

## Do benthivory and piscivory result in similar growth in walleye?

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Growth and condition of piscivorous and non-piscivorous walleye *Sander vitreus* classified on the basis of their stomach contents were compared to assess the consequences of their trophic flexibility. Piscivorous males showed a significantly higher growth trajectory than non-piscivorous ones, while there was no difference in the growth of females. No differences were found in the condition of piscivorous and non-piscivorous walleye for either sex. Trophic specialization of males, with some individuals foraging mainly on invertebrates and others including forage fishes in their diets, seems to be the most plausible explanation for the observed growth differences. The results also suggest that invertebrates are an important component in walleye diet throughout its ontogeny.

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Key words: backcalculation; feeding flexibility; foraging behaviour; growth models; linear mixed model; *Sander vitreus*.

### INTRODUCTION

Trophic flexibility is an important adaptive feature of the foraging behaviour of fishes (Dill, 1983). The evolution of flexible and diverse foraging tactics is expected when environmental conditions vary unpredictably and prey exhibit a wide range of antipredator defences (Godin, 1997). Generalist or opportunistic strategies should be particularly advantageous for consumers in cold temperate lakes as prey availability changes seasonally (Keast, 1979). In resource-limited habitats, feeding flexibility could lead to trophic polymorphism (*i.e.* the occurrence of forms of the same species displaying differential niche use) to avoid intraspecific competition (Robinson & Wilson, 1994; Skúlason & Smith, 1995). Although feeding plasticity is often associated with intermediate or low trophic levels (Snorrason *et al.*, 1994; Gu *et al.*, 1997; Bourke *et al.*, 1999), it can also occur in top predators (Chapman *et al.*, 1989; Vander Zanden *et al.*, 2000).

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While the timing of the onset of piscivory has been widely studied in fishes (Mittelbach & Persson, 1998; Persson & Brönmark, 2002), only a few works have considered the existence of alternative foraging strategies in the life history of piscivorous species. Pike *Esox lucius* L., for example, is often considered to be a specialist piscivore, but under some circumstances it continues to eat invertebrates as an adult (Chapman *et al.*, 1989; Beaudoin *et al.*, 1999). Although feeding flexibility has been reported for some piscivorous fishes, only a few studies have assessed its consequences on growth (Jonsson *et al.*, 1999; Blackie *et al.*, 2003).

Walleye *Sander vitreus* (Mitchill), formerly *Stizostedion vitreum* (Mitchill), is known to be a highly piscivorous species (Mittelbach & Persson, 1998), but in many lakes, individuals can feed on invertebrates during their whole ontogeny (Colby *et al.*, 1979). Because the energetic gain from feeding on a given prey is related to its profitability, individuals that maximize the profitability will feed more efficiently and have a higher fitness relative to other members of the population (Dill, 1983). For piscivorous fishes, the optimal food item should be prey fishes because of the high energy content and relatively small amount of waste (Weatherley & Gill, 1987). Therefore, piscivorous fishes usually grow faster and should have a better condition than those feeding on invertebrates (Jonsson *et al.*, 1999; Blackie *et al.*, 2003).

The objective of the present study was to compare feeding habits, growth and condition of piscivorous and non-piscivorous walleye. Assuming that stomach contents are a good index of the long-term foraging behaviour, hypotheses that piscivorous individuals exhibit higher growth and better condition than non-piscivorous ones were tested.

## MATERIALS AND METHODS

### STUDY AREA AND FISH SAMPLING

The data were collected in 2000 and in 2001 in 10 stratified headwater lakes of the Canadian Shield (lakes DF-2, DF-5, K-3 and K-8 were sampled in 2000; lakes AB-35, CSL-2, DA-4, K-1, K-2 and N-89 were sampled in 2001; Table I) located within a 47 680 km<sup>2</sup> area around Réservoir Gouin, Québec, Canada (Carignan *et al.*, 2000). The watersheds of these lakes were undisturbed and the fish communities were generally unexploited due to the limited access (all lakes were reached by aircraft). The general characteristics of the study lakes are given in Table I. All the lakes were sampled in July (except AB-35 in June and DF-2 and DF-5 in August).

Fishes were captured with experimental monofilament gillnets, 102.3 m long × 2.7 m deep, with stretched mesh panels of 20, 24, 33, 36, 50, 60, 76, 90 and 100 mm (with filament diameters of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32 and 0.32 mm, respectively). Gillnets were set perpendicular to the shore, with small and large meshes alternating from the shore among gillnets. The nets were set at regular intervals around the lake, the first being randomly located using aerial photography. The nets fished for periods of 17–19 h, always covering the periods between 1600 and 1030 hours. The fishing effort was six nets per night for lakes <50 ha, eight nets per night for lakes of 50–100 ha and 10 nets per night for lakes of 100–150 ha. For each fish caught, total length ( $L_T$ , ±1 mm) and mass ( $M$ , ±0.1 g) were noted; when possible, sex was determined by gonad examination. Opercular bone structures of walleye were removed for age determination (Babaluk *et al.*, 1993), and stomachs were removed and preserved in a 10% formalin solution for further analyses.

TABLE I. General characteristics and species composition of the study lakes

| Lake  | Surface area (km <sup>2</sup> ) | Mean depth (m) | Secchi disk depth (m) | Walleye sample size |                     | Catch per unit effort of fish community |      |      |      |      |      |      |   |     |   |
|-------|---------------------------------|----------------|-----------------------|---------------------|---------------------|---|------|------|------|------|------|------|---|-----|---|
|       |                                 |                |                       | Piscivorous (n)     | Non-piscivorous (n) | SAVI                                    | PEFL | ESLU | COCL | CACO | SECO | NOHU |   |     |   |
| AB-35 | 0.87                            | 6.4            | 4.4                   | 4                   | 5                   | 9.8                                     | 28.0 | 1.5  | —    | 2.5  | 9.8  | —    | — | —   | — |
| CSL-2 | 0.85                            | 3.1            | 2.7                   | 4                   | 8                   | 8.6                                     | 1.3  | 1.3  | 3.9  | 1.0  | —    | —    | — | 0.6 | — |
| DA-4  | 0.25                            | 3.0            | 1.1                   | 4                   | 2                   | 2.5                                     | 6.8  | 1.2  | 5.0  | 4.0  | 0.2  | —    | — | —   | — |
| DF-2  | 0.29                            | 2.9            | 3.0                   | 4                   | 6                   | 8.0                                     | 2.0  | 0.7  | 11.7 | 1.5  | —    | —    | — | 1.8 | — |
| DF-5  | 0.44                            | 3.4            | 2.6                   | 5                   | 11                  | 10.8                                    | 0.5  | 1.8  | 3.0  | —    | 0.2  | —    | — | 1.3 | — |
| K-1   | 0.32                            | 2.7            | 1.8                   | 5                   | 0                   | 3.5                                     | 4.0  | 1.7  | 0.3  | 0.2  | 2.0  | —    | — | —   | — |
| K-2   | 1.42                            | 4.3            | 1.9                   | 12                  | 22                  | 7.6                                     | 0.4  | 1.1  | 6.9  | 3.6  | 8.9  | —    | — | —   | — |
| K-3   | 0.82                            | 2.8            | 3.0                   | 1                   | 1                   | 3.6                                     | 5.6  | 3.3  | 6.1  | 1.1  | 0.5  | —    | — | 1.1 | — |
| K-8   | 0.75                            | 2.3            | 1.2                   | 6                   | 5                   | 6.5                                     | 11.4 | 1.1  | 3.9  | —    | 2.6  | —    | — | —   | — |
| N-89  | 0.67                            | 4.3            | 5.1                   | 9                   | 1                   | 4.5                                     | 4.5  | 0.4  | 11.3 | 0.4  | —    | —    | — | —   | — |

SAVI, walleye *Sander vitreus*; PEFL, yellow perch *Perca flavescens*; ESLU, pike *Esox lucius*; COCL, lake whitefish *Coregonus clupeaformis*; CACO, white sucker *Catostomus commersonii*; SECO, fallfish *Semotilus corporalis*; NOHU, spottail shiner *Notropis hudsonius*.

## DIET ANALYSIS

Prey found in walleye stomachs were classified into six functional categories: fishes, zoobenthos, amphipods, dipteran pupae, swimming insects and terrestrial insects. Each prey category was dried for 12 h at 60° C and then weighed ( $\pm 0.1$  mg). The numbers of individuals feeding on prey fishes only, invertebrates only and on a combination of these two categories ('mixed diet') were used to estimate food specialization in the study fish. The per cent  $M$  of fish in stomach contents was computed to determine the size–piscivory relationships of male and female walleye. Fish were classified as piscivorous or non-piscivorous for growth and fish condition analyses based on the presence or absence of fishes in their stomach. This classification was based on the assumption that a walleye having a prey fish in its stomach (with or without invertebrates) exhibited piscivorous behaviour. This assumption does not rule out the possibility that a walleye having only invertebrates in its stomach is not a piscivore. In this context, it was considered that any significant difference in growth between piscivores and non-piscivores would be conservative. Walleye with empty stomachs were not considered in the analysis.

## WALLEYE AGE AND GROWTH

Pairs of opercular bones were placed in a solution of soapy water overnight and then cleaned and dried before age determination. The bone structure was submerged in immersion oil and observed at  $\times 10$  magnification on a black background. Age determination was made by counting true annuli according to Babaluk *et al.* (1993). Two independent age readings were made by the same reader. When the results were different, two additional readings were made; if there was still disagreement, the sample was rejected. The successive annual growth increments were measured to the nearest 0.01 mm using a calibrated graticule mounted on a dissecting microscope. The  $L_T$  at previous ages were backcalculated following two proportional backcalculation methods: the scale-proportional hypothesis (SPH) and the body-proportional hypothesis (BPH) (Francis, 1990). A  $L_T$  and opercular length relationship was built for piscivorous and non-piscivorous walleye. Because the  $r^2$  values of these relationships were  $>0.90$ , no substantial differences were found in fish  $L_T$  between the backcalculation methods (SPH *v.* BPH) (Pierce *et al.*, 1996). In this study, only the results computed with the SPH method are presented.

## STATISTICAL ANALYSIS

### *Fish growth*

The slopes and elevations of growth curves were compared among piscivorous and non-piscivorous walleye using linear mixed models with repeated measures (MIXED procedure; SAS, 2001), which is a statistical framework conceived to model designs that include both fixed and random effects. Furthermore, linear mixed modelling is appropriate to handle repeated measures that are not independent, like backcalculated  $L_T$  from the same fish (Littell *et al.*, 1996). Because fish growth is generally not linear, polynomial functions were used to model the growth trajectory (*i.e.* quadratic and cubic terms). Age was thus treated as a continuous variable. Polynomial functions for modelling fish growth data have been shown to be comparable to the von Bertalanffy equation for some species including walleye, white sucker *Catostomus commersonii* (Lacepède) and pike (Chen *et al.*, 1992). Interaction terms were added to the model to investigate the non-additive effects of independent variables (Quinn & Keough, 2002). Growth was modelled by using a third-order polynomial function as:  $L_T = a + bA + cP + dF(L) + eAP + fA^2 + gA^2P + hA^3 + iA^3P$ , where  $L_T$  is fish total length,  $A$  is the age of fish at the backcalculated length (a fixed factor with repeated measures),  $P$  is the walleye's feeding type (a fixed factor),  $F$  is the walleye individual caught nested into the  $L$  factor (*i.e.* the lake from which the fish was caught, a random factor), and  $a-i$  are the regression coefficients.

The proper covariance structure (*i.e.* modelling of dependent errors due to repeated measures) was chosen by comparing the fit of the model with four different covariance structures (Littell *et al.*, 1996; Verbeke & Molenberghs, 2000): (1) autoregressive of order one, (2) compound symmetry, (3) Huynh-Feldt and (4) unstructured (Littell *et al.*, 1996). Models with different covariance structures were compared using the Akaike information criterion (AIC) (Littell *et al.*, 1996; Verbeke & Molenberghs, 2000). Because the number of observations ( $n$ ) was not 40 times greater than the number of explanatory variables ( $K$ ) (*i.e.*  $n K^{-1} < 40$ ), AIC corrected for a small sample size (AICc) was used (Anderson *et al.*, 2001). After having selected an appropriate covariance structure, the order of the polynomial was reduced when appropriate (Verbeke & Molenberghs, 2000); if higher-order terms (*i.e.* AGE<sup>3</sup> and AGE<sup>3</sup> × PISCIVORY) were not significantly related to  $L_T$ , they were dropped from the model (Verbeke & Molenberghs, 2000). The procedure was then applied to second-order terms (*i.e.* AGE<sup>2</sup> and AGE<sup>2</sup> × PISCIVORY) in the reduced model. This hierarchical procedure was used to reduce the model until a significant term was found, whether lower-order terms were significant or not (Verbeke & Molenberghs, 2000). If a model with an order lower than three was selected, the residuals were graphically checked to compare the fit of the untransformed model with the fit of an equivalent model in which both the independent and the dependent variables were log<sub>10</sub> transformed. Chen *et al.* (1992) suggested that such a transformation could greatly improve the fit of a second-order polynomial to model fish growth.

A minimum of three backcalculated  $L_T$  per individual was used. Furthermore, only lakes for which the sample size per age class was one or more individual fish per sex and feeding group (mean ± s.d.: males: 4.0 ± 2.4; females: 2.6 ± 3.1) were included in the model. The proportion of each feeding group was comparable across lakes (only a few lakes were excluded from the analyses because one of the two feeding group was absent). Analyses were restricted to ages for which at least two individuals per feeding group and per age class were available. For this reason, backcalculated growth trajectories were truncated at age 12 years. A total of 50 males and 38 females from seven (AB-35, CSL-2, DF-2, DF-5, K-2, K-8 and N-89) and six (AB-35, DA-4, DF-2, DF-5, K-2 and K-8) lakes, respectively, were used in these analyses. Globally, a total of 346 (149 piscivores and 197 non-piscivores) and 234 (83 piscivores and 151 non-piscivores) measurements of  $L_T$ -at-age were used in the analysis for males and females, respectively. Pair-wise comparisons between the adjusted  $L_T$  of piscivorous and non-piscivorous walleye (least squares means) were conducted for different ages to compare  $L_T$ -at-age. The sequential Bonferroni correction were used to account for multiple comparisons (Rice, 1989). To avoid over correction of the  $\alpha$  level by the sequential Bonferroni adjustment (Moran, 2003), *post hoc* tests were computed only for odd ages between 1 and 12 years (*i.e.* 1, 3, 5, 7, *etc.*). The growth of male and female walleye were analysed separately because walleye show sexual dimorphism (Henderson *et al.*, 2003).

### Fish condition

Conventional condition indices (e.g.  $k$ ; Murphy & Willis, 1996) are based on ratios that can lead to biased conclusions (Packard & Boardman, 1987). To avoid this problem, the effect of piscivory on fish condition was analysed by comparing the slope and elevation of the  $L_T$  and  $M$  relationships (Lai & Helser, 2004). To analyse the effect of piscivory on the  $L_T$  and  $M$  relationships for males and females separately, the variation in  $M$  was related to the two main variables ( $L_T$  and piscivory) and one interaction term ( $L_T \times$  piscivory) in a linear mixed model. To take into account the interlake variability in the slope and elevation of the male and female  $L_T$  and  $M$  relationships, the lake effect (LAKE) and interaction term (LAKE × log<sub>10</sub>  $L_T$ ) were considered as random variables in the model:  $\log_{10}M = a + b \log_{10}L_T + c P + d \log_{10}L_T P + e L + f L \log_{10}L_T$ . A total of 62 males and 47 females from 10 (all but AB-220) and nine lakes (all but AB-220 and K-3), respectively, were used in this analysis.

Normality, linearity and homoscedasticity of residuals were examined to determine if the assumptions of the linear mixed model were satisfied (Littell *et al.*, 1996). The

significance of the random factors (*e.g.* LAKE) in the mixed models was determined by the likelihood-ratio statistic. If random terms did not improve the fit of the model, they were dropped (Littell *et al.*, 1996). All statistical analyses were performed in SAS for Windows, version 8.2.

## RESULTS

### DIET

Walleye fed mainly on benthic invertebrates and fishes in the study lakes (Fig. 1). Terrestrial and swimming insects had low occurrence in the diet of walleye. Stomach content analysis revealed that 16% of males had a diet based exclusively on forage fishes, 35% had a diet based exclusively on invertebrates and 48% had a mixed diet including fishes and invertebrates (Fig. 1). Of the females, 16% had a diet based exclusively on forage fishes, 59% exclusively on invertebrates and 25% had a mixed diet (Fig. 1). The  $L_T$  of piscivorous walleye was not significantly correlated with the amount of prey fishes (per cent  $M$ ) in their stomach (Pearson correlation,  $P > 0.05$ ; males,  $r^2 = 0.03$ ; females,  $r^2 = 0.21$ ) (Fig. 2).

### GROWTH

A second order polynomial was retained to model the data given that third order terms were not significant. The AICc indicated that the autocorrelation between repeated measures of backcalculated walleye  $L_T$  was best modelled by an autoregressive covariance structure. Furthermore, examination of the

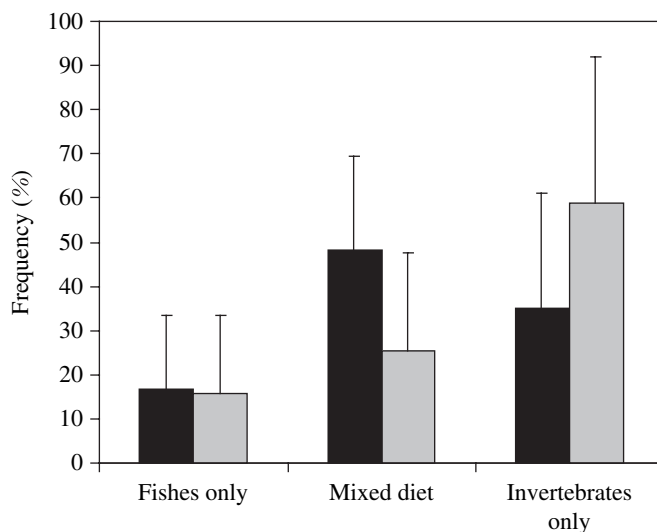


FIG. 1. Diet composition (mean  $\pm$  s.e. per cent frequency) of male (■;  $n = 63$ ) and female (□;  $n = 52$ ) walleye.

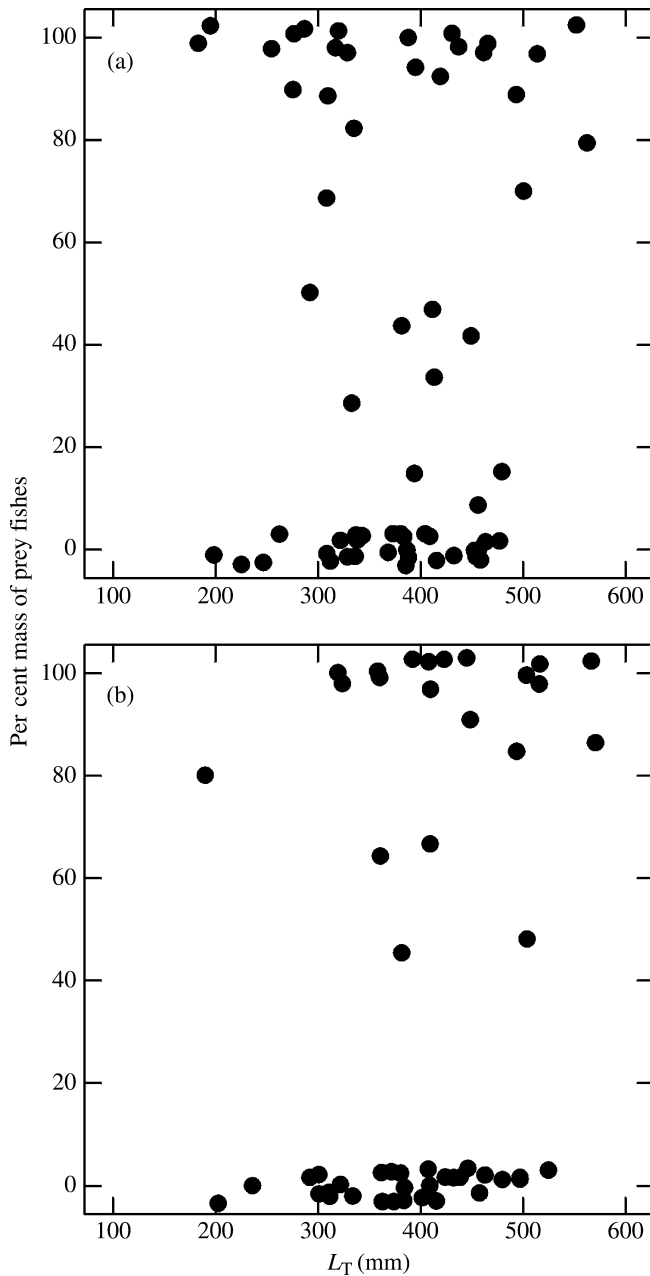


FIG. 2. Scatter plots of the per cent mass of prey fishes in stomachs of (a) male ( $n = 63$ ) and (b) female ( $n = 52$ ) walleye in relation to their total length. Note that the random jitter option was used to avoid the overlapping of points.

residuals indicated that a  $\log_{10}$  transformation did not improve the fit of the second order model. Model results showed no significant effect of piscivory on the growth of walleye for males (mixed model,  $n = 50$ ,  $P > 0.05$ ) but a significant effect of the interaction AGE  $\times$  PISCIVORY (mixed model,  $n = 50$ ,  $P < 0.01$ ;

Table II), indicating that the effect of piscivory varies with fish age. Significant differences were found between the adjusted  $L_T$  of piscivorous and non-piscivorous male walleye for age classes 7, 9 and 11 years [Fig. 3(a)]. The effect of piscivory on the backcalculated growth of females was not significant (mixed model:  $n = 38$ ,  $P > 0.05$ ), nor was the interaction of piscivory with age [mixed model,  $n = 38$ ,  $P > 0.05$ ; Table II and Fig. 3(b)]. The presence of the significant  $AGE^2$  term for both males (mixed model,  $n = 50$ ,  $P < 0.001$ ) and females (mixed model,  $n = 38$ ,  $P < 0.001$ ) indicated that the growth trajectories were not linear. The log-likelihood ratio test showed that the inclusion of the random term (*i.e.* LAKE) significantly improved the fit of the model for both males and females ( $P < 0.001$  and  $P < 0.01$ , respectively).

## FISH CONDITION

The results of the mixed model examining the effect of piscivory on the  $L_T$  and  $M$  relationships indicated that piscivorous and non-piscivorous fish had similar condition (mixed model; males:  $n = 62$ ,  $P > 0.05$ ; females:  $n = 47$ ,  $P > 0.05$ ; Table III). The log-likelihood ratio test showed that the inclusion of random terms (LAKE and LAKE  $\times$   $\log_{10} L_T$ ) did not significantly improve the fit of the model for either males or females ( $P > 0.05$  in both cases). Both random terms were thus dropped from the models.

## DISCUSSION

The results revealed that prey fishes and benthic invertebrates constitute the bulk of the walleye diet in the study lakes. The relative proportions of these two prey in stomach contents, however, were highly variable among individuals. The proportion of prey fishes in the diet was not correlated with walleye size. Thus, early stage walleye can prey on fishes (Mittelbach & Persson, 1998), but walleye can also feed on benthic invertebrates throughout its ontogeny.

TABLE II. Results for fixed effects in linear mixed models explaining variation in total length of piscivorous and non-piscivorous walleye based on (a) 50 individual growth curves for males from seven lakes and (b) 38 individual growth curves for females from six lakes. A minimum of three repeated measures per individual was used

| Effect                 | Numerator d.f. | Denominator d.f. | <i>F</i> | <i>P</i> |
|------------------------|----------------|------------------|----------|----------|
| (a)                    |                |                  |          |          |
| Age                    | 1              | 331              | 1765.38  | <0.0001  |
| Piscivory              | 1              | 80.6             | 0.66     | 0.4196   |
| Age $\times$ piscivory | 1              | 184              | 8.83     | 0.0034   |
| Age $\times$ age       | 1              | 320              | 411.45   | <0.0001  |
| (b)                    |                |                  |          |          |
| Age                    | 1              | 224              | 856.15   | <0.0001  |
| Piscivory              | 1              | 57.6             | 1.92     | 0.1708   |
| Age $\times$ piscivory | 1              | 159              | 2.83     | 0.0945   |
| Age $\times$ age       | 1              | 224              | 187.82   | <0.0001  |

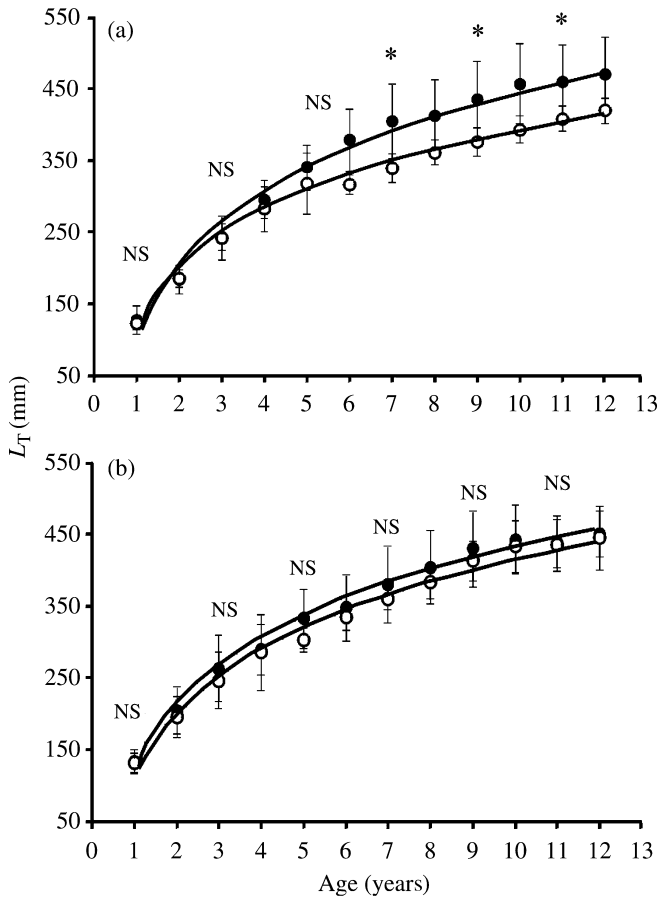


FIG. 3. Mean  $\pm$  S.E. backcalculated lengths of piscivorous (●) and non-piscivorous (○) walleye for (a) males (piscivorous  $n = 23$ ; non-piscivorous  $n = 27$ ) and (b) females (piscivorous  $n = 13$ ; non-piscivorous  $n = 25$ ). Note that to avoid an over correction of the  $\alpha$  level by Bonferroni adjustment, *post hoc* tests were only computed for odd ages. Mean values with asterisks (\*) are significant after a sequential Bonferroni correction; NS, differences not significant between piscivorous and non-piscivorous walleye for a given age. Curves were fitted for each group using a logarithmic function to show growth trends.

Such a large contribution of invertebrates to the walleye diet might be related to the relatively low abundance of prey fishes in these oligotrophic, unproductive lakes, and by resource competition with pike, which is present in all of the study lakes.

Prey fishes are considered to be more profitable than benthic invertebrate for piscivorous predators (Mittelbach & Persson, 1998). This higher profitability can be explained by the higher energy content and small amount of waste of prey fishes (Weatherley & Gill, 1987) and their larger size, which may increase their encounter rate with piscivores (Persson, 1987; Noakes & Godin, 1988). Therefore, if the environment does not provide an adequate size spectrum of prey fishes to allow predators to take larger and larger prey as they grow, growth may cease (Mittelbach, 1983). In such conditions, feeding at a lower

TABLE III. Results of linear mixed models explaining the variation in the  $\log_{10}$  mass of piscivorous and non-piscivorous walleye for (a) 62 males from 10 lakes and (b) 47 females from nine lakes

| Effect          | Numerator d.f. | Denominator d.f. | <i>F</i> | <i>P</i> |
|-----------------|----------------|------------------|----------|----------|
| (a)             |                |                  |          |          |
| $\log_{10} L_T$ | 1              | 59               | 678.37   | <0.0001  |
| Piscivory       | 1              | 59               | 2.99     | 0.0892   |
| (b)             |                |                  |          |          |
| $\log_{10} L_T$ | 1              | 44               | 2779.46  | <0.0001  |
| Piscivory       | 1              | 44               | 2.70     | 0.1073   |

$L_T$ , total length.

level of the food web might be advantageous for predatory fishes (Chapman *et al.*, 1989; Beaudoin *et al.*, 1999). In cases where forage fishes were absent, benthic invertebrates have been found to constitute the main food items of piscivores like pike (Beaudoin *et al.*, 1999). The results suggest that invertebrates could be an important component of the diet of walleye throughout their ontogeny, even in the presence of forage fishes, *e.g.* yellow perch *Perca flavescens* (Mitchill). Because of changes in the availability of prey fishes over time, the seasonal dynamics of temperate lakes may favour such a flexibility in resource use (Chapman *et al.*, 1989). Furthermore, prey fishes availability in the study area might have been reduced due to predation by pike, whose diet consists of 46% prey fishes on average (by *M*) (Y. Paradis, A. Bertolo & P. Magnan, unpubl. data). It was also shown in lakes of the same area that the presence of pike is negatively related to the relative abundance of prey fishes (Bertolo *et al.*, 2005). The important contribution of invertebrates to the diets of piscivorous species is consistent with the findings of Vander Zanden & Vadeboncoeur (2002) and Vadeboncoeur *et al.* (2002), who showed that benthic production plays a central role in supporting higher trophic level production, including piscivores.

Piscivorous males showed a significantly higher growth trajectory than non-piscivorous males, supporting the notion that prey fishes are more profitable than benthic invertebrates for piscivorous individuals. Similar differences in growth of piscivores and non-piscivores based on stomach content data have been observed in other studies. For example, Blackie *et al.* (2003) showed that lake charr *Salvelinus namaycush* (Walbaum) classified as piscivores on the basis of their stomach contents had a better growth rate than those classified as insectivores. These growth differences were explained by trophic specialization of lake charr, with some individuals specializing on prey fishes and others on invertebrates (Blackie *et al.*, 2003; Alfonso, 2004). Jonsson *et al.* (1999) also showed that brown trout *Salmo trutta* L. feeding on fishes had higher growth than brown trout feeding on invertebrates. These authors explained this difference by the presence of fast growing individuals in the population, which switched to piscivory at a younger age and at a smaller size than the slow growing ones. Jonsson *et al.* (1999) suggested that the ontogenetic shift to piscivory could be inferred from a sudden increase in growth. A similar pattern was observed for perch *Perca fluviatilis* L. (LeCren, 1992; Persson *et al.*, 2000).

Both piscivorous and non-piscivorous walleye showed continuous growth trajectories in the study lakes, suggesting that there is not an ontogenetic shift. The effects of piscivory were examined by comparing adjusted  $L_T$ -at-age, which revealed that piscivorous males diverged from non-piscivorous ones at age 7 years. This result suggests that trophic specialization takes place gradually in male walleye, where some individuals specialize on prey fishes and others on invertebrates.

No difference in growth between piscivorous and non-piscivorous individuals was found for female walleye. A first hypothesis is that females show less fidelity than males to a given prey during their ontogeny, making the use of stomach contents unreliable to assess their long-term foraging behaviour. Alternatively, if the assumption that stomach content data are a good index of the long-term foraging behaviour of individuals is valid, these results suggest that males and females do not allocate their energy to growth and reproduction in the same way. Energy allocation to reproductive and somatic growth is known to be different for males and females of many species, where males allocate less energy to gonads than females (Moyle & Cech, 1996). In contrast to males, an optimal strategy for females would favour an energy intake that fosters growth to increase ovarian production (Hughes, 1997). Therefore, food specialization in female walleye, if any, would be expected to affect their reproductive investment before affecting growth. Unfortunately, due to logistic constraints, namely the weight and space that would be taken up by the entire specimen in the aircraft, it was not possible to bring back the whole sampled fish. Thus, it was not possible to investigate the reproductive investment of female walleye.

The correlation between growth and the presence and absence of prey fishes in the stomach contents of individuals reported in the literature and confirmed in the present study for males suggests that the presence of prey fishes in the stomach could be a good proxy for long-term piscivory. The results showed, however, that this pattern is sex dependent and suggest that the analysis of short-term and long-term feeding behaviour should explicitly take sex into account. Therefore, analysing growth from pooled data of both sexes, as has been done in other studies (Jonsson *et al.*, 1999; Blackie *et al.*, 2003), might lead to a biased conclusion.

The comparison of growth and condition of piscivorous and non-piscivorous walleye is based on the backcalculated  $L_T$  of individuals from 12 age classes from different lakes. Analysing such relatively long growth trajectories and considering lake as a random factor allowed the assumption that the results reported here are representative of the study area. The use of long-term indices of foraging behaviour, such as stable isotopes (Beaudoin *et al.*, 1999), would help to confirm the reliability of stomach contents to infer diet specialization of individuals in future studies.

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