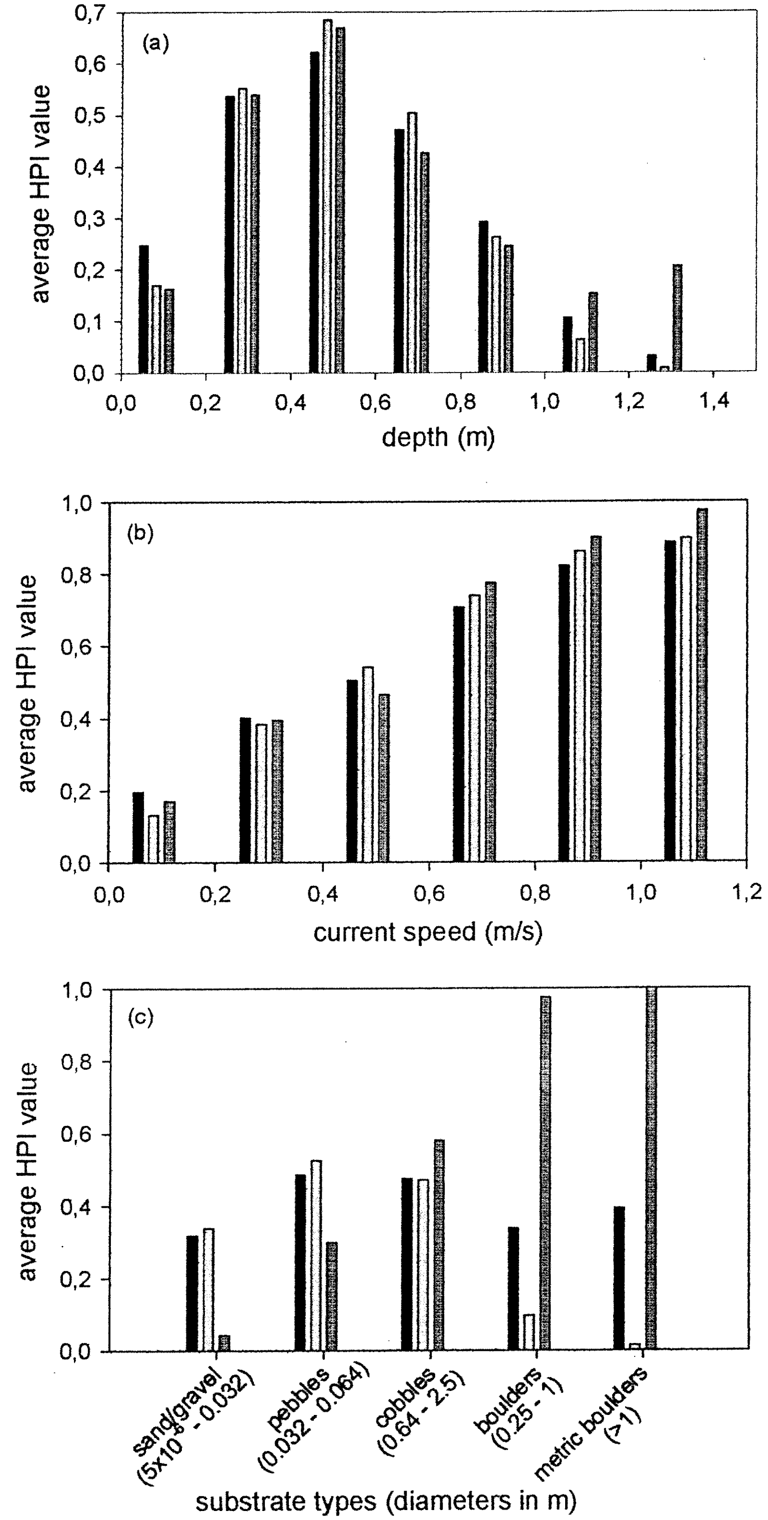

Fig. 6: Average predictions of habitat quality by HPI developed in low (black bars), intermediate (gray bars) and high (darker gray bars) cloud cover in function of depth (a), current velocity (b), and substrate type (c).

contrasted values to avoid an infinite increase of the index in relation to a specific physical variable.

The riverbed of the reach was composed of substrate types that ranged from sand to metric boulders. For a given substrate type, the predictions of habitat quality performed by the three HPI differed (Figure 6c). The HPI developed under low cloud cover predicted greater habitat quality where pebbles and cobbles were present (average 0.48 in both cases). Lower habitat quality were predicted where sand/gravel, boulder, and metric boulders were present (average HPI 0.32, 0.34, and 0.39 respectively). The HPI developed under intermediate cloud cover predicted greater habitat quality where pebbles were present (average HPI 0.53). Its habitat predictions decreased when the diameter of substrate was smaller or larger than pebbles (Figure 6c). The worst habitat predicted by this index were composed of metric boulders (average HPI 0.01). Conversely, the habitat quality predicted by the HPI developed under high cloud cover was greater as the diameter of substrate increased (Figure 6c). Hence, the worst habitat according to this index (average HPI 0.04) were situated in sand/gravel substrate type and the best habitat (average HPI 1) were situated in metric boulders.

Comparison between the real fish distribution and the distribution pattern predicted using habitat quality indices developed under different cloud covers.

The habitat quality maps (figure 5) were compared to the real fish distribution map randomly selected for low (Figure 7a) and high (Figure 7b) cloud cover. Polynomial regressions of the second order were performed between the ten habitat quality classes (0

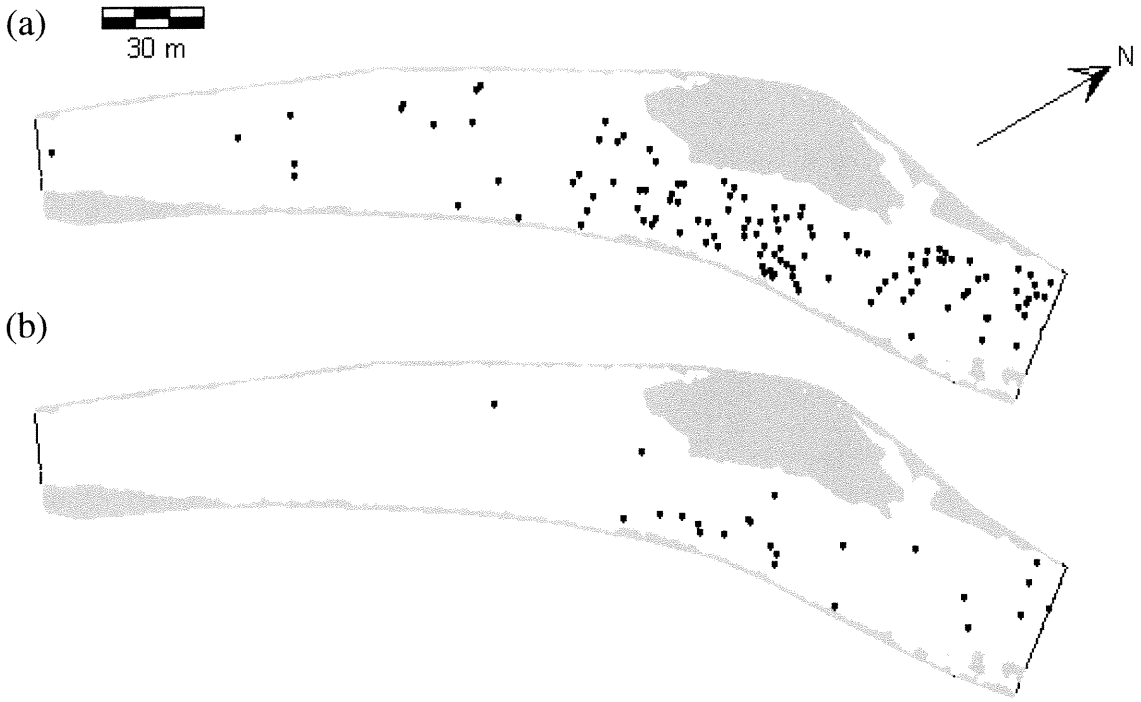

Figure 7. Real fish distribution under low (a) and high (b) cloud cover

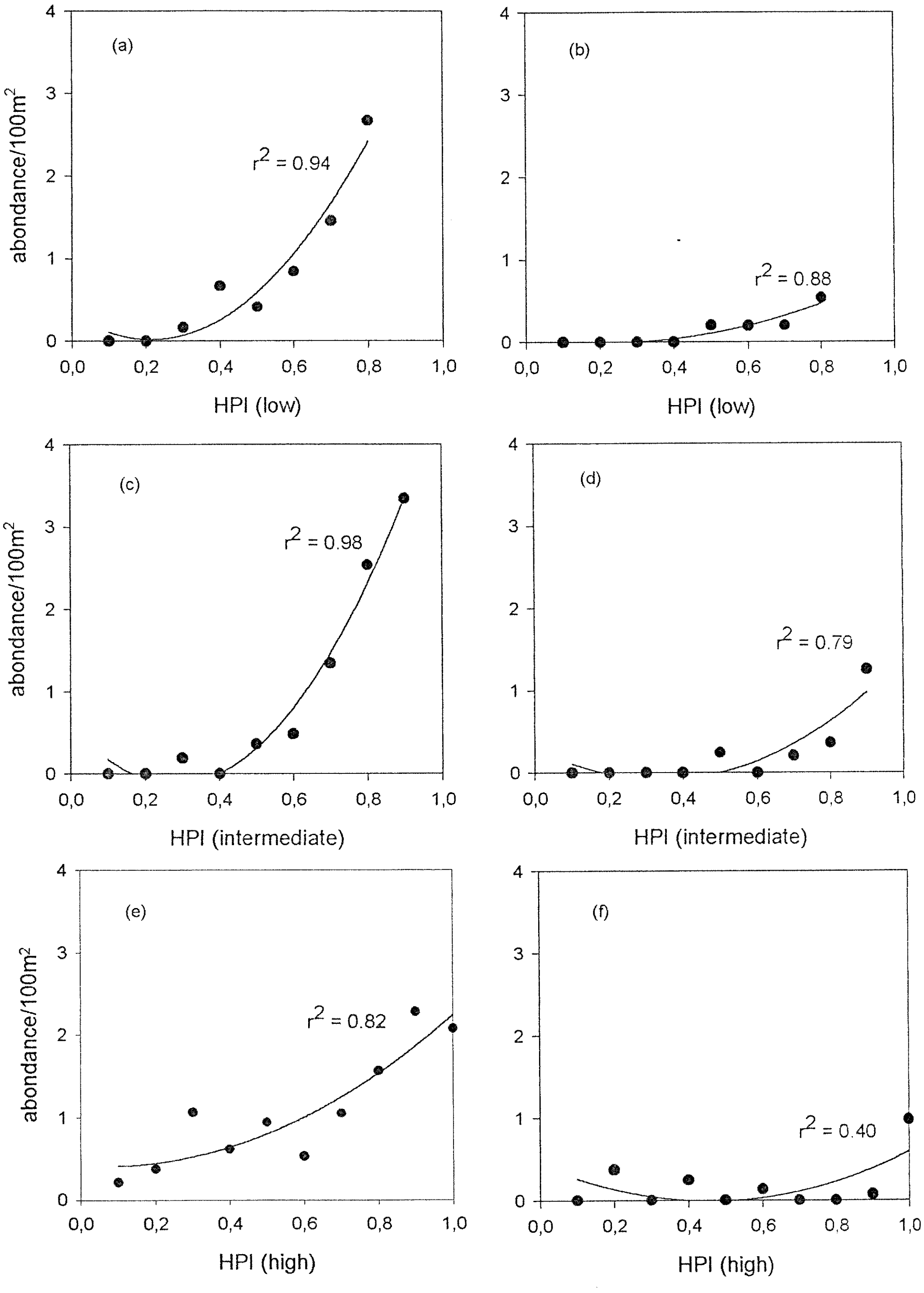

Figure 8: Relationships between fish densities observed under low (a,c,e) and high (b,d,f) cloud cover and the habitat quality value predicted by three different HPI developed under particular cloud cover conditions (in parantesis).

to 1 with intervals of 0.1) predicted by each of the three HPI and the parrs densities observed into each of these habitat class under low and high cloud cover. Significant positive relationships ($p<0.005$) were found between real fish densities under low cloud cover and HPI predictions for all indices (Figure 8). However, the indices developed under low and intermediate cloud cover explained a greater part of the variability of the fish densities (94% and 98% respectively) than index developed under high cloud cover (82%). Relationships between fish densities under high cloud cover were positive and statistically significant only for indices developed under high and intermediate cloud cover ($p<0.005$). The index developed under cloud cover of 100% was unable to adequately predict fish distribution in this high cloud cover conditions despite the fact that the data are spatially autocorrelated (Figure 8).

Discussion

Our results suggest that cloud cover explains a larger fraction of among-day variations of the number of fish adopting a diurnal feeding behaviour than water temperature. Furthermore, the predictions performed by habitat quality indices differs if they are developed under different cloud cover.

One approach that can be used to interpret our findings on foraging strategies of salmon parrs is to assume that they have evolved, like many other traits, to maximise fitness (Metcalfe and Steele 2001). Foraging strategies are suggested to be selected in accordance to food availability (Metcalfe et al. 1999, Reiriz et al. 1998, Lampert 1987) and predation risk (Eklöv 1997, Warburton and Brown 1997, Sih 1987). Fish select a foraging strategy that maximises the ratio between the food intake and the predation risk. Any factors that diminish this ratio could force fish to hide in substrate interstices.

Food intake vary according to conditions that will influence the capture efficiency of organisms (Metcalfe and Steele 2001). According to mechanistic models, the food capture efficiency of fish that holds station on or above substrate, as salmon parrs, depend partly on their ability to detect a food item, move out and intercept it before it is carried downstream (Metcalfe et al. 1997, Hugues and Dill 1990). The time available to the fish to detect and recognise a food item is very important to determine the efficiency to capture this item. Hence, any conditions that will influence the reactive distance of the fish will also influence the time available to capture a prey and therefore influence the capture efficiency. In the case of Atlantic salmon parrs, it has been demonstrated that, in low turbidity conditions (like Escoumins river) light intensity positively influences their reactive distance to preys (Benfield and Minello, 1996) and their food intake. Hence, fish foraging rate and efficiency may increase with light intensity.

However, predation risk by the common merganser (*Mergus merganser*), a visual feeder observed over our reach, is higher during day (Cramp and Simmons, 1977). Interestingly, there are indications that light intensity may decrease predation risk affecting parrs. To detect fish, the common merganser submerge its head and visually scan underwater (Alvo, 1995). However, this strategy is useful where the water depth is relatively important (< 4m) and in slow current. In the Escoumins River, where the mean depth is nearly 0.4 m and mean current velocity over 0.8 m/s, a prey detection directly from the surface (as used by the juveniles of merganser; Foreman 1976) is probably easier. Hence, cloud cover, that directly influence the light reflection on the surface of the water, can possibly increase the efficiency of merganser to detect salmon parrs. Hence, in high cloud cover conditions, the light reflection is lower, the capacity of merganser to detect fish from the surface is increased and the predation risk become greater. Oppositely, when the cloud cover is lower, the sunlight is reflected on the surface of the water, the capacity of merganser to detect fish is could possibly decreased and the predation risk is lower. We can assume that under low cloud cover, parrs consider that energetic gains are higher than costs due to predation, and then decide to forage. In contrast, in high cloud cover, fish consider that the energetic gains are not high enough to compensate for the predation costs and then choose to hide in substrate interstices. Interestingly, for the two dates for which the average did not represent well cloud cover conditions, fish abundance was more directly related to cloud cover measured in the middle of survey than to the average measure. It suggests that the evaluation of the benefits and the costs associated to a certain level of cloud cover is performed by fish within minutes after a sudden change into cloud cover.

The relationship between water temperature and the number of fish observed was not significant. Our work contrasts with the study by Fraser et al. (1995) who show a clear positive relationship between the two variables. However, the range of temperatures observed during this study was narrower and had higher mean than their (16,5°C to 21,7°C in this study compared to 2°C to 18,5°C in the Fraser et al. study). It is impossible to deny any effects of the water temperature below our range on fish foraging behaviour. However, our data show that, when summer high water temperatures occur, cloud cover is the variable that better explains the variability of the foraging strategy of Atlantic salmon parrs.

One can argue that the differences into the number of fish observed in this study is not a behavioural response of fish to cloud cover but only a result of the inability of divers to notice fish when light conditions are affected by an important cloud cover. We did not performed any experiment to test this possibility. However, we noticed that the critical distance at which a fish reacts to the presence of divers (approximately 0.5 m to 1.0 m) is always shorter than the size of the field of vision of divers even in bad light conditions (approximately 2 m in contrast to about 4 m in good light conditions). Hence, divers could always see parrs before they noticed our presence and flee. These observations were judged sufficient to assume that if there were the same number of fish irrespective of the cloud cover conditions, divers would see them.

The purpose aimed at the development and the comparison of three habitat quality index was to determine if water temperature and cloud cover have an effect on the development of this kind of biological models and further determine in which conditions the sampling must be done to give better results. Our analysis show that the quality of the predictions performed by a habitat quality index depends on which cloud cover conditions it was developed. The regressions performed between fish densities and NHM predictions suggest that fish distribution under low cloud cover is better predicted by habitat quality index developed under low ($R^2 = 0.94$) or intermediate ($R^2 = 0.98$) cloud cover than by index developed under high cloud cover ($R^2 = 0.82$). The difference into the predictions quality are greater ($R^2 = 0.88$ and 0.79 for habitat quality indices developed under low and intermediate cloud cover respectively) when they are compared to fish distribution in high cloud cover, which is not adequately predicted by the HPI developed under high cloud cover ($R^2 = 0.40$). According to this result, we assume that this HPI should be considered as invalid since it cannot predict fish distribution despite the autocorrelation that came from the fact that development and comparison are made over the same reach. However, because of that same autocorrelation, we cannot assess about the validity of the two other HPI.

One can argue that the invalidity of the HPI developed under high cloud cover is not caused by the behavioural variability shown by salmon parrs but on the lower number of data used to developed this index (n = 64) comparing to the other indices (n = 282 for low cloud cover and n = 210 for intermediate cloud cover). We verified the effect of sample size on the performance of our HPI by randomly selected 64 data (32 presences and 32 absences) in the data sets corresponding to conditions used and avoided by fish under low and intermediate cloud covers. From these data, two new HPI were developed, one for each cloud cover (low and intermediate). We then performed regressions between fish density on high and low cloud covers and HPI for these two index following the five steps procedure described in the statistical analysis section of the method.

The results of these analysis show that despite the lower number of data, these indices are able to predict fish distribution either under low cloud cover ($R^2 = 0.95$ and 0.91 for HPI developed under low and intermediate cloud cover respectively) and high cloud cover ($R^2 = 0.90$ and 0.85 for HPI developed under low and intermediate cloud cover respectively). These results suggest that the lower performances of the HPI developed under cloud cover of 100% in predicting fish distribution is not a cause of the number of data used but is related to the behaviour variability of salmon parrs.

Our work demonstrates the effect of cloud cover on foraging behaviour of salmon parr and further into the development of habitat quality indices. We suggest that the development of a valid HPI must be performed under cloud cover as low as possible to insure good performances into habitat quality predictions. We also conclude that other samplings that aimed to quantified habitat quality and that involve underwater visual observations of salmon parrs should take cloud cover in consideration when field sampling design are planned. Otherwise, results could be questioned.

Conclusion

Dans le premier chapitre de ce mémoire, la modélisation numérique bidimensionnelle des microhabitats (MNH) a été utilisée afin de répondre à certaines incertitudes reliées aux ensemencements de saumons de l'Atlantique de pisciculture dans les rivières. Afin de faciliter la revue de ce travail, les résultats peuvent être divisés en deux parties : le comportement des poissons ensemencés d'une part, et celui des poissons sauvages après l'ensemencement d'autre part. Les résultats suggèrent que les tacons ensemencés ont beaucoup de difficultés à s'installer à proximité de l'endroit où ils sont ensemencés mais que ceux qui restent sont capables de détecter les meilleurs habitats et d'y établir un territoire alimentaire. Les données ne supportent pas l'hypothèse que les poissons de pisciculture se soient déplacés à cause de la saturation des habitats disponibles par les poissons sauvages. Les analyses et observations laissent plutôt spéculer que le faible taux d'installation serait dû soit aux conditions d'élevage en pisciculture ou bien au stress induit par la procédure d'ensemencement.

Au niveau de la réponse des juvéniles naturels à l'ensemencement, aucun changement dans la distribution spatiale de saumons de l'Atlantique n'a été détecté. La diminution de la densité de poissons sauvages observée après l'ensemencement aurait pu être interprétée comme étant un déplacement des poissons sauvages en amont ou en aval de la section suivant l'ensemencement. Par contre, cette diminution était incluse dans l'étendue de la variabilité naturelle mesurée au deuxième chapitre ce qui porte à croire que cette variation de densité est naturelle et non pas due à l'ensemencement. Il est par contre malheureux qu'aucune mesure du couvert nuageux n'ait été prise à l'époque de ces observations, l'effet de cette variable environnementale n'ayant été découvert que l'année suivante, car les conclusions finales auraient pu être renforcées.

Le deuxième chapitre du mémoire a tenté d'approfondir l'approche de l'IPH en mettant en relief les conditions pouvant influencer la qualité des indices développés à partir d'observations visuelles en apnée du comportement alimentaire des poissons. Or, il a été démontré que le couvert nuageux influence négativement le comportement alimentaire des juvéniles de saumons de l'Atlantique et par le fait même la qualité des IPH. En effet, un IPH développé en conditions ensoleillées aura de meilleures qualités prédictives qu'un IPH développé en conditions nuageuses. Les conclusions de ce travail ont donc permis d'assurer une bonne utilisation de la méthode et pourraient difficilement être mises de côté lors de l'établissement dans l'avenir de plans d'échantillonnage portant sur le comportement des juvéniles de saumon de l'Atlantique.

Dans son ensemble, ce mémoire est une première tentative afin i) d'utiliser les qualités prédictives de l'IPH visant à dissiper des incertitudes reliées à l'écologie des poissons et ii) d'élucider certaines considérations méthodologiques quant au développement des MNH dans le but d'étudier l'écologie du saumon de l'Atlantique. En ce sens, il serait bien que de telles découvertes puissent permettent une plus grande utilisation (assurée) de ce type de modélisation en écologie compte tenu de ces possibilités.

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