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MORTALITÉ HIVERNALE DE L'ÉPERLAN ARC-EN-CIEL D'EAU DOUCE

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RÉSUMÉ

La compréhension des facteurs affectant la survie des éperlans arc-en-ciel (*Osmerus mordax*) juvéniles est primordiale puisqu'il constitue la principale nourriture de la ouananiche du lac Saint-Jean (*Salmo salar*). Ce saumon d'eau douce connaît actuellement une très faible abondance, mais également une très faible croissance. Les fluctuations inter-annuelles d'abondance de ce poisson fourrage peuvent devenir un facteur clé dans la production de plusieurs espèces de poissons de pêche sportive. Ces fluctuations pourraient être contrôlées par les facteurs climatiques, particulièrement près des limites nordiques de distribution de l'espèce, situées tout près du lac Saint-Jean.

Notre objectif principal était d'évaluer l'effet des facteurs climatiques sur le recrutement des jeunes éperlans arc-en-ciel d'eau douce de l'année, en évaluant l'effet de la longueur de la saison de croissance sur l'accumulation lipidique et la taille des individus, et l'effet de la sévérité de l'hiver sur la mortalité sélective liée à la taille et la diminution des lipides pendant cette période. Des échantillons ont été récoltés dans trois lacs québécois situés entre 45°02'N et 48°20'N, et ayant entre 990 et 1980 degrés-jours. Les lacs ont été visités le plus tard possible à l'automne 2002 et 2003 et le plus tôt possible au printemps 2003 et 2004. Trente-deux poissons provenant de chacun des lacs et de chacune des périodes d'échantillonnage ont été utilisés pour l'extraction des lipides, et un sous-échantillon de dix poissons a été sélectionné pour la lecture de la microstructure de l'otolithe. Un index de croissance a été mesuré en utilisant le rayon de l'otolithe à 75 jours, correspondant à la durée du stade larvaire. Les poissons des populations nordiques ont un meilleur taux de croissance et d'accumulation de lipides que ceux des populations du sud. Pour les trois lacs échantillonnés, aucune mortalité hivernale sélective liée à la taille n'a été détectée pendant le stade larvaire. L'épuisement des réserves lipidiques ne semble pas être le seul facteur responsable de la mortalité hivernale. Conséquemment, la courte saison de croissance et la sévérité de l'hiver ne semblent pas responsables des importantes fluctuations d'abondance de l'éperlan arc-en-ciel.

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INTRODUCTION GÉNÉRALE

Les populations de poissons constituent une ressource naturelle importante dans la région du Saguenay – Lac-Saint-Jean. La ouananiche (*Salmo salar*) est certainement un des poissons les plus recherchés par les pêcheurs sportifs québécois et représente donc des retombées économiques très importantes pour l'industrie du tourisme. Cependant, depuis quelques années, l'abondance et la croissance de ce saumon d'eau douce ont varié drastiquement (MRNF, données non publiées). Plusieurs efforts ont été accomplis dans le but de rétablir la population de ce poisson, mais n'ont pas donné les résultats escomptés. Depuis 1995, un programme de recherche a été mis en place et vise à mieux comprendre la biologie de ce saumon d'eau douce afin d'assurer la conservation des populations du lac Saint-Jean. Plusieurs études démontrent que la ouananiche se nourrit principalement d'éperlans arc-en-ciel (*Osmerus mordax*) (Mahy 1975, Desjardins 1989, Nadon 1991, Lefebvre 2003). Cette grande sélectivité désavantage la ouananiche, puisqu'elle dépend en bonne partie du succès de recrutement de l'éperlan arc-en-ciel pour se nourrir. Il est maintenant établi que les fluctuations de l'abondance de l'éperlan arc-en-ciel ont une incidence directe sur la croissance et la mortalité de la ouananiche du lac Saint-Jean (Legault, données non publiées). Afin de garantir le retour et la pérennité de ces populations, il est primordial de mieux comprendre les facteurs qui affectent la survie de l'éperlan.

L'éperlan arc-en-ciel est retrouvé sur la côte est de l'Amérique du Nord (Lachance 1995). Il est généralement anadrome, vivant en mer et retournant en rivière pour frayer. Par contre, plusieurs populations vivent en eaux douces exclusivement (Bernatchez et Giroux 2000). Au lac Saint-Jean, à 48°45'N de latitude, l'éperlan est près de la limite nord de sa distribution en eaux douces au Québec (Delisle et Veilleux 1969). Ces informations laissent croire que les facteurs climatiques pourraient être en partie responsables des variations d'abondance que l'on observe au niveau des populations au lac Saint-Jean.

Chez de nombreuses espèces de poissons, la survie des juvéniles tend à être plus faible et plus variable comparativement aux autres stades de vie (Mion et al. 1998). La mortalité hivernale a été identifiée comme étant le facteur le plus important pour la régulation du recrutement des espèces d'eaux douces tempérées (Miranda et Hubbard 1994a, Henderson et al. 1988). Pendant l'hiver, l'alimentation est limitée par les températures froides et la nourriture qui devient rare (Keast 1968, Johnson et Evans 1996). À cette période, les poissons dépendent uniquement de leurs réserves d'énergie sous forme de lipides pour répondre à leurs besoins métaboliques de base (Johnson et Evans 1996). Il s'agit donc d'une période critique pour les jeunes de l'année.

Il est aussi courant d'affirmer que la taille des individus pendant les stades larvaires et juvéniles est un déterminant majeur de la survie (Sogard 1997). Les réserves de lipides sont constituées par les poissons au printemps et à l'été. Par contre, les jeunes de l'année qui éclosent au début de l'été, comme c'est le cas pour l'éperlan arc-en-ciel, ont une période beaucoup plus courte pour accumuler des lipides (Foy et Paul 1999). Pour les jeunes poissons de l'année, on observe des individus de tailles différentes, reflétant la croissance de ceux-ci. Ces poissons ont des proportions similaires de réserves lipidiques par rapport à leur taille. Par contre, les poissons de petite taille ont proportionnellement un métabolisme standard plus élevé que les individus de plus grande taille, ce qui provoque un épuisement des réserves énergétiques plus rapidement chez les premiers (Miranda et Hubbard 1994a). Ainsi, pour les poissons qui ne s'alimentent pas pendant l'hiver, la relation entre la longueur du poisson et la quantité d'énergie emmagasinée à la fin de la première saison de croissance pourrait déterminer si le poisson peut survivre à la période hivernale. Plus un poisson aura atteint une grande taille et des réserves lipidiques importantes au début de son premier hiver, plus il aura de chances d'y survivre (Thompson et al. 1991). D'ailleurs, la perte d'énergie métabolique est la cause la plus souvent citée comme étant responsable de la mortalité liée à la taille (Oliver et al. 1979; Post et Evans 1989; Thompson et al. 1991). À la lumière de ces informations, il est essentiel que la taille des poissons et leurs réserves énergétiques soient considérées dans l'évaluation du taux de survie du stade juvénile.

Les variations latitudinales peuvent avoir un effet important sur la croissance et la survie des jeunes poissons. En 1990, Conover a démontré que l'hypothèse de la variation contre-gradient pourrait être étendue à plusieurs espèces. Cette hypothèse provient du fait qu'une diminution de la longueur de la saison de croissance d'un facteur de 2 ou 3, ne provoque pas la même diminution de taille des poissons à la fin de cette même période.

Ainsi, la taille des poissons peut être indépendante de la longueur de leur première saison de croissance. Non seulement la saison de croissance est plus courte au nord, mais l'hiver y est également plus long, plus sévère. L'hiver peut être une force de sélection importante, où les individus qui croissent plus rapidement pendant leur premier été, ont plus de chances de survivre (Fullerton et al. 2000). Néanmoins, l'influence de la taille pour la mortalité hivernale peut différer selon les populations d'une même espèce (Miranda et Hubbard 1994a).

La sévérité de l'hiver pourrait donc être un des facteurs responsables des variations d'abondance que l'on observe au niveau des populations d'éperlans du lac Saint-Jean. Ainsi, le fait de connaître les conditions infligeant un taux de mortalité hivernale élevé aux éperlans arc-en-ciel juvéniles permettrait de mieux prévoir leur recrutement. De telles informations sont essentielles lorsque l'on vise une meilleure gestion des populations de ouananiches, qui dépendent directement de l'abondance de ce poisson fourrage. Dans le contexte actuel des changements climatiques, il est également intéressant de mieux comprendre les différences physiologiques des populations de poissons à différentes latitudes. Dans l'éventualité où les limites de distribution de plusieurs espèces pourraient être modifiées, la connaissance des adaptations à la saisonnalité permettront sans doute de mieux gérer les changements.

L'objectif principal de cette étude est d'évaluer l'effet des facteurs climatiques sur le recrutement des éperlans arc-en-ciel juvéniles d'eau douce. Il est possible de supposer que les éperlans arc-en-ciel juvéniles auront une taille indépendante de la latitude, selon l'hypothèse de la variation contre-gradient. Les hivers plus longs au nord pourraient également induire de la mortalité sélective liée à la taille.

OVERWINTER MORTALITY OF FRESH WATER RAINBOW SMELT

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1. ABSTRACT

Rainbow smelt (*Osmerus mordax*) is an important forage fish for many predators such as salmonids. Consequently, inter-annual variability of smelt population is a key factor affecting the production of many game fish. Inter-annual fluctuations of freshwater rainbow smelt populations may be driven by climatic factors, especially at their northern distributional limits. Our objective was to evaluate the effect of climatic factors on recruitment of young-of-the-year (YOY) freshwater rainbow smelt, with evaluation of the effect of length of growing season on lipid accumulation and length of fish, and the effect of winter severity on lipid depletion and size-selective overwinter mortality. Samples were collected in three lakes located between 45°02'N and 48°20'N in the province of Quebec with annual degree-days ranging from 990 to 1980. Lakes were sampled in late autumn 2002 and 2003 and in early spring 2003 and 2004. Thirty fish from each lake and from each sampling period were used for lipid extraction and a sub-sample of ten fish were selected for otolith microstructure examination. Growth during larval stage was measured using the otolith radius at age 75 d. Fish of northern populations have a better growth and lipid accumulation rate than fish of southern populations. For the three sampled lakes, no size-selective overwinter mortality was detected for the larval stage. Lipid exhaustion does not seem to be the sole factor affecting overwinter mortality. Consequently, shorter growing season and severe winter at northern latitudes are not likely responsible for the important fluctuations in rainbow smelt abundance.

2. INTRODUCTION

Surviving a first winter is an important factor for the recruitment of freshwater fish (Oliver et al. 1979; Adams et al. 1982; Henderson et al. 1988; Post and Evans 1989; Miranda and Hubbard 1994a; Ludsin and DeVries 1997; Fullerton et al. 2000). During winter, feeding is reduced by cold temperatures and food scarcity (Keast 1968; Johnson and Evans 1996). To meet metabolic requirements during fasting period, such as winter, fish need lipids, their major source of energy reserves. (Shul'man 1960; Johnson and Evans 1996). Young-of-the-year (YOY) fish are particularly subject to overwinter mortality due to energy depletion (Post and Evans 1989). They have a time constraint for somatic growth and lipid acquisition, because storage and utilization of energy reserves are closely linked to body size (Schultz and Conover 1997).

Many authors have demonstrated that a major cause of size-selective overwinter mortality is starvation of smaller individuals, favouring larger individuals of the population (Oliver et al. 1979; Henderson et al. 1988; Post and Evans 1989). It is also recognized that larger fish emerge from winter in better energetic condition (Cargnelli and Gross 1997). Smaller fish are less tolerant to starvation in contrast with larger fish having more energy reserves, in the form of lipids, and a lower metabolic rate (Post 1990). If mortality is more important for smaller than larger fish during winter, the size distribution at the end of the first growing season can be a major determinant for the recruitment (Gutreuter and Anderson 1985).

In 1990, Conover showed evidence that countergradient variation in growth rate can be very widespread. This hypothesis has been suggested after the observation of a variety of temperate fish species. The duration of the first growing season can declined by a factor of 2 or 3, but their body size at the end of the first growing season did not decline with the same factor. This suggests that length of fish can be independent of the length of the growing season (Conover and Present 1990). In spite of a shorter growing season, fish in populations of northern latitudes may have a better growth rate than fish of southern populations. This hypothesis has been supported for many species in saltwater such as Atlantic silverside (*Menidia menidia*) (Conover and Present 1990), Arctic charr (*Salvelinus alpinus*) (DeLabbio et al. 1990; Torrissen and Barnung 1991), mummichog (*Fundulus heteroclitus*) (Schultz et al. 1996), striped bass (*Roccus saxatilis*) (Conover et al. 1997) and Atlantic halibut (*Hippoglossus hippoglossus*) (Jonassen et al. 2000). The different capacity of growth between latitudes have been studied for only few freshwater species, and the countergradient variation in growth rate have been observed only for largemouth bass (*Micropterus salmoides*) (Williamson and Carmichael 1990), lake sturgeon (*Acipenser fulvescens*) (Power and McKinley 1997), and emerald shiners (*Notropis atherinoides*) (Pegg and Pierce 2001).

At northern latitudes, a short growing season implies also a long, or more severe winter. In the study of Fullerton et al. (2000) on the largemouth bass, results indicated that increasing winter severity increase also energy depletion. For many fish species, low lipid content (in many smaller fish) means a lower ability to survive to prolonged or severe winter (Cunjak and Power 1987; Johnson and Evans 1990; Sogard and Olla 2000).

Rainbow smelt (*Osmerus mordax*) spawn early in spring, just after ice breaking. Hatching take place 2 or 3 weeks after, depending on water temperature. This species has a short life cycle, being able to reproduce at 2 years old (Scott and Crossman 1974). Rainbow smelt is an important forage fish for a lot of predators, like salmonid species (Scott and Crossman 1974, Kircheis and Stanley 1981; Kirn and LaBar 1996). However, the abundance of this species show important natural inter-annual fluctuations (Kircheis and Stanley 1981) affecting the production of salmonids and others game fish. For example, abundance of young-of-the-year (YOY) rainbow smelt decreased from 29,4 to 0,2 individuals by 1000 m^{-3} between 1996 and 2001 in lake Saint-Jean (unpublished data, Michel Legault, Ministère des Ressources Naturelles et de la Faune du Québec). Many biotic (predation, diet, parasitism) and abiotic (climate, hydrology) factors can be responsible for these important fluctuations. Among them, the climatic factors may play an important role, particularly near the northern distributional limits of the species. In the province of Québec, rainbow smelt have been found at the southern border of the province (45° of latitude), and as north as 50° of latitude (Delisle and Veilleux 1969).

The objective of this study is to evaluate the effect of climatic factors on recruitment of YOY freshwater rainbow smelt, with evaluation of lipid accumulation and growth. It is possible to suppose that length of young rainbow smelt is independent of latitude, in accordance with the hypothesis of the countergradient variation. Longer winter at northern latitude can also induce size-selective mortality.

3. MATERIALS AND METHODS

3.1 Study sites

Lake Memphrémagog (Memphré), lake Kénogami and lake Jacques-Cartier (J-Cartier) are located in the province of Québec. They have different latitudes and altitudes (Table 1) in order to work on different lengths of growing season and winter. The number of freezing-days was calculated as the number of days where the mean air temperature is below 0°C. The number of degree-days was calculated as the sum of all degrees above 5°C. All temperature records were provided by the National Climate Archive of Environment Canada. There is a difference of approximately 3° of latitude between the southern lake (Memphrémagog) and the northern lake (Kénogami). Lake Jacques-Cartier is elevated in altitude (791,2 m), so fish in this lake experience shorter growing season and longer winter than fish in the northern lake (Kénogami). The length of the growing season increase by a factor of 2 between lake Jacques-Cartier and lake Memphrémagog and a difference of 65 freezing-days exist between these two lakes during the cold season.

Table 1. Geographic and climatic description of the three lakes studied.

Lake	Latitude	Longitude	Altitude	Season	Freezing-days	Degree-days
Memphrémagog	45°7'N	72°13'W	266,7 m	2002-2003	133	1785
				2003-2004	113	1982
Kénogami	48°25'N	71°9'W	127,8 m	2003-2004	140	1587
Jacques-Cartier	47°33'N	71°13'W	791,2 m	2003-2004	178	986

The three studied lakes contain populations of rainbow smelt. These populations are naturally present in the lake Memphrémagog and Kénogami (Delisle and Veilleux 1969). In Jacques-Cartier, rainbow smelt was introduced between 1960 and 1964 (Fournier and Lépine, 1998). Stocked fish come from three locations: 22 400 smelt were introduced from Lake aux Sables (46°52'N, 72°21'W) between 1960 and 1962, 6 600 smelt were introduced from the lake Kénogami (48°25'N, 71°9'W) in 1962 and 1963, and 14 838 smelt were introduced from the Boyer river (46°53'N, 70°51'W) in 1963 and 1964 (unpublished data, Gaétan Fournier, SEPAQ).

3.2 Field collection

A minimum of 32 fish was sampled in each lake, for each sampling season. Fish were sampled as late as possible in autumn, after the fall turnover, and as early as possible in spring, after ice break-up. Lake Memphrémagog was sampled for two seasons (2002-2003 and 2003-2004) and the two others lakes for only one season (2003-2004). The sample of lake Memphrémagog was divided in two sub-samples for the season 2002-2003, one from each part of the lake: south and north. Only the south part of the lake was sampled in 2003-2004. Sampling occurred on 29 October 2002, 7 may 2003, 21 October 2003 and 3 May 2004 in lake Memphrémagog; 14 October 2003 and 1 June 2004 in lake Kénogami; 15 October 2003 and 2 June 2004 in lake Jacques-Cartier. Sampling was made at night, in order to eliminate net avoidance by rainbow smelt. A mid-water trawl with a rigid frame and an opening of 2 m by 2 m was used for sampling. For a precise description of this trawl, see Legault (2002). Between 2 and 11 traits of this trawl were necessary to catch our 32 fish, with duration between 15 and 45 minutes for each trait. Specimens were immediately placed on ice after capture, and frozen in the next 12 hours.

3.3 Lipid extraction

Thirty-two fish were selected for lipid analysis in each lake and in each season, in proportion of the total length frequency distributions. Lipids were extracted in each fish using the method described in Schultz and Conover (1997). Briefly, each fish was thawed, and wet weight was measured. Sagittal otoliths and gut content were removed. Each fish was dehydrated in a freeze-dryer for 72 hours. The total content of lipids was extracted in petroleum ether, using a Soxhlet extractor. With a large extractor (Body I.D. × Length (mm): 105 × 300; Condenser [standard taper] Joint: 103/60), it was possible to process 12 samples at the same time. Because the size of the extractor decreased the number of cycle processing in the same time period, extraction lasted 6 hours (in comparison of 5 hours in Schultz and Conover 1997). However, this duration corresponded to the results of Dobush et al. (1985) who obtain that extraction during between 3 to 6 hours efficiently maximizes non-polar lipids while removing virtually no non-lipid material. At each step of the extraction, each sample can be discarded when an external event can affect the weight of fish. So the number of fish for each sample varies between 22 and 32 fish.

3.4 Otolith microstructure examination

Ten fish were selected for otolith microstructure examination in each lake and in each season, in proportion of the total length frequency distributions. Rainbow smelt otolith microstructures were examined using the method described in Sirois et al. (1998). Sagittal otoliths were mounted on a microscope slide with thermoplastic glue (Crystal Bond). Otoliths were polished with 1 to 5 μm grit aluminium oxide lapping film. Otolith radius at age 75 days and total radius of the otolith were measured using a light microscope at 100-400× magnification. Preliminary trials with otoliths from fish sampled in lake Jacques-Cartier, where growing season is the shorter, determined that a minimum count of 75 daily growth increments is possible for all fish. The measure of otolith radius at age 75 days was considered to represent the growth during the larval stage. Length of fish at age 75 d was back-calculated using the biological intercept method (Campana 1990). Some otoliths in the lake Jacques-Cartier were discarded from the analysis because the otoliths show artefacts. So the number of fish in the lake Jacques-Cartier sample is 14, and 20 fish for each of the 4 others samples.

3.5 Statistical analysis

A Kolomogorov-Smirnov test was performed to verify that total length frequency distributions were the same between all fish caught and fish selected for samples (lipid and otolith analysis). ANOVA was performed to compare growth rate and lipid accumulation rate, with a Tukey-Kramer *a posteriori* test. A Kolmogorov-Smirnov was also performed to compare autumn and spring total length and percent lipids distributions and also to detect size-selective mortality. For all statistical test, $\alpha=0.05$ was the level of significance.

4. RESULTS

4.1 First growing season: growth and lipid accumulation

Mean growth rate of fish during the larval stage in the two northern lakes, Jacques-Cartier and Kénogami, were significantly greater than in the three samples of the lake Memphrémagog (except during autumn between Kénogami and Memphrémagog south for the season 03-04), as shown with the results of Tukey-Kramer *a posteriori* test (Fig. 1). Fish in the two northern lakes shown a significantly higher growth rate during their first growing season (ranging between 0.51 and 0.58 mm/d) compared with fish from the southern lake (ranging between 0.39 and 0.45 mm/d).

During autumn, the mean percent lipids in fish at the end of their first growing season in the two northern lakes (Jacques-Cartier and Kénogami) are significantly greater than in the three samples of the lake Memphrémagog as shown with the results of Tukey-Kramer *a posteriori* test (Fig. 2). Fish in the two northern lakes have more than 8.17% of lipids, compared with fish from the southern lake with less than 3.66% of lipids. Fish in northern lakes have a significantly better lipid accumulation rate during their first growing season.

Fig. 1. Mean growth rate (mm/d ± SD) during the larval stage for the five samples collected in (a) autumn and (b) spring. Letters above each bar show the results of a Tukey-Kramer *a posteriori* test.

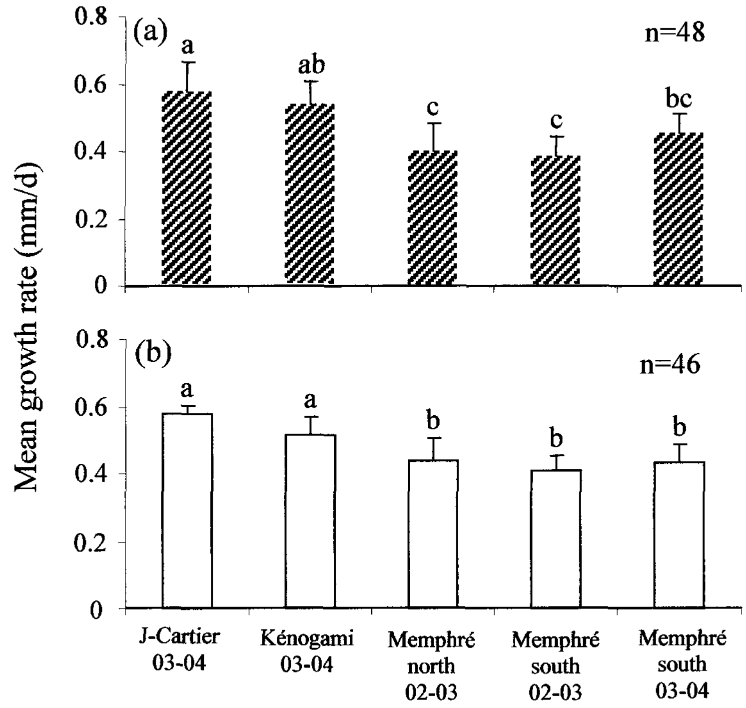
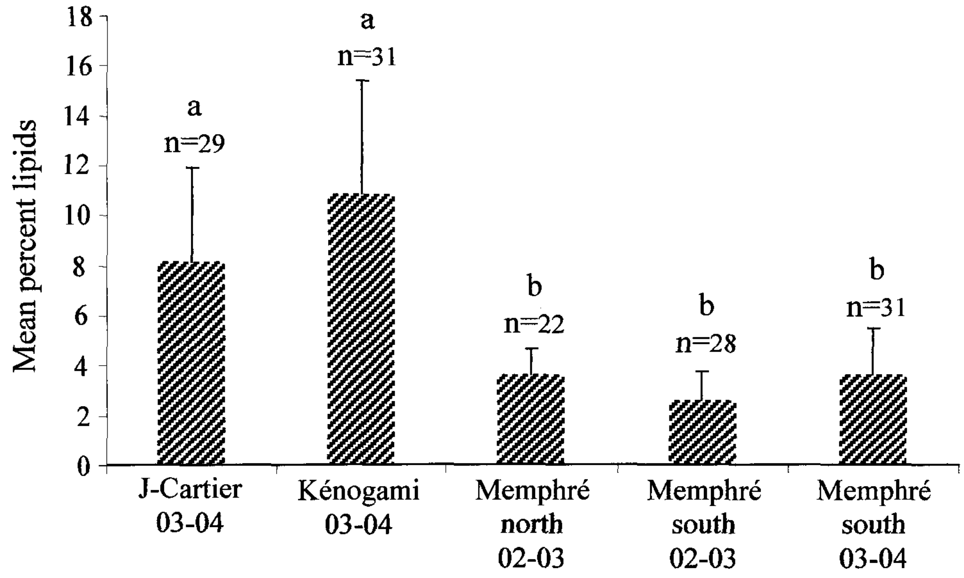


Fig. 2. Mean percent lipids (± SD) in fish of the five samples collected in autumn. Lipid percentage is calculated with dry weight. Letters above each bar show the result of a Tukey-Kramer *a posteriori* test.



Lipid accumulation for all populations is hyperallometric (slopes of total length versus lipids exceeding 3), during the two seasons (Fig. 3-4 and Table 2). During autumn, slopes of the two northern lakes (Jacques-Cartier and Kénogami) are higher (6.80 and 8.98 respectively) compared with the three samples of lake Memphrémagog (4.07, 4.59 and 4.64). The same pattern is observed during spring for slopes of lake Jacques-Cartier and Kénogami (8.57 and 6.61 respectively), compared with the three samples of lake Memphrémagog (3.09, 3.36 and 4.50 for spring slopes). Fish surviving to winter have the same pattern of hyperallometric lipid accumulation than fish from autumn samples.

Fig. 3. Relationships between total length (ln mm) and lipids (ln g) in autumn for lake (a) J-Cartier 03-04, (b) Kénogami 03-04, (c) Memphrémagog north 02-03, (d) Memphrémagog south 02-03 and (e) Memphrémagog south 03-04. Regression details are given in table 2.

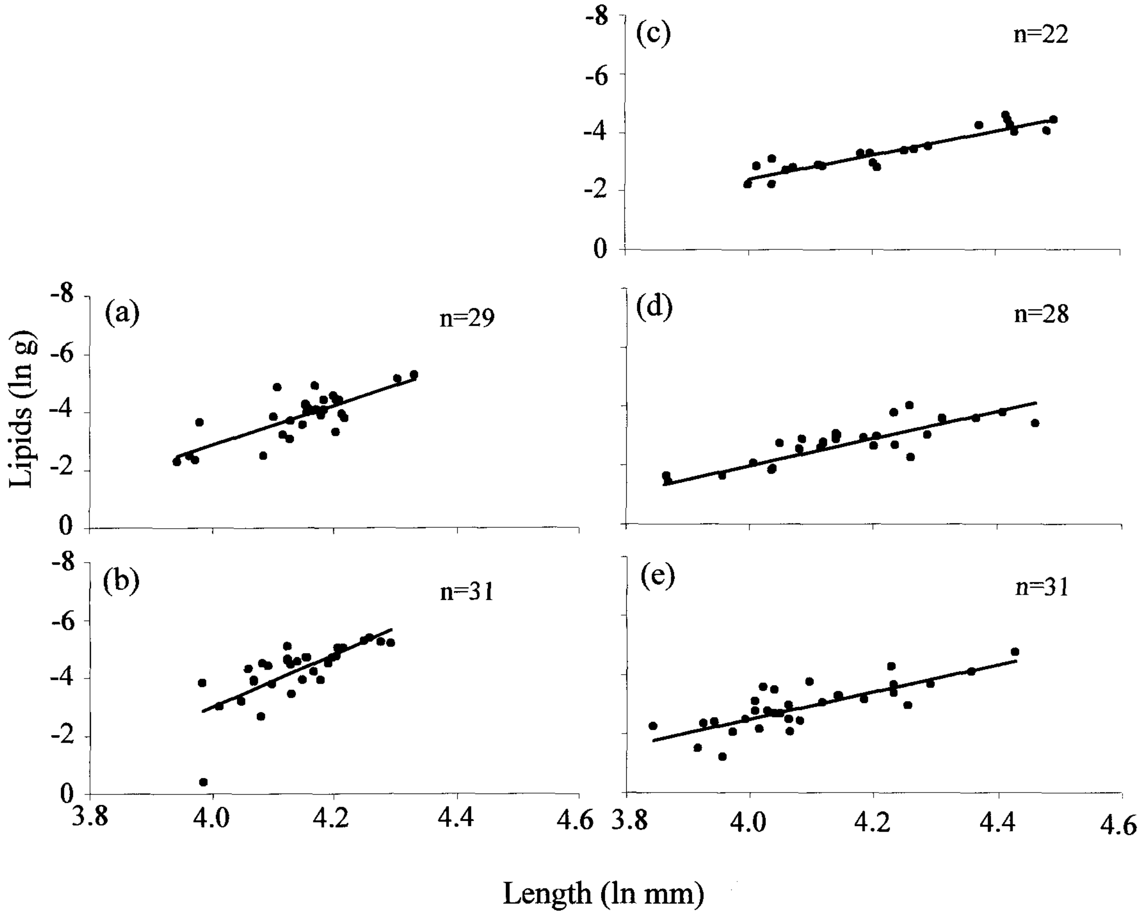


Fig. 4. Relationships between total length (ln mm) and lipids (ln g) in spring for lake (a) J-Cartier 03-04, (b) Kénogami 03-04, (c) Memphrémagog north 02-03, (d) Memphrémagog south 02-03 and (e) Memphrémagog south 03-04. Regression details are given in table 2.

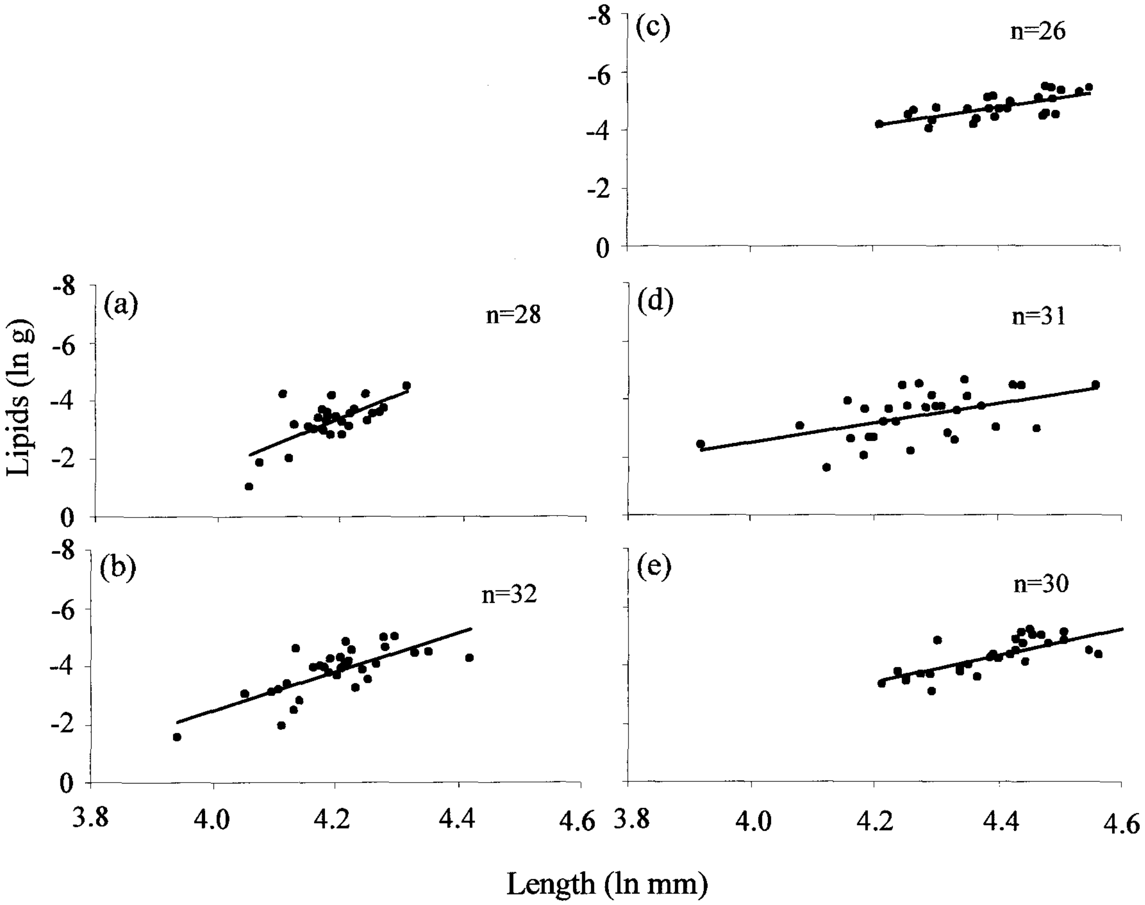


Table 2. Slopes, intercepts and r^2 of the regression between total length (ln mm) and lipids (ln g) shown in fig. 3 and 4 for fish collected in autumn and spring.

	Season	Slope	Intercept	r^2
J-Cartier 03-04	autumn	6.80	-32.38	0.61
	spring	8.57	-40.66	0.47
Kénogami 03-04	autumn	8.98	-40.93	0.53
	spring	6.61	-31.99	0.53
Memphré north 02-03	autumn	4.07	-21.86	0.86
	spring	3.09	-16.88	0.45
Memphré south 02-03	autumn	4.59	-24.39	0.68
	spring	3.36	-18.98	0.26
Memphré south 03-04	autumn	4.64	-24.07	0.63
	spring	4.50	-23.50	0.57

4.2 Winter severity: size-selective mortality

Total length frequency distributions were different between autumn and spring for the five samples (Fig. 5). In the two northern lakes, the total length frequency distributions showed fish measuring between 40 to 80 mm during autumn, compared with fish measuring between 50 to 85 mm during spring. In lake Memphrémagog, total length frequency distributions during spring showed an increase of 10 mm with the total length frequency distributions of autumn. A Kolmogorov-Smirnov test confirmed that total length frequency distributions are significantly different between the two seasons (Jacques-Cartier 03-04 $p=0.0042$; Kénogami 03-04 $p<0.0001$; Memphrémagog north 02-03 $p=0.0139$; Memphrémagog south 02-03 $p<0.0001$; Memphrémagog south 03-04 $p<0.0001$). Fish caught in spring were significantly longer than fish sampled in autumn.

There was an overlap of the autumn and spring back-calculated length frequency distributions of fish at the end of the larval stage for the five samples (Fig. 6). Fish from autumn sample in the northern lakes measure between 40 and 65 mm after 75 days of growth, and fish from the spring sample measure between 35 and 55 mm after the same growth period. In the southern lake, fish from autumn sample measure between 25 and 50 mm, and fish from the spring sample measure between 30 and 55 mm. A Kolmogorov-Smirnov test confirmed that back-calculated length frequency distributions at 75 d were not significantly different between the smelt captured in autumn and in spring (Jacques-Cartier 03-04 $p=0.1373$; Kénogami 03-04 $p=0.4038$; Memphrémagog north 02-03 $p=0.1642$; Memphrémagog south 02-03 $p=0.4038$; Memphrémagog south 03-04 $p>0.9999$).

Fig. 5. Total length frequency distributions of all fish captured (shown in percent of the sample) in each of the five samples: (a) J-Cartier 03-04, (b) Kénogami 03-04, (c) Memphrémagog north 02-03, (d) Memphrémagog south 02-03, (e) Memphrémagog south 03-04, during autumn (striped bars) and during spring (shaded bars).

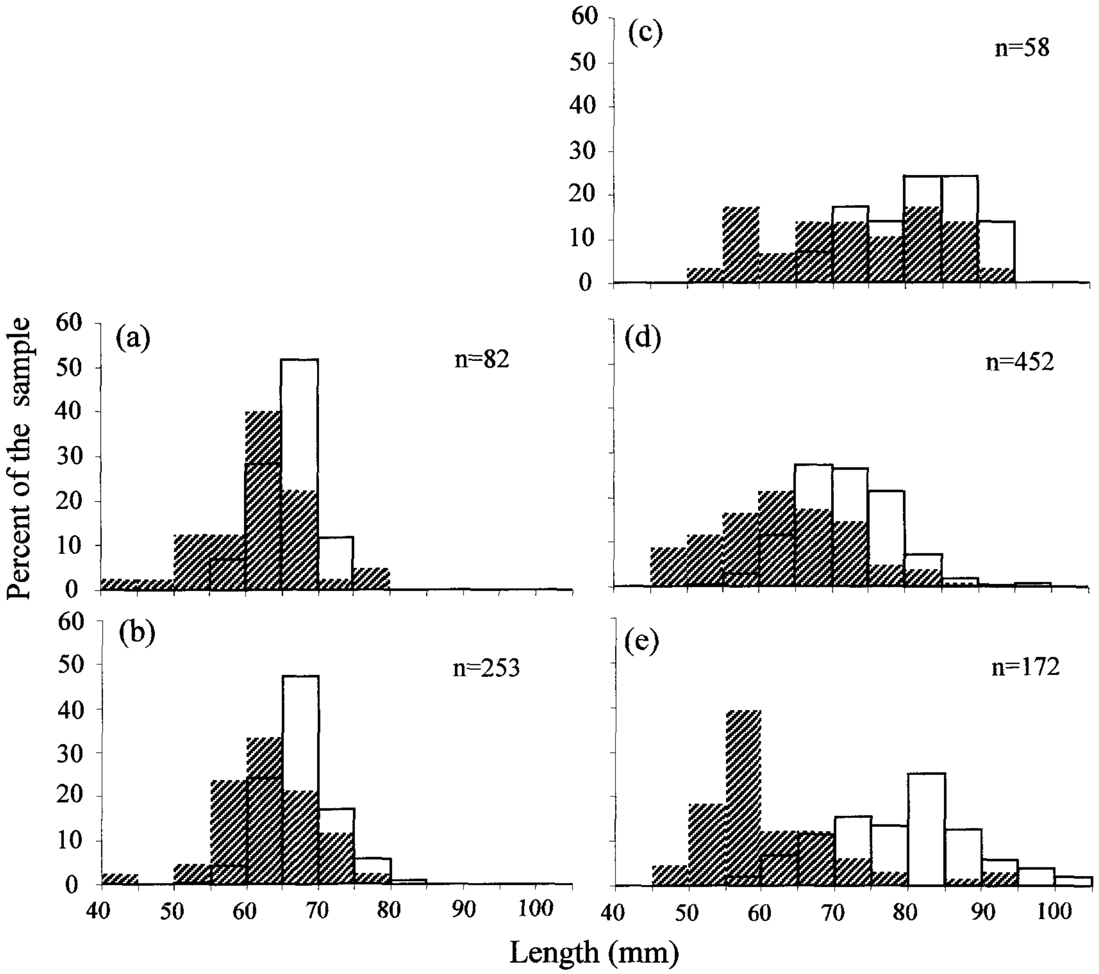
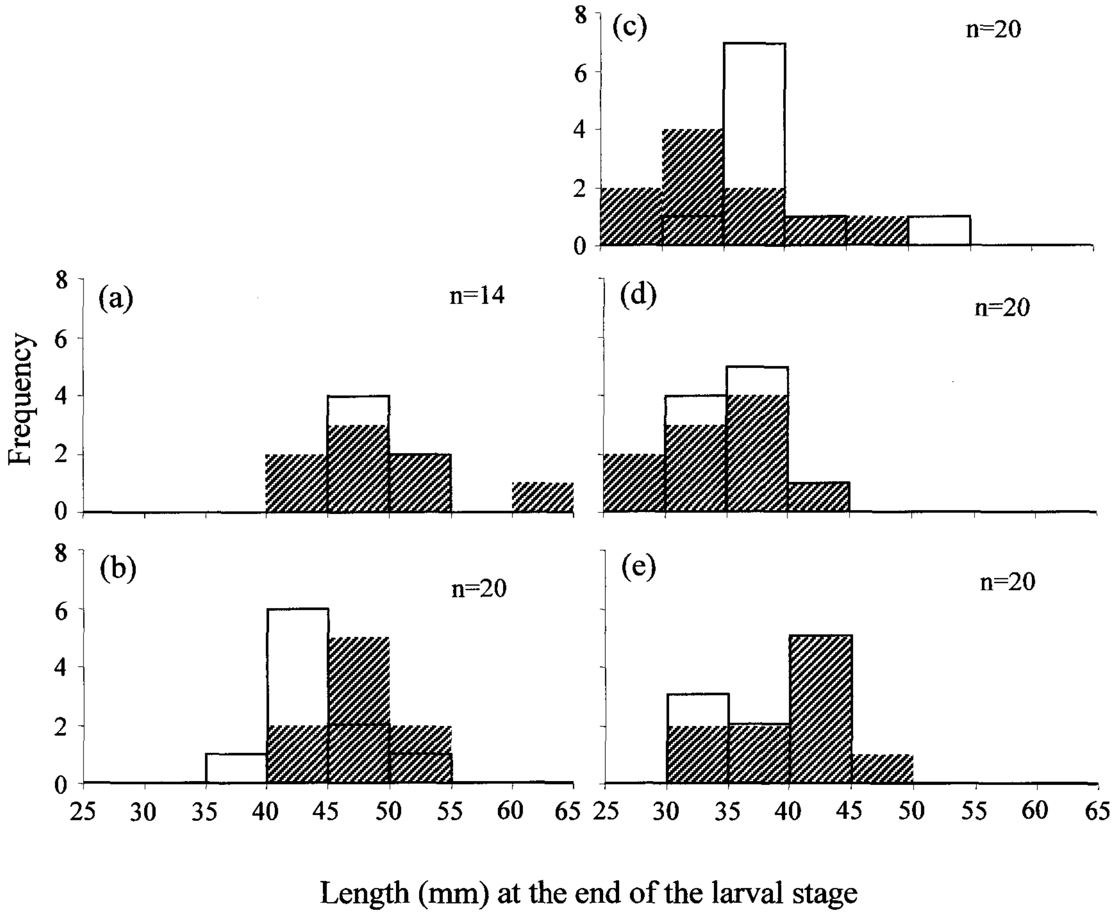
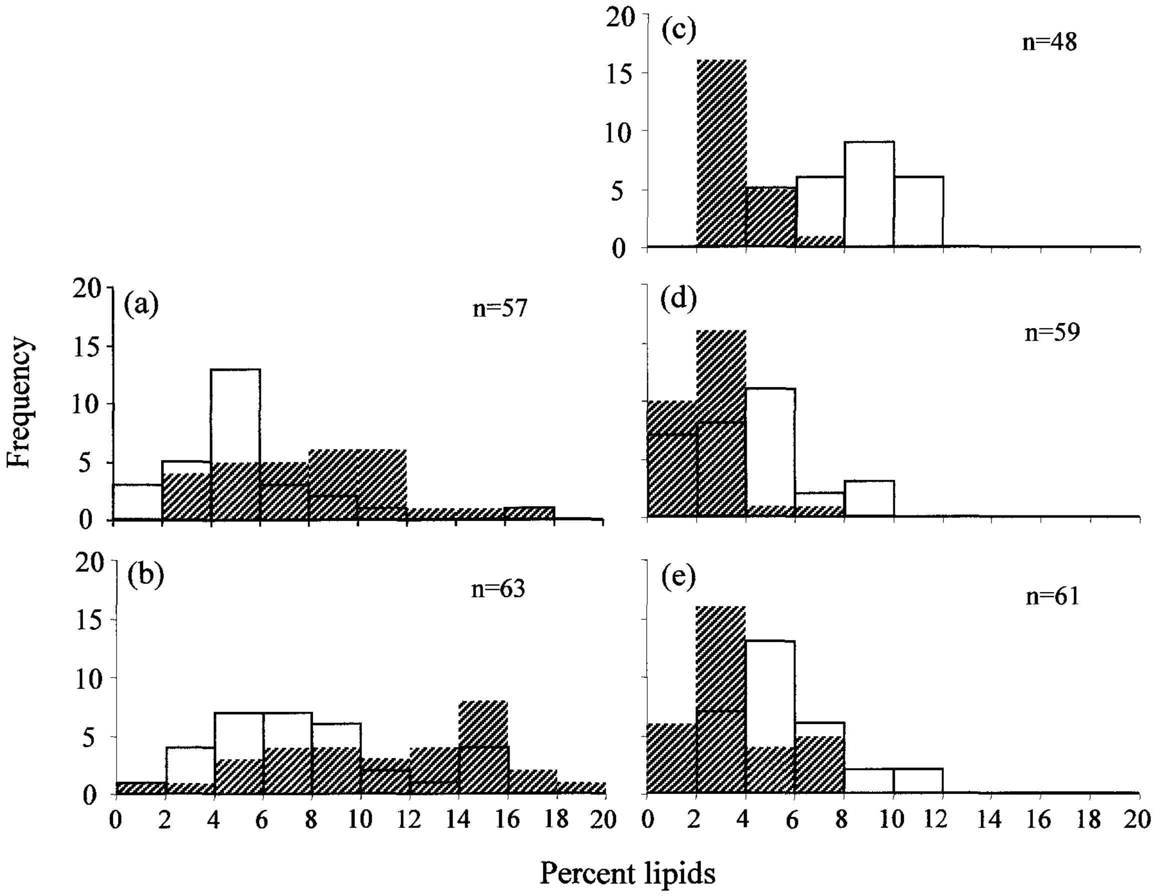


Fig. 6. Back-calculated length frequency distributions of fish for lake: (a) J-Cartier 03-04, (b) Kénogami 03-04, (c) Memphrémagog north 02-03, (d) Memphrémagog south 02-03, (e) Memphrémagog south 03-04, during autumn (striped bars) and spring (shaded bars).



Different patterns of lipid frequency distributions were observed between autumn and spring for the five samples (fig. 7). A Kolmogorov-Smirnov test confirm that lipid frequency distributions were significantly different between the two seasons (Jacques-Cartier 03-04 p=0.0030; Kénogami 03-04 p=0.0139; Memphrémagog north 02-03 p<0.0001; Memphrémagog south 02-03 p=0.0059; Memphrémagog south 03-04 p=0.0002). During winter, the percentage of lipids in fish from lakes Jacques-Cartier and Kénogami depleted significantly. During this same period, the percentage of lipids in fish from lake Memphrémagog increased significantly. Fish caught during spring have less lipids compared with fish caught during autumn in lakes Jacques-Cartier and Kénogami, but inversely, have more lipids in the lake Memphrémagog.

Fig. 7. Percent lipids frequency distributions of the five samples: (a) J-Cartier 03-04, (b) Kénogami 03-04, (c) Memphrémagog north 02-03, (d) Memphrémagog south 02-03, (e) Memphrémagog south 03-04, during autumn (striped bars) and during spring (shaded bars). Lipid percentages were calculated using fish dry weights.



5. DISCUSSION

5.1 First growing season: growth and lipid accumulation

Freshwater rainbow smelt showed significant differences in growth rate during their first growing season according to the latitude, inversely related to the length of the growing season (Fig. 1). In accordance with Conover 1990, the hypothesis of the countergradient variation can also be applied to the freshwater smelt such as the largemouth bass (Williamson and Carmichael 1990), the lake sturgeon (Power and McKinley 1997), and the emerald shiners (Pegg and Pierce 2001). At northern latitude, when growing season is short, high growth rates were favoured (Conover and Schultz 1995). The hypothesis was supported by larval growth rate as revealed by otolith microstructure. Fish at northern latitude have a compensatory better growth rate to achieve a minimal size at the end of their first growing season (Fig. 1). The differences of latitude, length of growing season and winter severity are probably agents of selection to increase growth rate (Henderson et al. 1988, Post and Evans 1989, Conover 1992, Schultz and Conover 1997, Schultz et al. 1998). An experimental approach will be able to confirm that this difference in growth rate is an adaptive response to evolution, provoked by these agents of selection.

Fish at northern latitude experience severe winter conditions and accumulate more fat than those inhabiting warmer environments. In general, fish for which food is available throughout the year accumulate considerably less fat than those which go without food for a long period (Shul'man 1960). According to this affirmation, fish at northern latitudes (lake Jacques-Cartier and Kénogami) accumulated significantly more lipids than fish at southern latitude (lake Memphrémagog), in spite of a shorter growing season (Fig. 2). It is also in accordance with the results of Schultz and Conover (1997), showing a lipid accumulation rate varying latitudinally: northern populations accumulate fat more rapidly than fish in southern populations.

Hyperallometry in energy reserves appears to be common among fish living in seasonal environments (Shuter and Post 1990, Larson 1991, Schultz and Conover 1997). This way of accumulating lipids means that individuals with a better growth rate store disproportionately more lipids (Schultz and Conover 1997). Our results suggest that hyperallometry is common for freshwater rainbow smelt, but also more important for fish of northern populations (Fig. 3-4, Table 2). Growing rapidly provided many advantages to these fish. For example, high lipid reserves in larger fish may contribute to their relatively high survival rates during periods of energy depletion, such as winter (Shuter and Post 1990). Northern fish have adapted to grow rapidly and larger fish have a higher survival because they accumulate disproportionately more lipids than smaller fish.

5.2 Winter severity: size-selective mortality

Fish caught during spring are significantly longer than fish sampled in autumn for the five samples (Fig. 5). Two assumptions are possible to explain this observation. First, fish are able to feed during winter, at least during an important part of the season. This result is inconsistent with the results of Foltz and Norden (1977) showing that smelt fed little during winter in the lake Michigan. Without discarding the possibility to have an important variation between different lakes, it is surprising to observe this variation in locations southern to the lake Memphrémagog (approximately 1° southern in latitude). However, fish in our three lakes, can be able to feed for a short period just after our autumn sampling, and just before our spring sampling. The second assumption suggests that difference of the total length frequency distributions of fish after winter is the effect of the size-selective overwinter mortality. The hypothesis of the countergradient variation suggests that adaptation of a better growth rate at higher latitude is produced by the size-selective overwinter mortality (Conover 1990, Good et al. 2001). In this case, this hypothesis suggests that size-selective mortality is more important in lake Jacques-Cartier and Kénogami than in lake Memphrémagog. But the hypothesis concerning this kind of mortality is often contradictory in the literature.

Many authors have failed to find size-selective overwinter mortality. For example, for the largemouth bass, Kohler et al. (1993) and Toneys and Coble (1979) did not found evidence of size-related winter mortality in Oklahoma, Illinois and Wisconsin lakes and reservoirs. Also, Jackson and Noble (1999) had not found any total length frequency difference between one year fish catch during spring, and fish catch during the previous autumn. Inversely, size-selective overwinter mortality have been demonstrated for a lot of species, and play a fundamental role in regulating recruitment of one year striped bass in

Hudson river (Hurst and Conover 1998). Chaput and Robichaud (1995) observed size-related overwinter mortality for YOY striped bass; Post and Evans (1989) and Toneys and Coble (1980) have the same results for smaller yellow perch (*Perca flavescens*), and Oliver et al. (1979) for smallmouth bass (*Micropterus dolomieui*). Also, Cargnelli and Gross (1996) found that overwinter survival of large YOY bluegill (*Lepomis macrochirus*) was 231% higher than overwinter survival of fish comparatively smaller at the end of their first summer of life.

Our study does not detect differential growth during the larval stage that can induce size-selective overwinter mortality (Fig. 6). This kind of mortality can be possible, but can be induced in the last days of the growing season. This is particularly true in the lake Memphrémagog, where the number of degree-days is twice the length of the growing season of the lake Jacques-Cartier. Hence, growth during autumn can be decisive for the size-selective mortality, particularly in the lake Memphrémagog. This is inconsistent with Conover (1990), but in accordance with Garvey et al. (1998) suggesting that survival of small age-0 largemouth bass comparing to large counterparts may generally increase with latitude. Predation and energy depletion might be important for size-selective mortality because mild winter at south can extend the period of predation risk (Miranda and Hubbard 1994b, Garvey et al. 1998). Also, this kind of mortality can be dependent of year as shown in the results of Hurst and Conover (1998). Size-selective overwinter mortality can be important only in particular conditions, and were not observed in the two years of our sampling.

Overwinter mortality caused by starvation is a key factor to delimit the northern distributional limit of many species. Shuter and Post (1990) suggest that the northern distributional limit of 11 families and 25 genera out of the 24 families of fish found in Canadian waters may be shaped by overwinter starvation mortality of YOY. In the present study, percent lipids in fish at northern latitudes (near the rainbow smelt northern distributional limit) depleted significantly during winter. The level of lipids in fish from two northern lakes after winter depletion is not a critic situation, because the percent lipids of fish in the lake Memphrémagog during autumn is always at a lower level (Fig. 7). The possibility of overwinter mortality caused by energy exhaustion is not discarded. However, this kind of mortality affects probably a small part of the population in these northern lakes. A great proportion of fish at these latitudes are well adapted with their hyperallometric lipid accumulation compared to southern fish. They accumulate a sufficient amount of lipids before winter to survive to this period of energy depletion.

Lipids are the most important energy reserves in fish during fasting, such as winter (Shul'man 1960, Love 1970), even though they deplete during this period (Oliver et al. 1979; Miranda and Hubbard 1994a). However, in our study, the percent of lipids had increased in fish between autumn and spring in the lake Memphrémagog (Fig. 7). These results can be explained by the same two assumptions discussed previously: fish in this lake can feed during winter, and fish can experience strong size-selective overwinter mortality. It is difficult to conclude on these two possible assumptions without further investigations.

However, our results suggest that size-selective mortality is likely to occur in lake Memphrémagog, where fish show slow growth and low lipid accumulation. The difference in winter severity could induce strong size-selective mortality in particular conditions. Inversely, size-selective mortality is less likely to occur at northern latitudes, where fish have developed adaptations to longer winter, with high growth and lipid accumulation rates.

All results in this study detect no significant difference between the two northern lakes, despite their different climatic conditions (38 freezing-days and 601 degree-days). This result can be attributed to diverse factors, like parasitism, diet and predation. All of these factors should be investigated for a better understanding of the dynamics of each lake. However, it is important to remember that rainbow smelt in lake Jacques-Cartier have been introduced recently, between 1960 and 1964 (Fournier and Lépine 1998). If the adaptive response to evolution is the best hypothesis to explain the countergradient variation in growth rate and lipid accumulation, the adaptation of rainbow smelt in lake Jacques-Cartier is incomplete.

In spite of a shorter growing season in northern lakes, young rainbow smelt have a higher growth rate, and a better lipid accumulation rate in their first growing season than their southern counterparts. These results can be an adaptive response to evolution, but a laboratory experience is necessary to support this hypothesis. This higher growth rate does not seem to be controlled by the size-selective overwinter mortality, as shown by the back-calculated length frequency distributions at the end of the larval stage. An analysis of the back-calculated length of fish in the lake Memphrémagog later in the season, and a periodic winter sampling (to quantify feeding during winter), can clarify many possibilities mentioned in the discussion. This study clearly demonstrated an important adaptation of northern populations to seasonality. No evidence of size-selective overwinter mortality has been found, and the starvation can not be the single factor affecting this kind of mortality. Consequently, shorter growing season and severe winter at northern latitudes are not likely responsible for the important fluctuations in rainbow smelt abundance.

6. ACKNOWLEDGMENTS

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CONCLUSION GÉNÉRALE

Les résultats obtenus lors de cette étude permettent d'affirmer qu'il existe une adaptation des jeunes éperlans aux conditions prévalant près de la limite nord de leur distribution. Malgré la saison de croissance plus courte, les jeunes éperlans ont un meilleur taux de croissance au nord, leur permettant d'atteindre une taille minimale pour survivre à l'hiver. Le taux d'accumulation de lipides de ces mêmes poissons est également meilleur au nord, leur permettant d'accumuler plus de lipides que les poissons du sud. Ils sont ainsi capable de survivre aux hivers plus longs et plus rigoureux des latitudes élevées.

Les résultats concernant la longueur des poissons indiquent que les poissons capturés au printemps sont plus longs que ceux capturés à l'automne. Il est possible de poser deux hypothèses pour expliquer ce phénomène. Premièrement, les poissons pourraient avoir une alimentation active pendant une partie de l'hiver ou du moins, après notre échantillonnage automnal, et avant notre échantillonnage printanier. La seconde hypothèse concerne la mortalité sélective liée à la taille. Il a été impossible de détecter dans aucun échantillon ce type de mortalité à la fin de la phase larvaire. Il pourrait donc être intéressant de vérifier la présence de ce phénomène après cette période, soit pendant la croissance automnale. Cette évaluation serait particulièrement intéressante pour le lac Memphrémagog, où la saison de croissance est beaucoup plus longue que dans les deux autres lacs.

La mortalité sélective liée à la taille n'a pas été détectée dans les trois lacs, mais cette possibilité demeure très probable dans le lac Memphrémagog, où les poissons ont un taux de croissance et d'accumulation de lipides faible. Ainsi, la mortalité hivernale liée à la taille pourrait se produire dans certaines conditions, comme par exemple lorsque l'hiver est particulièrement long. Inversement, ce type de mortalité est peu probable pour les populations du nord, puisqu'elles se sont adaptées aux conditions rigoureuses en adoptant un meilleur taux de croissance et d'accumulation de lipides que les populations du sud. D'ailleurs, la diminution de lipides des poissons du lac Jacques-Cartier et Kénogami ne semble pas atteindre un seuil critique, puisque le pourcentage de lipides dans ces poissons au printemps est plus élevé que celui des poissons du lac Memphrémagog à l'automne.

Il semble que les jeunes éperlans arc-en-ciel évoluant dans les lacs du nord se sont adaptés aux conditions climatiques qui y sévissent. Les résultats obtenus indiquent que la mortalité par inanition au cours de l'hiver n'est pas un facteur important régissant les fluctuations importantes d'abondance observées au lac Saint-Jean. Il est donc intéressant de souligner que la limite nord de distribution de cette espèce n'est pas appelée à changer avec le réchauffement climatique, puisque cette limite ne semble pas sculptée par les conditions climatiques.

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