# Fish habitat modeling: from conceptual framework to functional tools[1]

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**Abstract**: Natural and anthropogenic perturbations do not always equally affect all parts of an ecosystem, and all parts of an ecosystem do not equally contribute to maintain fish communities. The increasing pressure to use natural resources and to modify habitats led to the development of approaches to identify areas of key importance for fish communities. Following these approaches, aquatic systems could be perceived as puzzles, composed of a multitude of pieces with temporally flexible physical attributes and biological roles. Such a spatially explicit framework requires models that may allow one to predict fish distribution patterns and fish net energy gain once they have adopted a specific distribution pattern. Despite the conceptual appeal of spatially explicit approaches, functional tools may be obtained only after their assumptions have been tested and their models have been validated. Efforts must be deployed to identify temporal and spatial scales at which fish distribution and abundance should be estimated and modeled. Studies on fish behaviour and the energetic consequences of these behaviours must be conducted to insure that bioenergetic criteria used to define fish habitat quality do not depend on arbitrary assumptions about fish activity costs.

**Résumé** : Les perturbations naturelles et anthropiques n'affectent pas toujours également toutes les parties d'un écosystème et toutes les parties d'un écosystème ne contribuent pas également au maintien des communautés de poissons. La pression grandissante d'utiliser les ressources naturelles ont amené le développement d'approches permettant d'identifier les régions d'une importance clé pour les communautés de poissons. Suivant ces approches, les rivières relativement peu profondes pourraient être perçues comme des mosaïques de parcelles ayant chacune sa valeur énergétique spécifique pour les poissons et les rivières plus profondes et les lacs pourraient ressembler à des sculptures de blocs ayant chacun sa valeur de croissance potentielle pour les poissons. Un cadre de référence spatialement explicite requiert des modèles qui permettent de prédire les patrons de distribution des poissons et le gain énergétique net des poissons une fois qu'ils ont adopté un patron de distribution spécifique. Malgré l'attrait conceptuel des approches spatialement explicites, des outils fonctionnels ne pourront être obtenus qu'une fois leurs prémisses testées et leurs modèles validés. Des efforts doivent être déployés pour identifier les échelles temporelles et spatiales auxquelles la distribution et l'abondance des poissons devraient être estimées et modélisées. Des études sur le comportement des poissons et les conséquences énergétiques de ces comportements doivent être effectuées pour s'assurer que les critères bioénergétiques utilisés pour définir la qualité de l'habitat des poissons ne dépendent pas de prémisses arbitraires au sujet des coûts de l'activité des poissons.

## Introduction

Physical, chemical, and biological attributes of lakes and rivers and of the watershed that supplies them with water and nutrients are extremely variable among systems. This situation represents a challenge for ecologists trying to forecast how changes in environmental conditions may affect fish communities. Despite an apparently overwhelming variability in environmental conditions, models have been developed to predict some of the biological properties that we find useful. Contributions of a suite of scientists from Ryder (1965) to Downing et al. (1990) and to Randall et al. (1995)

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to develop relationships between fish production sensu largo (fish yield, biomass, or production; further referred to as fish production for simplicity) and characteristics of lakes or rivers exemplify, in my mind, what aquatic science is all about: acquiring knowledge that leads to the development of tools that can be manageable and useful for both fundamental and practical purposes.

Current models that attempt to predict the effects of changes in environmental conditions on fish communities generally focus on variables averaged over one or many years and over entire lakes or rivers (e.g., total fish yield or production, seasonal mean biomass, mean chlorophyll *a* concentration, average phosphorus concentration, mean depth, mean flow, total number of degree-days per growing season). However, all natural or anthropogenic perturbations of environmental conditions may not equally affect all parts of an ecosystem. Similarly, all parts of an ecosystem may not equally contribute to the maintenance of fish communities. Furthermore, the impact on fish of any given natural or anthropogenic perturbation may vary with time. Recognition of this situation has led to the development of approaches to locate, enumerate, and evaluate fish habitats and hence to identify areas of key importance for fish communities

2

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

(Bovee 1982; Brandt et al. 1992; Minns and Bakelaar 1999). Such a spatially explicit framework requires models that may allow one to predict fish distribution patterns and fish habitat quality. Despite the conceptual appeal of spatially explicit fish habitat models, functional tools may be obtained only after underlying assumptions have been tested and models have been validated. In this context, my objectives are to (*i*) present attempts to develop methods to estimate and model fish distribution, abundance, and production and (*ii*) discuss problems and solutions related to the use of an energetic criterion, the potential growth under given environmental conditions, to define fish habitat quality. My emphasis on an energetic criterion reflects my own interest in bioenergetics and not a contention about the superiority of this criterion. The capacity of a habitat to provide suitable spawning or overwintering conditions can be expected to give complementary and equally useful information (Cunjak 1988; Knapp and Preisler 1999).

## Empirical models of freshwater fish production

Empirical models of freshwater fish production provide indications on the boundaries within which fish communities and aquatic systems may function. The most important conceptual problem of these models may be their potential circularity (phosphorus concentration may affect fish through bottom-up processes, but fish excretion may affect phosphorus availability and primary production: McQueen et al. 1986; Kraft 1992; Vanni 1996). Maybe the use of nutrient loading (D'Arcy and Carignan 1997) instead of nutrient concentration in aquatic systems as a truly "independent" variable could contribute to solving this potential circularity. The most important functional limitation of the empirical models of fish production, which may or may not be related to the conceptual problem, is their confidence intervals that often span an order of magnitude. Most attempts to improve the precision of predictions made by such empirical models have focussed on the selection of potentially more powerful independent variables (for instance, the use by Downing et al. (1990) of primary production instead of the morphoedaphic index to predict fish production). However, estimation of the fish production per se may not be a simple exercise.
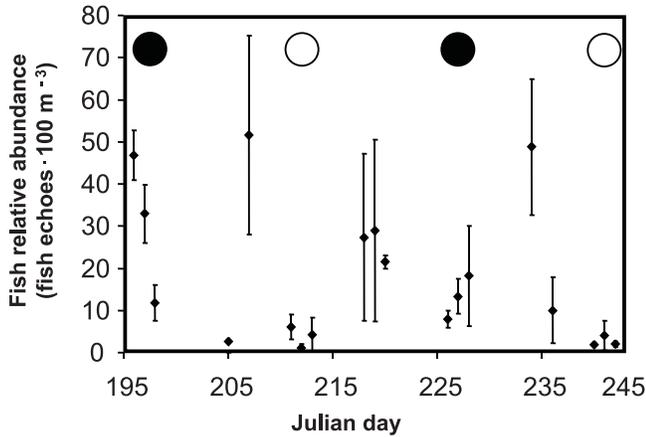
## Estimation of fish production

### Temporal considerations

Most empirical models that try to predict fish production are based on the analysis of results obtained using different sampling strategies and sampling gears. While these differences may contribute to the unexplained variance of empirical relationships, any approach based on the combination of data collected in many lakes is also subjected to an assumption regarding the temporal stability of the systems studied. Sampling designs often require that data (fish abundance and size) be collected in different lakes at different moments. The assumption is made that these data sets are comparable and that the moment of sampling has no effect on the planned comparison. We tested this assumption by assessing the extent of temporal variation in fish abundance estimates within a system, Lake Croche, at the Station de Biologie des

Laurentides de l'Université de Montréal. The littoral zone of this lake is of poor quality. Benthic invertebrates are rare, and fish catch using beach seines is low. Hydroacoustic surveys suggest that fish migrate every day from the littoral zone towards the pelagic zone at dusk and back to the littoral zone at dawn (Gauthier and Boisclair 1997). The hypolimnetic zone of Lake Croche (below a depth of 5–6 m) is anoxic during most of the summer, and consequently, vertical migrations do not explain the occurrence of fish in the pelagic zone of this lake at night. This situation led us to believe that many fish from this lake use the lower part of the littoral zone during the day, out of reach of our seines, and migrate towards the pelagic zone at dusk. We estimated the number of fish targets (target strength >52 dB according to Gaudreau and Boisclair 1998) detected by a hydroacoustic system using a horizontal scanning approach. This approach consists of directing the transducer of the hydroacoustic system such that the axis of the acoustic beam is parallel to water surface (Gauthier et al. 1997). Fish targets were subsequently transformed into estimates of fish relative abundance (FRA, fish echoes·100 m$^{-3}$ insonified). During these surveys, hydroacoustic signals were sent from a floating platform set in the pelagic zone of the lake towards the shore. Using this approach, fish cannot be detected within 5–15 m from the shore of Lake Croche because the hydroacoustic beam crosses the slope of the littoral zone before reaching the shore. The isobath where the hydroacoustic beam intersects the littoral is further referred to as the hydroacoustic shore. Sounding was performed at 4-h intervals for 15 consecutive days (Comeau and Boisclair 1998). On most of the sampling dates, the number of targets detected (and hence the number of fish in the pelagic zone) increased at dusk and decreased at dawn with peak FRA at night approximately 10-fold larger than values during the day. Pelagic seining indicated that hybrids of northern redbelly and finescale dace (*Phoxinus oes* × *Phoxinus neogaeus*) were the only planktivorous fish using the pelagic zone of Lake Croche at night (Gauthier and Boisclair 1997). We also noted that maximum FRA at night could vary 12-fold among nights, with the lowest values observed on a night of a full moon (see also Luecke and Wurtsbaugh 1993). Since our study covered only half a moon cycle, we repeated the sampling of Lake Croche to cover two consecutive moon cycles (Gaudreau and Boisclair 2000). On each moon phase (new, first quarter, full, and last quarter), day and night horizontal hydroacoustic surveys were performed over 3 consecutive days spanning from the day before to the day after a specific moon phase. The average number of fish migrating towards the pelagic zone of this lake at night could vary eightfold depending on the moon phase (Fig. 1). These results indicate that in lakes where fish exhibit distribution patterns similar to those found in Lake Croche, the temporal sampling schedules may greatly affect fish abundance, biomass, and production values. Interestingly, the magnitude of the variation that we observed for fish abundance estimates obtained using different temporal sampling schedules is similar to the variation of fish production estimates for a given primary production. This situation suggests that better sampling schedules may contribute to reducing the confidence intervals of empirical models of fish production.
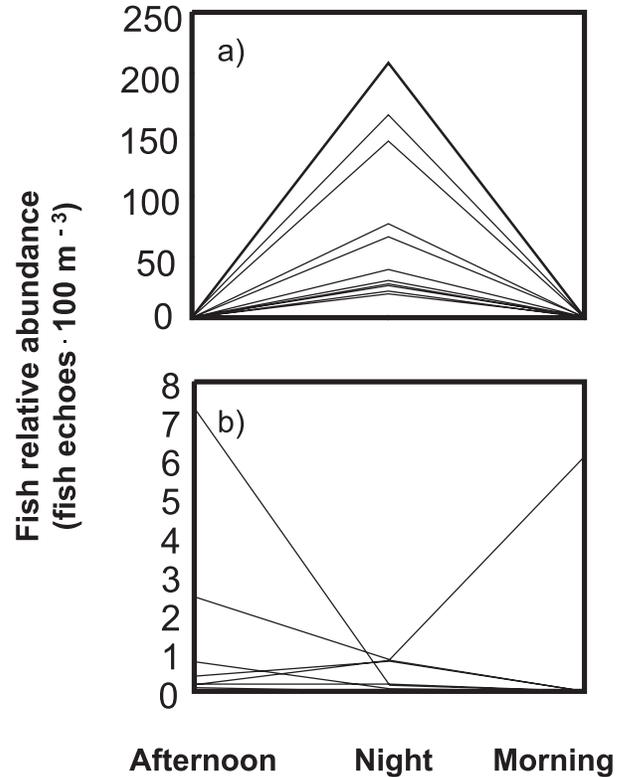
**Fig. 1.** FRA at 01:00 in the surface waters of a bay of Lake Croche estimated by hydroacoustic surveys performed using a horizontal scanning approach during two consecutive moon cycles. Solid and opened circles represent the new and full moon phases, respectively. Error bars indicate ±1 SD. Julian days 205 and 235 were not sampled because of storms.

**Fig. 2.** Daily variations of FRA in the pelagic area of (*a*) Lake Hertel and (*b*) Lake Croche. Each line represents a different 100-m segment of the perimeter of the lakes in which we performed hydroacoustic surveys using the horizontal scanning approach. Distribution patterns of Lakes Cromwell and Silver (not shown) are identical to those of Lakes Hertel and Croche, respectively.





### Spatial considerations

Once fish abundance has been evaluated, estimates of fish biomass produced (e.g., kilograms per year) are divided by total lake or river area to obtain production rates (e.g., kilograms per hectare per year). This procedure assumes that the complete area of lakes or rivers contributes to the production of fish or that the exact magnitude of area effectively producing fish has no effect on the biological interpretation of the relationship obtained. High variance of fish density estimates obtained in the littoral zone of lakes and patchiness of fish density values observed in rivers (Duncan and Kubecka 1996; Fischer and Eckman 1997) suggest that not all areas of lakes or rivers contribute equally to fish productivity. This situation may also occur in the pelagic zone of lakes. Gaudreau and Boisclair (1998) performed horizontal scanning of 25–100% of the perimeter of two lakes containing pelagic piscivorous fish, Lake Croche (brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*)) and Lake Silver (also has brown trout (*Salmo trutta*)), and two lakes lacking this functional group, Lakes Cromwell and Hertel. These lakes are in the Eastern Townships, Montreal, and Laurentians regions of Quebec. Hydroacoustic sampling was performed from a boat located 15–55 m from shore depending on the lake. During sampling, the acoustic beam was directed from a boat towards the closest shore of the lake. Sounding was conducted at 4-h intervals over one 24-h period in each lake. FRA was estimated for 7–12 sequential segments of 100 m of the perimeter of each lake and for two distance classes from the hydroacoustic shore (0–10 m and, when possible, 10–20 m). Average FRA values for any given lake, time of day, and distance from the hydroacoustic shore varied 3- to 84-fold among segments (Fig. 2), supporting the assumption that not all areas of a lake contribute equally to the maintenance of fish communities. Although 1-day sampling does not allow us to determine whether fish consistently use the same segments of the perimeter of the lake (day after day), it is interesting to note that in Lakes Hertel and Cromwell, migration towards the pelagic zone was temporally synchronised among segments (Fig. 2*a*). Peak FRA values, and hence peak migration towards the pelagic zone, occurred at night in all segments. No such temporal synchronism was observed in Lakes Croche and Silver (Fig. 2*b*). These results contrast with the expectation that the presence of pelagic piscivores should induce well-structured fish migrations (Gliwicz and Jachner 1992). The distribution patterns that we observed suggest that the presence of pelagic piscivores may, in fact, induce planktivorous fish to perform feeding migrations that are difficult to predict by their predators. Our data do not permit us to assess the relative effect of the presence of pelagic piscivores and of the sampling design on the presence or absence of temporal synchronism in fish migration. However, our data may be sufficient to suggest that there may be conditions that induce or impede such synchronism. I can only speculate that this synchronism may affect the intensity of predator–prey interactions and the occurrence of nutrient pulses created by fish migrating into the pelagic zone and excreting nutrients (Schindler et al. 1996). While both the occurrence of these nutrient pulses and their effect on the pelagic food web remain to be tested, knowledge that fish may or may not simultaneously migrate towards the pelagic zone may promote new approaches to evaluate the mechanism by which they could affect the pelagic food web.

4

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

We complemented our evaluation of fish spatial distribution by performing studies to assess variations of fish abundance in the nearshore (approximately 25–40 m from shore) and farshore (approximately 60–75 m from shore) areas of the pelagic zone of three lakes. The complete perimeter of Lakes d'Argent, Cristal, and Orford (Lower Laurentians and Eastern Townships regions of Quebec) was insonified (horizontal scanning) twice at 12:00 and twice at 24:00 on dates within 3 days of the new moon. This strategy was adopted to observe the full magnitude of fish migration and to permit the comparison among lakes (same moon phase). Surveys were performed from a boat cruising approximately 50 m from shore, first with the transducer looking towards the littoral zone of the lakes (nearshore area) and second with the transducer looking towards the centre of the lakes (farshore area). Hydroacoustic recordings were divided into 100-m segments and FRA was estimated for each segment of 100 m in both the nearshore and the farshore areas. FRA was further estimated for three classes of distance from the transducer (11–16, 16–21, and 21–26 m). The volume sampled in each class of distance was calculated independently. On average, FRA increased sevenfold as the distance from the transducer increased (Fig. 3). It is doubtful that acoustic beam spreading over a distance of 15 m may cause such an increase in FRA. One explanation may be that, during horizontal scanning, because the acoustic beam crosses the water surface, hydroacoustic noise caused by even gentle turbulence may increase with the distance from the transducer. Hence, FRAs were analysed independently for each class of distance from the transducer. Nonparametric analyses of variance, using the different 100-m segments sampled at a given time of day as replicates, indicated that the three lakes differed in fish distribution patterns. In Lake Cristal, more fish were observed during the day than during the night (a situation totally opposite of that in Lake Croche), but FRA in the nearshore area did not differ significantly from that in the farshore area (Fig. 3a). In Lake Orford, there was no statistically significant difference between FRA obtained during the day and during the night, but significantly more fish were observed in the nearshore area than in the farshore area (Fig. 3b). Lake d'Argent also had statistically higher FRA values in the nearshore area, but fish abundance during the night was higher than that during the day (maybe similar to Lake Croche; Fig. 3c). These observations suggest that the highest fish abundance in the pelagic zone of lakes does not always occur at night and consequently that data for evaluating fish production or trophic interactions in this zone should be collected using both day and night surveys. More importantly, these data suggest that the degree of coupling between fish distribution patterns and prey distribution patterns may differ among lakes. Zooplankton biomass is generally expected to be highest in the pelagic zone of lakes and to increase at night (Gliwicz 1986; but see Levy 1990). This is also true in our study area (Gauthier and Boisclair 1997; Masson and Pinel-Alloul 1998; Avois et al. 2000). Yet, our data indicate that at least in some lakes, fish abundance is lowest in the pelagic zone when zooplankton is expected to be highest in this area and that fish may not exploit the full extent of the pelagic zone (significantly more fish in the nearshore area than in the farshore area). The lack of coupling between fish and zooplankton distribution patterns

**Fig. 3.** Day–night variations of mean FRA in the nearshore (N) and farshore (F) areas of the pelagic zone of (*a*) Lake Cristal, (*b*) Lake Orford, and (*c*) Lake d'Argent. The complete perimeters of the lakes were insonified during two consecutive horizontal scanning surveys performed at 50 m from the shore. First, the transducer was directed towards the shore (nearshore estimates), and second, the transducer was directed towards the middle of the lake (farshore estimates). Nearshore and farshore values were divided into three classes of distance from the transducer.
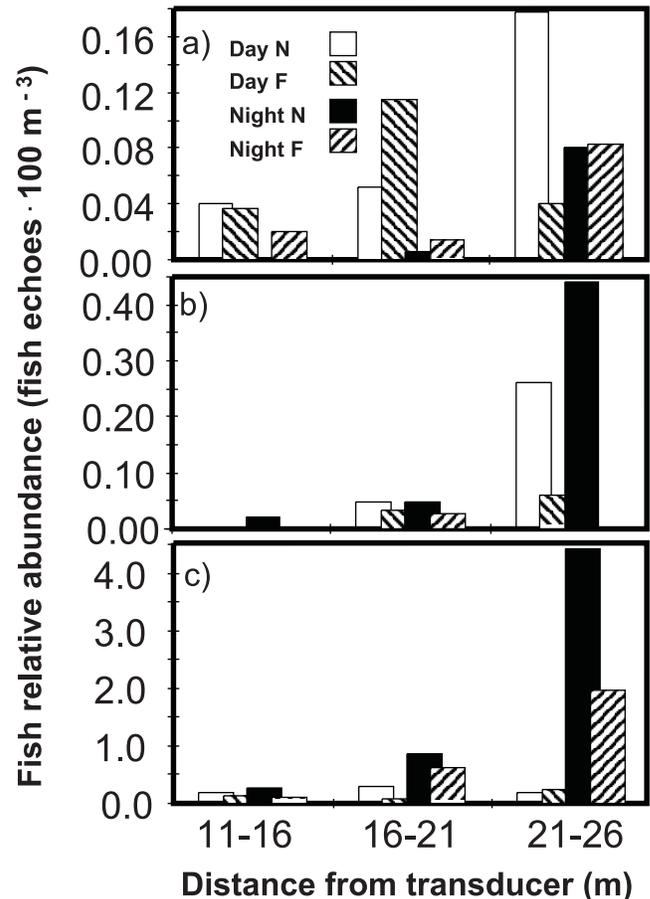


may have the positive effect of providing a refuge for zooplankton that allows a predator and its prey to persist at higher biomass levels (Leslie and Gower 1960), or it may have the negative effect of causing lost opportunities to transfer energy from one trophic level to the next. While the net result of this situation may depend on the balance between the "refuge" and the "lost opportunity" effects, it is tempting to speculate that part of the variance of fish production for a given phosphorus concentration or primary production may be related to the extent of the spatiotemporal coupling between fish and their prey.

## Space × time × energy axes

Fish production (Ricker 1975), regardless of the scale of observation, is the product of fish biomass (fish abundance × fish size) and fish growth. However, fish often perform migrations between areas of lakes that differ in environmental conditions at approximately 12-h intervals, and these migration patterns may change from one week to the next. In

rivers, environmental conditions such as water depth and current velocity may vary on a small spatial scale and, together with water temperature, may differ from one day to the next because of more or less sudden changes of flow produced, for instance, by rain. While it may be possible to estimate fish abundance and size over small spatial and short temporal scales, it is often difficult to estimate fish growth per se on a weekly basis and practically impossible to determine growth on a daily basis. Yet, ecologists are not necessarily destined to try to develop relationships between production rates estimated at some spatiotemporal scales and a composite of environmental variables estimated at all sorts of spatial and temporal scales.

The spatial and temporal heterogeneity of biotic and abiotic conditions should force us to view lakes not as more or less connected littoral, epilimnetic, and hypolimnetic zones but as sculptures of blocks each having a temporally flexible ecological value. Similarly, shallow rivers should be perceived as mosaics of tiles with fluctuating physical and biological attributes. Modeling such spatially and temporally dynamic structures is daunting because it pulls us away from the traditional use of variables averaged spatially and temporally. Furthermore, it represents a conceptual challenge because it requires that we identify the biotic and abiotic variables that affect fish production at the scales selected and that we quantify their effects at these scales. Finally, but not least, this approach constitutes a technical challenge because it requires that we organise and represent the information used as inputs to the model and the predictions themselves in a manageable way. Considering those challenges, I can only recognise the merits of the pioneering work of Brandt et al. (1992) who provided an inspiring example suggesting that it may be feasible, with "spatially explicit models," to integrate bioenergetic models and the spatial structures of physical conditions such as water temperature to estimate potential fish growth in a series of volumes in a lake (Goyke and Brandt 1993; Mason and Brandt 1996). Spatially explicit models focus on among- *and* within-system variations of fish habitat quantity and quality. My conception of the future development of spatially explicit models of fish habitats is based on two questions. How will fish distribute themselves under given sets of environmental conditions? How will fish perform once they have adopted a specified distribution pattern?

## Fish distribution

Studies on fish distribution in lakes indicate that fish distribution is heterogeneous (Duncan and Kubecka 1996; Fischer and Eckman 1997; Gaudreau and Boisclair 1998). The development of models to predict fish distribution requires that lakes be sampled according to a standardised temporal and spatial design based on the use of similar gear and assumes that general rules that determine fish distribution exist. While methodological standardisation may be feasible, it does not appear to facilitate the work. Our own studies suggest that sampling during the day and during the night, at different moments of the moon phase, in the littoral, nearshore, and farshore areas of the pelagic zone and, at least in some cases, in the profundal zone of lakes may be required. Nevertheless, when the same sampling protocol is applied in a few lakes (Gaudreau and Boisclair 1998, 2000),

results suggest that similarities of fish distribution patterns among lakes may exist (for instance, among Lakes Croche, Silver, and d'Argent or between Lakes Hertel and Cromwell) and that simple variables may be used to explain different distribution patterns (for instance, the presence or absence of pelagic piscivorous fish). Much remains to be done to establish the existence of general rules that define fish distribution patterns. Although this venture appears more than challenging, studies of fish distribution patterns in rivers, to which both engineers and biologists have contributed over decades (Bovee 1982; Leclerc et al. 1994; Whalen and Parrish 1999), suggest that practical and manageable models may be achievable. Recent studies suggest that it may be possible to predict fish distribution in rivers with models based on relatively few variables. For instance, Guay et al. (2000) recorded the water depth, current speed, and substrate diameter in 308 parcels of 1 m$^2$ occupied by Atlantic salmon (*Salmo salar*) juveniles in a 750-m-long calibration section of the Sainte-Marguerite River (Saguenay region of Quebec). The same physical characteristics were recorded in that section for an equal number of parcels in which no salmon were observed. This data set permitted the development of a multivariate logistic regression that predicts the probability of observing a fish under specified combinations of water depth, current speed, and substrate diameter. This "probabilistic" model was used to predict the spatial distribution of fish in an adjacent section of the same river (validation section, length of 750 m). During this exercise, we produced a map in which the validation section was divided into 10 habitat types (varying from 0 to 1 by intervals of 0.1) defined by the probability of finding a fish according to the probabilistic model (see fig. 5 in Guay et al. 2000). Real fish density (from 0 to 2.5 fish·100 m$^{-2}$) was estimated in each of these types of habitats by snorkeling the entire validation section. We found a strong relationship between real fish abundance and the predictions made by the probabilistic model ($r^2 = 0.81$–$0.98$ depending on water flow). Similar findings were obtained by Boudreau et al. (1996) and Bourgeois et al. (1996) using a slightly different approach. Considering that rivers, because of their dynamic physical attributes related to flow, may represent more challenging habitats to model, I can only presume that similarly efficient models may be developed for lakes. An important contribution of these studies may be that once fish distribution patterns are better understood, the spatial and temporal scales at which we should estimate the interactions between fish and environmental conditions may become clearer.

## Fish performance

Yearly or seasonal fish yield and production have often been used as measures of how well fish are doing in lakes and rivers or, alternatively, as a measure of the quality of these habitats. Spatially explicit habitat modeling requires that the currency used to describe fish performance be compatible with the spatial and temporal scales employed for the study of fish distribution patterns. Bioenergetic models may permit us to reconcile the scales used to analyse fish spatial and temporal distribution patterns and to estimate fish performance. The general form of bioenergetic models (also see Winberg 1956; Kitchell et al. 1977) can be written as

(1)     surplus = ingestion – (expenditures + losses)

where "surplus" is the sum of somatic and gonadal growth (surplus energy, sensu Ware 1982), "expenditures" are the costs of performing any metabolic work (standard metabolism, digestion, activity), and "losses" are products released during excretion and egestion (Brett and Groves 1979). The structure of bioenergetic models suggests that surplus energy, which is a valid measure of fish performance, can be predicted for any environmental condition and for any time interval at which fish ingestion, expenditures, and losses can be measured, even if this time interval is too short to estimate surplus energy per se. Equation 1 is fundamentally flawless: "surplus" has to be what is left once "expenditures" and "losses" are subtracted from "ingestion." However, approaches used to transform a theoretical entity into a functional predictive tool are by no means similarly perfect. Bioenergetic models require so much data and pressure to produce predictions is such that data are often replaced by *realistic* assumptions (Ney 1993). In fact, each equation and parameter used to implement bioenergetic models represents an assumption. It may be appropriate to view predictions of eq. 1 as estimates of the net energy gain expected to occur during a specified time interval under given environmental conditions. These predictions are further referred to as expected net energy gain (ENEG).
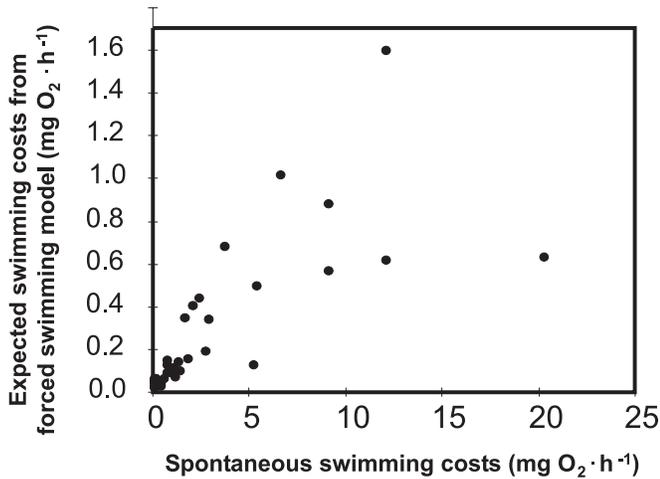
My work has focussed on two components of fish bioenergetic budgets: the modeling of ingestion and activity rates. Ingestion rate is an obvious choice because it is the fuel for growth. My interest in activity rates stems from research suggesting that this component of fish bioenergetic models may represent a potentially large and variable fraction of energy budgets (Boisclair and Leggett 1989). Hence, improper assumptions about activity rates could severely bias ENEG values predicted by bioenergetic models. Despite the controversy and the criticisms (Hayward 1990; Hewett et al. 1991), the effective role of fish activity rates in bioenergetic models remains unresolved, probably because of the difficulty in estimating this component of the energy budget. One approach employed for that purpose has been to estimate activity rates by difference using eq. 1 (Kerr 1982; Boisclair and Leggett 1989). This approach is amenable only for relatively long temporal scales because it presumes that both ENEG (generally growth) and consumption rates are known. Using this approach, Boisclair and Rasmussen (1996) developed models to predict seasonal activity rates of yellow perch (*Perca flavescens*). They found that 69% of the estimated variation in activity rates could be explained using only fish weight and water transparency as independent variables. Consequently, these analyses suggest that relatively simple models can predict a key bioenergetic component. However, if the objective is to use a traditional statistical framework to predict ENEG using ingestion, expenditures, and losses as independent variables, it is important that these variables be statistically independent. This requirement necessitates the development of approaches to estimate fish activity rates per se.

Methods to estimate fish activity rates per se require three kinds of information: the amount of time that fish spend swimming, the intensity of the movement (generally swimming speed), and models to transform the number and inten-

sity of movements into energy expenditures. Experiments performed in flume respirometers have been used to develop relationships between oxygen consumption, body weight, and swimming speed (Beamish 1978). During these experiments, fish are forced to swim against a current of constant speed and direction. However, it has long been recognised that the costs of swimming at a constant speed and direction may not correspond to those of swimming at the same average speed but with accelerations, decelerations, and turns (Beamish and Dickie 1967). Empirical analyses by Boisclair and Tang (1993) suggested that the energetic costs of spontaneous swimming (including changes of speed and direction) for a given fish weight and average swimming speed may be 6 to 14 times higher than those estimated by forced swimming models. These results supported the hypothesis that accelerations and turns are very expensive and led to experiments to develop models aimed at estimating the spontaneous swimming costs of fish using a more detailed suite of swimming characteristics as independent variables. Over the past 10 years, we have performed 45 respirometry experiments with brook trout ranging from 1 to 42 g wet weight (Krohn and Boisclair 1994; Tang and Boisclair 1995; Tang et al. 2000). During these experiments, fish are free to swim, without any current, in rectangular respirometers (27–108 L) held at water temperatures ranging from 4 to 21°C. Fish swimming characteristics such as the average and the variance of swimming speed, acceleration rates, and turning rates were estimated using the stereocinematographic method (Boisclair 1992*a*). Swimming characteristics varied among experiments such that, for instance, average speed ranged from 3.8 to 16.5 cm·s$^{-1}$. Spontaneous swimming costs ranged from 0.05 to 20.3 mg O$_2$·h$^{-1}$. These data permitted the development of models in which fish weight and different swimming characteristics explained 35–91% of the variation in spontaneous swimming costs. More importantly, these experiments confirmed that, for a given fish weight, the energetic costs of spontaneous swimming at a specific average swimming speed are, on average, ninefold higher than the expected costs of forced swimming at the same speed (Fig. 4). Our studies indicate that the use of forced swimming models for fish that change their speed and direction may greatly underestimate the costs of habitat utilisation and overestimate ENEG and habitat value.

The approach that we developed to estimate fish activity rates from videorecordings of their movements allows us to estimate activity rates that are *almost* statistically independent from growth and consumption rates; calculations of both growth and activity rates require estimates of fish weight. By combining this approach with existing models for estimating fish ingestion rates, we have tried to obtain models for predicting fish ingestion and activity rates under small spatial and short temporal scales (Boisclair 1992*b*; Boisclair and Sirois 1993; Sirois and Boisclair 1995; Marchand and Boisclair 1998). So far, we have performed 32 daily experiments with brook trout (0.6–3.5 g wet weight) held in 1- to 8-m$^3$ enclosures under variable water temperatures (17–21°C) and fish (0.5–3 fish·m$^{-3}$) and zooplankton (0.01–0.29 g dry·L$^{-1}$) densities. Variables such as fish numerical density, water temperature, and fish weight explained 33–82% of the variations of fish ingestion and activity rates (Table 1). While there are arguments to suggest that these

**Fig. 4.** Relationship between the respiration rates of brook trout predicted by a forced swimming model (Boisclair and Tang 1993) and the observed spontaneous costs of swimming for these fish during 45 respirometry experiments.



**Table 1.** Empirical relationships between specific components of fish bioenergetic models and environmental conditions during 32 daily experiments with brook trout held in enclosures.

$I/\text{SMR} = 11.31 - 0.33N - 0.47T - 0.48W$, $R^2 = 0.82$

$A/\text{SMR} = 3.94 - 0.43T + 0.38W$, $R^2 = 0.33$

**Note:** Growth ($G$), ingestion ($I$), and activity ($A$) rates are presented as multiples of standard metabolic rate (SMR). Independent variables that explained a significant fraction of variations of these bioenergetic components are fish numerical density ($N$, $\text{n·m}^{-3}$), average fish weight ($W$, g wet), and water temperature ($T$, °C).

experiments may be biologically meaningful (Marchand and Boisclair 1998), the lack of information on the density of fish that is realistic for study in 1- to 8-m$^3$ enclosures set in lakes makes it difficult to evaluate whether these models have more than a purely academic value. My perspective is that the most important contribution of these findings is that they indicate that it may be possible to develop models for predicting variations of fish bioenergetic components, and hence for predicting ENEG, on relatively small spatial scales and short temporal scales. These characteristics are required to perform spatially explicit modeling.

Modeling ENEG in rivers involves different challenges than that in lakes. One important difference between lakes and rivers is the presence of current, which has direct consequences on the estimation of fish activity rates. In rivers, current speed is expected to increase exponentially from the bottom towards the surface of a river (Dingman 1984). Current speed at any given distance from the bottom may vary within a few seconds (Kirkbride and Ferguson 1995). Hence, the cost of habitat utilisation for fish that constantly remain close to the bottom of rivers may be expected to be adequately described using forced swimming models. However, fish that perform frequent feeding attempts from the bottom towards the surface of rivers may face highly variable current speeds. In such cases, fish movements may involve important changes in swimming speed and direction. While this situation may resemble the definition of spontaneous swimming, in contrast with the experimental conditions used to develop spontaneous swimming models, current is always present in rivers. It could be argued that the cost of swimming at a given average speed (for instance, during a movement towards drifting prey) may be higher in rivers than expected by spontaneous swimming models because movements in a constantly moving and changing environment may require more vigorous and frequent accelerations. The magnitude of the energetic consequences of turbulent currents on fish swimming costs may be expected to depend on the interaction between fish behaviour and current structure. Video observations of the behaviour of Atlantic salmon juve-

niles suggest that there may be interesting parallels between fish behaviour and current structure (F. Burton and D. Boisclair, unpublished data). For instance, attacks directed by Atlantic salmon juveniles towards drifting prey occur at intervals ranging from a few seconds to a few minutes. The duration of the forward (upstream) phase of attacks, which is expected to be the most energy-demanding part of the attack, ranges from 0.5 to 2 s. Recordings of the structure of water turbulence suggest that significant troughs in current speed (three- to eightfold decrease of current speed) may occur at 5- to 30-s intervals. Furthermore, the duration of such troughs may range from 0.5 to 5 s (Roy et al. 1999). Thus, current troughs may be sufficiently intense, frequent, and long to represent windows of opportunity during which fish could save significant energy. This situation, combined with the presence of eddies (Vogel 1994) creating upstream forces downstream of rocks often used as waiting positions by salmon, may decrease the costs of habitat utilisation estimated using effective fish swimming speed. It can be expected that studies on the behaviour of fish in turbulent currents, the structure of turbulent currents, and the energetics of swimming under such conditions may have a significant effect on estimates of ENEG for fish that live in rivers and on estimates of habitat quality values in rivers.

## Epilogue

Empirical models of fish production provide simple and manageable tools that allow us to define general tendencies about the effect of average conditions found in aquatic systems on fish communities. The strength of spatially explicit models resides in their ability to explicitly represent determinant habitats to be protected. In the context of the constantly increasing pressure not only to exploit fish populations but also to alter their habitats both locally and globally, this attribute may not be trivial. The weakness of fish habitat models is the long list of assumptions that affects the validity of their predictions. Testing these assumptions may be the only means to transform a promising conceptual framework into functional tools.

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