The relationship between piscivory and growth of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) in headwater lakes of the Canadian Shield

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Abstract: We used data from a survey of 36 headwater lakes of the Canadian Shield to investigate the relationship between piscivory and growth, abundance, and longevity of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*). The occurrence of northern pike (*Esox lucius*) and walleye (*Sander vitreus*) explained variations in the abundance of both white sucker and yellow perch, suggesting strong predation-induced mortality. The longevity of both species tended to be negatively related to increased piscivory. White sucker grew better and had a better condition in lakes with piscivores. Yellow perch showed only small among-lake differences in growth and condition. The superior competitive ability of white sucker over yellow perch could explain why yellow perch did not show improved growth or longevity where population densities were low in lakes with piscivores and white sucker. Furthermore, yellow perch growth was inversely related to the biomass of piscivorous fish in their first year of life. Stomach content data suggest that small yellow perch, which rely on zooplankton, might restrict their use of pelagic resources to reduce their predation risk by piscivores, thus reducing their growth. Our results show that the effects of piscivores can be species-specific and dependent on community structure.

Reésumé : Nous avons utilisé les données d'un inventaire de 36 lacs du bouclier canadien pour examiner la relation entre la piscivorie et la croissance, l'abondance ainsi que la longévité du meunier noir (*Catostomus commersoni*) et de la perchaude (*Perca flavescens*). L'occurrence du grand brochet (*Esox lucius*) et du doré jaune (*Sander vitreus*) ont expliqué les variations d'abondance du meunier noir et de la perchaude, suggérant une forte mortalité due à la prédation. La longévité des deux espèces tendait à diminuer en fonction du gradient de piscivorie. Le meunier noir a affiché une meilleure croissance et une meilleure condition dans les lacs avec piscivores. La perchaude n'a montré que des faibles différences de croissance entre les lacs étudiés. La supériorité compétitive du meunier noir sur la perchaude pourrait expliquer pourquoi la perchaude n'a pas profité de la réduction de sa densité dans les lacs avec piscivores et meuniers noirs. De plus, la croissance de la perchaude était inversement reliée à la biomasse des piscivores dans leur première année de vie. L'analyse des contenus stomacaux suggère que les perchaudes juvéniles, qui dépendent du zooplancton, pourraient réduire leur utilisation des ressources pélagiques pour diminuer leur risque de prédation par les piscivores, réduisant ainsi leur croissance. Nos résultats illustrent que les effets de la piscivorie peuvent être spécifiques à l'espèce et dépendants de la structure de la communauté.

Introduction

Piscivory is known to exert strong effects on abundance, biomass, and diversity of prey fish (Carpenter and Kitchell 1993; Chapleau et al. 1997). Food web theory suggests that such a top-down control can potentially lead to major changes in the biomass of lower trophic levels in lake ecosystems (Carpenter and Kitchell 1993). For example, by lowering the levels of intraspecific competition, the reduction of prey fish density by piscivores might lead to better growth in surviving individuals. In contrast, the dynamics of competitive interaction among prey species could be such that some species would not experience any growth improvement in response to a decrease in intraspecific competition related to piscivory (e.g., low competitive ability compared with other prey fish species). It is thus important to understand how different prey species respond to piscivory to better understand the effects of changes at the top of lacustrine food webs.

It is well documented that the growth of widely distributed species such as white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) can differ among popu-

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Table 1. Selected watershed characteristics and morphometric variables of the study lakes.

Variable	Lake group I (n = 10)	II (n = 17)	III (n = 9)	F	P
Lake area (km^2)	0.67±0.61	0.36±0.17	0.46±0.20	2.65	0.09
Maximum depth (m)	14.8±7.4	14.3±6.1	11.9±4.7	0.83	0.44
Mean depth (m)	5.3±2.2	4.6±1.8	4.7±1.7	0.43	0.65
Watershed area (km^2)	3.6±3.6	3.0±1.9	4.9±6.4	0.65	0.53
Residence time (years)	2.2±1.4	1.4±0.8	1.4±1.1	2.35	0.11
Lake slope (%)	7.0±3.2	8.9±4.0	6.2±2.0	1.84	0.17

Note: Data are means ± SD. Lake groups: I, no piscivores; II, with northern pike (*Esox lucius*); III, with northern pike and walleye (*Sander vitreus*). F and P values as determined by ANOVA conducted on log-transformed data are also shown.

lations (Trippel and Harvey 1987; Boisclair and Leggett 1989*a*; Chen and Harvey 1999). However, factors explaining such variations are still unclear. Different pathways, related to a combination of density-dependent (i.e., biotic) and density-independent (i.e., abiotic) factors, could lead to among-lake variability in fish growth. A strong variation in the length-at-age of 32 white sucker populations was observed by Chen and Harvey (1999), who related these among-lake differences to spatial (genetic difference owing to isolation) and physicochemical (lake pH) factors. Many studies have been conducted on *Perca* spp., and several nonmutually exclusive interpretations have been suggested to explain variations in their growth, including prey type (Tyson and Knight 2001), habitat productivity (Abbey and Mackay 1991), water temperature (Power and van den Heuvel 1999), and the presence of competing species (Hayes et al. 1992). Boisclair and Leggett (1989*a*, 1989*b*) found that neither the quantity nor the mean size of the ingested prey was able to fully explain the strong among-population variations in yellow perch growth rates. They suggested that the low growth of yellow perch was related to an increase in their metabolic demand caused by frequent interactions with cyprinid fish (Boisclair and Leggett 1989*c*). This example suggests that community structure could affect fish growth patterns by modifying the behaviour of individuals. The presence of piscivorous fish could also have strong effects on prey fish behaviour and consequently on their growth because they are forced to use suboptimal foraging habitats (Werner et al. 1983). In contrast, as mentioned above, predation can have an indirect positive effect on fish growth by reducing the level of intra- and inter-specific competition (Rudstam et al. 1996; Paukert et al. 2002).

Because yellow perch and white sucker show ontogenetic differences in habitat use and body size, they are potentially exposed to different predation risks during their whole life. Yellow perch is a generalist feeder that shows ontogenetic shifts in both diet and habitat: after hatching in the littoral zone, the individuals migrate to the pelagic zone to feed on zooplankton and then return to the littoral zone when they have a sufficient gape size to integrate benthic prey into their diet (Post et al. 1997). In contrast, white sucker has a short planktivorous stage and relies on benthic resources during most of its ontogeny (Scott and Crossman 1973). Because of its pelagic phase and the use of zooplankton as an alternative resource in the presence of competitors, yellow perch is probably more exposed than white sucker to piscivorous predators that occur at the interface of the pelagic and littoral zones. Given that the duration of the planktonic stage is important in determining the growth pattern of 0+ yellow perch (Post et al. 1997), piscivorous predators might affect the growth of 0+ yellow perch by forcing them to an earlier habitat shift, thus reducing their feeding on zooplankton. Furthermore, because white sucker can reach larger sizes than yellow perch, it is probably less vulnerable to gape-limited predators than yellow perch. Because the interplay of behavioural and numeric effects of piscivorous fish is likely to be habitat and species dependent, white sucker and yellow perch might respond differently to the presence of piscivores.

In this paper, we test the hypothesis that predation by piscivorous fish is related to variations in the growth of white sucker and yellow perch using data from a survey of 36 Canadian Shield lakes that contain at least one of these two species. We expected predation by piscivorous fish to be associated with (*i*) a higher growth and (or) condition of both prey species because of their relatively low abundance and (*ii*) a poor growth and (or) condition of those size classes of yellow perch that rely on zooplankton, owing to a presumably restricted access to the pelagic resources. The study lakes are in the same geographic region and have similar morphometry, so they are comparable in many respects. In contrast, the biomass of large piscivorous predators differs greatly among the study lakes, thus allowing the analysis of their effect on the growth of both white sucker and yellow perch. Lake morphometric variables were included in the analysis to control for their potential indirect effects on fish growth.

Methods

Study area and biological background

Thirty-six thermally stratified headwater lakes were selected on the basis of comparable size, basin morphometry, and catchment properties (Table 1). The lakes were accessible only by aircraft, belong to the same hydrographic region, and are located in a 30 000 km^2 area surrounding the Gouin Reservoir, Haute-Mauricie, Quebec, Canada (48°50′N, 75°00′W) (see fig. 1 in Carignan et al. 2000). Lake morphometry and catchment properties were determined from aerial photographs and from 15–25 echosounder transects (Carignan et al. 2000). The catchments of these lakes were only exposed to limited perturbation until 1995, when nine of them experienced forest fires and nine were logged by forestry companies. The effects of forest fires and logging

Table 2. Relative biomass (BPUE) (g fresh weight·net^{-1}·night^{-1}) and numbers (CPUE) (individuals·net^{-1}·night^{-1}) of major fish taxa in the study lakes.

Variable		Lake group I (n = 10)	II (n = 17)	III (n = 9)	F	P
Brook trout	BPUE	694±519 (6)	0±0 (0)	0±0 (0)	nt	
	CPUE	5.6±6.4	0±0	0±0	nt	
Yellow perch	BPUE[a]	704±674 (3)	177±135 (13)	144±174 (9)	3.1	0.068
	CPUE[a]	64.5±59.5a	11.8±7.3b	8.1±5.9b	7.4	0.0034*
White sucker	BPUE[b]	3476±1812 (10)	1715±2519 (13)	2201±2227 (8)	3.1	0.059
	CPUE[a]	18.9±12.0a	2.9±3.4b	3.9±3.1b	12.7	0.0001*
Northern pike	BPUE	0±0 (0)	2696±1384 (17)	2228±1154 (9)	nt	
	CPUE	0±0	2.5±1.4	1.5±0.7	nt	
Walleye	BPUE	0±0 (0)	0±0 (0)	3573±1609 (9)	nt	
	CPUE	0±0	0±0	8.1±3.6	nt	
Lake whitefish	BPUE	0±0 (0)	1454±908 (3)	3243±2584 (8)	nt	
	CPUE	0±0	6.1±7.4	8.0±7.0	nt	
Prey fish	BPUE[c]	255±204a (9)	104±189ab (12)	36±60b (6)	4.9	0.016
	CPUE[a]	45.8±49.5a	18.3±23.9ab	6.3±9.8b	5.71	0.009*

Note: Data are means ± SD. Means with different letters are significantly different as determined by a Tukey multiple range comparison test ($P < 0.05$). Prey fish are all small-bodied species (mainly cyprinids) pooled. The occurrence of each fish species is indicated in parentheses. nt, not tested owing to low sample size. An asterisk denotes significant after the sequential Bonferroni correction. Lake groups: I, no piscivores; II, with northern pike (*Esox lucius*); III, with northern pike and walleye (*Sander vitreus*).

[a] ANOVA performed on data that were log transformed.

[b] ANOVA performed on data that were square-root transformed.

[c] ANOVA performed on data that were rank transformed.

were studied on these lakes for the 3 years following the perturbation (between 1996 and 1998). Carignan et al. (2000) showed that fire and logging were associated with higher concentrations of nutrients and major ions in these lakes. Planas et al. (2000) found significant effects of the perturbations on the biomass of both benthic and pelagic algae, which were higher in logged and burned lakes between 1996 and 1998. Furthermore, Patoine et al. (2000) found that the biomass of small-sized zooplankton (mostly rotifers) was higher in burned-watershed lakes, while the biomass of larger zooplankton (mostly calanoids) was lower in logged-watershed lakes. Between 1996 and 1997, St-Onge and Magnan (2000) found some negative effects of these perturbations on the abundance of small size classes of both yellow perch and white sucker but did not observe such an effect for larger individuals. In addition, watershed perturbations had no effect on the growth of yellow perch in these lakes (St-Onge and Magnan 2000; growth of white sucker was not estimated in this study). Despite the lack of any clear effects on yellow perch growth, we cannot exclude the possibility that such perturbations could affect the entire structure of the food web over the long term and indirectly affect fish growth. Since we focus here on the effects of fish community structure, we adopted two different approaches to control for the effects of perturbations on fish growth. First, to avoid the potential noise in fish growth owing to the watershed perturbation, we used only back-calculated lengths-at-age of fish from the period preceding the watershed perturbations in our analysis. Second, variables describing the degree of perturbation in the watershed (see below) were included in the list of independent variables used to explain variation in the length–weight relationships.

Twenty-three fish species were found in this survey. Northern pike (*Esox lucius*), white sucker, lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*, formerly *Stizostedion vitreum*), yellow perch, and brook trout (*Salvelinus fontinalis*) were the most important in terms of relative biomass (for a complete list, see St-Onge and Magnan 2000). For this analysis, the numbers and relative biomasses of other small prey fish (mostly cyprinids) were pooled into a single prey category (Table 2). The relative biomasses (grams of fish per gill net per night; see below) of these seven taxa were used as explanatory variables in subsequent analyses to explain variations in white sucker and yellow perch growth.

For the purpose of the present study, we classified the fish communities into three categories: group I, absence of large piscivorous predators; group II, presence of northern pike; and group III, co-occurrence of northern pike and walleye. Fish community and watershed perturbation were not confounding factors in this study, since a similar proportion of the lakes with each type of fish community experienced watershed perturbations.

Fish sampling

Nineteen lakes were sampled in 1996 and 17 in 1997. Each lake was sampled once between June and August. The sampling date (as Julian days) was not significantly different among lake groups (one-way analysis of variance (ANOVA), $F_{[2,35]} = 1.1$, $P = 0.36$). Fish were captured with experimental monofilament gill nets that were 102.3 m long × 2.7 m high with stretched mesh panels of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm (filament diameter of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32, and 0.32 mm, respectively). Gill nets were set perpendicular to the shore, with small and large meshes alternating from the shore among gill nets. The nets were set at regular intervals around the lake, with the first net location being randomly located on aerial photographs. The fishing effort was six nets per night for lakes <50 ha, eight nets per night for lakes of 50–100 ha, 10 nets per night for lakes of 100–150 ha, and 12 nets per night for lakes >150 ha. The nets fished for 17–19 h, covering the period between 1600 and 1030. For all fish captured, total length (±1 mm) and weight (±0.1 g) were noted. This procedure led to comparable among-lake estimates of catch and biomass per unit effort (CPUE and BPUE, respectively, numbers and grams of fish captured per net per night). To determine age and growth, we used fin rays for white sucker and opercular bones for yellow perch. Details on age determination can be found in St-Onge and Magnan (2000) for yellow perch and in Brodeur et al. (2001) for white sucker. Longevity was measured as the 90th percentile of the fish ages observed in a given lake.

Stomach content analysis

To get indirect information on habitat use, we analyzed the stomach contents of both yellow perch and white sucker. The diet of a subsample of these two species was determined to compare their feeding habits among lake groups. The stomach content was analyzed for yellow perch, while the anterior two thirds of the gut was analyzed for white sucker, since this species lacks a true stomach (Tremblay and Magnan 1991). Prey items were classified into four functional groups as zoobenthos, zooplankton (microcrustaceans and *Chaoborus* larvae), dipteran pupae, and prey fish. Each prey category was dried (12 h at 60 °C) and then weighed to the nearest 0.0001 g. Because of the reduced sample size, it was not possible to analyze gut contents for many size classes. However, to investigate the potential ontogenetic shifts occurring in white sucker and yellow perch among lake groups, we pooled the data into two arbitrary size classes (i.e., small and large fish), corresponding to fish <200 and ≥200 mm for white sucker and <90 and ≥90 mm for yellow perch. Statistical analyses were carried out only for those lakes where we had at least three gut contents per size class, although the sample size was >10 in most of the lakes. We analyzed (mean ± SD) 29.5 ± 26.0 and 32.6 ± 26.9 stomachs per lake for white sucker <200 and ≥200 mm, respectively, and 25.3 ± 24.7 and 37.9 ± 35.8 stomachs per lake for yellow perch <90 and ≥90 mm, respectively. Since logging and fire occurred before the fish were collected, these watershed perturbations might have affected the fish diet. However, since watershed perturbation was not different among the lake groups (i.e., fish community types), it could only have added noise in the analysis of this last factor but not biased the results.

Statistical analyses

Relative abundance, longevity, and diet

We analyzed the variations among lake groups in the relative abundance (CPUE and BPUE) of the seven fish taxa studied as well as in the longevity of yellow perch and white sucker with one-way ANOVA followed by Tukey multiple range comparison tests. A two-way ANOVA was used to test the effects of fish size and lake group on the feeding habits. When necessary, data were $\log(x + 1)$ or square root transformed to normalize the residuals. Percentage data (i.e., the proportion of different prey types in the stomachs) were arcsine transformed prior to analysis. If these procedures were not successful, ANOVAs were conducted on rank-transformed data (Quinn and Keough 2002).

Growth

We used two approaches to investigate the determinants of fish growth in our study lakes: (*i*) comparison of growth trajectories among lake groups with linear mixed models to determine the effect of piscivores on fish growth and (*ii*) multiple linear regression to determine if length-at-age of the main age classes is affected by factors other than piscivores (e.g., lake morphometry).

Linear mixed models (procedure MIXED, SAS statistical package; SAS 1999) were used to compare fish growth trajectories among lake groups because this statistical approach properly handles both fixed (e.g., lake groups) and random (e.g., lakes) factors. Furthermore, linear mixed modeling is appropriate for use with repeated measures, like back-calculated lengths from the same fish, that are not independent (Littell et al. 1996). Within this framework, both the autocorrelation among back-calculated lengths and their covariance can be modeled by selecting an appropriate covariance structure (see below) for the matrix of repeated measures (Littell et al. 1996). This is particularly important not only to obtain correct estimates of the regression coefficients but also because the use of an inappropriate covariance structure may lead to invalid significance tests (Littell et al. 1996).

We modeled the data by using a third-order polynomial growth function:

$$\begin{aligned}\mathrm{TL} = {} & a + b \times \mathrm{AGE} + c \times \mathrm{GROUP} \\ & + d \times \mathrm{LAKE(GROUP)} + e \times \mathrm{AGE} \times \mathrm{GROUP} \\ & + f \times \mathrm{AGE}^2 + g \times \mathrm{AGE}^2 \times \mathrm{GROUP} \\ & + h \times \mathrm{AGE}^3 + i \times \mathrm{AGE}^3 \times \mathrm{GROUP}\end{aligned}$$

where TL is fish total length, AGE is fish age (a fixed factor with repeated measures), GROUP is the lake group (a fixed factor), LAKE is the lake from which the fish were caught (a random factor nested into the GROUP factor), and a to i are the regression coefficients. Since yellow perch data were only available for ages 1 and 2, second- and third-order terms were not included and their growth was thus modeled as linear.

The proper covariance structure was chosen by comparing the fit of the model with four different covariance structures (Littell et al. 1996; Verbeke and Molenberghs 2000): (*i*) autoregressive of order one (AR1), (*ii*) compound symmetry (CS), (*iii*) Huynh–Feldt (HF), and (*iv*) unstructured (UN). The AR1 covariance structure assumes that the repeated measures have the same variance, whereas their correlation decreases with increasing lag between them. The CS covariance structure assumes the same variance for all of the repeated measures and that all pairs of repeated measures on the same fish have the same correlation. The HF covariance structure is a generalization of the CS structure, with heterogeneous variance among the repeated measures. Finally, the more general UN covariance structure makes no assumption on the homogeneity of variances or about correlations between repeated measures. The number of parameters needed to estimate these four covariance structures varies: two for AR1 and CS, $1 + n$ for HF, where n is the number of repeated measures, and $n(n + 1) \times 0.5$ for UN (Littell et al. 1996). An objective comparison of different covariance structures can be done by using goodness-of-fit criteria such as the Akaike information criterion (Littell et al. 1996; Verbeke and Molenberghs 2000). The Akaike information criterion takes into account both the fit of the data and the number of parameters involved in the construction of the covariance matrix, favouring those models with a small number of parameters in the covariance structure (Littell et al. 1996). The selection of the best-fitted and more parsimonious model was carried out by choosing the model with the smaller Akaike information criterion value.

After having selected an appropriate covariance structure, we checked if the order of the polynomial could be reduced (Verbeke and Molenberghs 2000). Thus, if higher-order terms (i.e., AGE^3 and $\mathrm{AGE}^3 \times \mathrm{GROUP}$) were not significantly related to fish length, they were dropped from the model. The procedure was then applied to higher-order terms (i.e., AGE^2 and $\mathrm{AGE}^2 \times \mathrm{GROUP}$) 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 and Molenberghs 2000).

If a model with an order lower than three was selected, we used the residual plot 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 transformed. Chen et al. (1992) suggested that such a transformation could greatly improve the fit of a second-order polynomial to model fish growth.

Back-calculated data related to the year of perturbation and the postperturbation period were excluded from the analysis. A minimum of four back-calculated lengths per white sucker and two per yellow perch were used. Moreover, we included in the model only those lakes for which the sample size per age class was three or more individual fish and we restricted the analysis to those ages for which we had at least two lakes per group and per age class. Therefore, back-calculated growth trajectories of white sucker and yellow perch were truncated at age 6 and age 2, respectively. A total of 590 white sucker and 303 yellow perch from 17 and 19 lakes, respectively, were used in this analysis. Globally, a total of 3528 and 606 measures of length-at-age were used in the analysis for white sucker and yellow perch, respectively. If a significant GROUP or $\mathrm{GROUP} \times \mathrm{AGE}^n$ effect was detected, we compared the growth trajectories among lake groups. This was done by pairwise comparisons of adjusted lengths (i.e., least square means of lengths) at different ages. A sequential Bonferroni correction was applied to control for multiple comparisons.

We used stepwise multiple regression to test the hypothesis that differences in lengths-at-age for both white sucker and yellow perch were related to differences in the structure of the fish community (BPUEs of piscivorous fish and of other fish taxa) and in lake morphometry (i.e., altitude, lake area, shoreline development, maximum depth, average lake slope, residence time, basin area, and drainage area to lake area ratio).

Fish condition

The effect of fish community structure on fish condition was analyzed through length–weight relationships. To analyze the effect of lake group on the length–weight relationship for both white sucker and yellow perch, we investigated whether the variation in the fish body weight (W) was related to three main variables and two interactions terms in a linear mixed model:

$$\begin{aligned}\log W = a + b \times \log \mathrm{TL} + c \times \mathrm{GROUP} \\ + d \times \mathrm{LAKE(GROUP)} + e \times \mathrm{GROUP} \times \log \mathrm{TL} \\ + f \times \mathrm{LAKE(GROUP)} \times \log \mathrm{TL}\end{aligned}$$

Julian day and the percentages of watershed burned or logged were used as covariables in this analysis but were discarded if not significantly related to the dependent variable. Pairwise comparisons of adjusted weights (i.e., least square means of log W) allowed us to compare the condition of fish among lake groups. When the slopes among lake groups were significantly different, we compared the adjusted weights for three different sizes representing the range encountered in the populations (i.e., the 25th, 50th, and 75th percentiles of log TL; Littell et al. 1996). Significantly different slopes among lake groups indicate that the differences in fish condition among lake groups vary with fish size, making it necessary to compare their elevation at different values (percentiles) of the independent variable. In the model, we included only the lakes for which the total number of fish measured per lake was ≥10. Comparisons of the length–weight relationships were made for a range of body lengths corresponding to a complete overlap among lake groups. Thus, based on the visual inspection of raw data, we restricted the analysis to white sucker ranging between 100 and 400 mm and to yellow perch <140 mm. A total of 1270 white sucker and 2006 yellow perch from 17 and 24 lakes, respectively, were used in the analysis.

Residual scatterplots, normal probability plots, and partial residual plots were used to determine if the assumptions of models were satisfied (i.e., normality, linearity, and homoscedasticity of residuals). These assumptions were met for all models presented in this paper.

Results

Relative abundance (CPUE and BPUE)

In the absence of both northern pike and walleye (group I), the CPUEs of both white sucker and yellow perch were significantly higher than in lake groups II and III (Table 2). The variations in BPUEs among lake groups of both white sucker and yellow perch tended to be similar to the variations observed in CPUEs, although only marginally significant (Table 2).

Growth

Mixed models

It was not possible to model the white sucker growth data by a third-order polynomial function, since the maximum likelihood estimation technique procedure failed to converge. Therefore, we dropped all of the third-order terms from the model. White sucker growth was best modeled by a log-transformed second-order polynomial model with a UN covariance structure. The lake group effect was significant ($P = 0.044$), as were both the first- and the second-order interactions between lake group and age (log AGE × GROUP and log AGE^2 × GROUP) (Table 3). Also, both the first- and second-order terms of log AGE were significant (Table 3). This suggests that the observed growth pattern for this species (*i*) is not linear (the log AGE^2 term is significant) and (*ii*) differs among the lake groups (the log AGE^2 × GROUP and log AGE × GROUP terms are significant). In all cases, length-at-age tended to be relatively high in group III, low in group I, and intermediate in group II (Fig. 1). However, pairwise comparisons of adjusted lengths did not show any significant differences between pairs of lake groups.

Yellow perch growth was best modeled by a log-transformed model with a UN covariance structure. Yellow perch showed no significant differences among lake groups, but we found a significant interaction between log AGE and GROUP (Table 3). Age was also significantly related to length (Table 3). Post hoc comparisons of adjusted lengths did not show any significant difference among lake groups.

Table 3. Results of linear mixed models explaining the variation in length of (*a*) white sucker (*Catostomus commersoni*) (1–6 years old, 17 lakes) and (*b*) yellow perch (*Perca flavescens*) (1–2 years old, 19 lakes).

	Type 3 test of fixed effects		
Effect	df	*F*	*P*
White sucker			
log AGE	1,575	190.7	<0.0001
GROUP	2,13.9	3.93	0.044
log AGE × GROUP	2,581	29.7	<0.0001
log AGE^2	1,501	648.2	<0.0001
log AGE^2 × GROUP	2,514	12.9	<0.0001
Yellow perch			
log AGE	1,300	4111.2	<0.0001
GROUP	2,15.9	2.38	0.13
log AGE × GROUP	2,300	6.16	0.0024

Note: AGE, fish age (years); GROUP, lake group (see Table 1). log AGE^2 and log AGE^2 × GROUP represent terms for a second-order polynomial model with interactions. A total of 590 and 303 individual growth trajectories were used in this analysis for white sucker and yellow perch, respectively.

Stepwise regressions

The stepwise regression approach revealed that the biomass of piscivorous fish had a strong positive effect on the length of white sucker from age 1 to 6 (Table 4). The length of white sucker at age 1 was directly related to the BPUE of piscivorous fish and white sucker and indirectly related to that of yellow perch (Table 4). The significance level of this latter independent variable (i.e., yellow perch BPUE) proved to be very sensitive to one outlier and was unrelated to the length of white sucker at age 1 after this outlier was omitted from the analysis. In contrast, the BPUEs of piscivorous fish and white sucker were not sensitive to outliers and together explained nearly 55% of the variation in white sucker length-at-age (Table 4). A similar picture was observed for white sucker length-at-age 3, with the BPUE of piscivorous fish, white sucker, and lake whitefish being retained in the regression model (Table 4). For length-at-ages 2, 4, 5, and 6, only the BPUE of piscivorous fish was retained in the models (Table 4). In all models, piscivorous fish biomass was directly related to white sucker length-at-age and explained the largest proportion of the explained variation (Table 4). All stepwise regressions were significant after the sequential Bonferroni correction.

The yellow perch length-at-age 1 was negatively related to the BPUE of piscivorous fish (Table 4). Yellow perch length-at-age 2 was directly related to the total BPUE of yellow perch. Both models were significant after the sequential Bonferroni correction. No lake morphometric variables were selected in any of the models built for the two species.

Length–weight relationships

We found a significant lake group effect in the length–weight relationships for both white sucker and yellow perch (Table 5). Furthermore, there was a significant interaction between the $\log_{10}$ TL and the lake group in both cases, indicating that the slope of the length–weight relationship differed among lake groups. The among-lake pairwise comparisons of white sucker adjusted weights at 180, 205, and 286 mm (the 25th, 50th, and 75th percentiles of log TL, respectively) revealed that in all cases, group I differed significantly from groups II and III, while the latter two were not significantly different (Table 5). For yellow perch, none of the adjusted weights were significantly different among lake groups, but adjusted weights tended to be lower in lake group I, intermediate in group II, and highest in group III (Table 5). The significance of these hypotheses was assessed after a sequential Bonferroni corrected level because a total of nine post hoc comparisons were made for each species. Julian day and the percentages of watershed burned or logged were not significantly related to the dependent variable and therefore were not included in the model.

Longevity

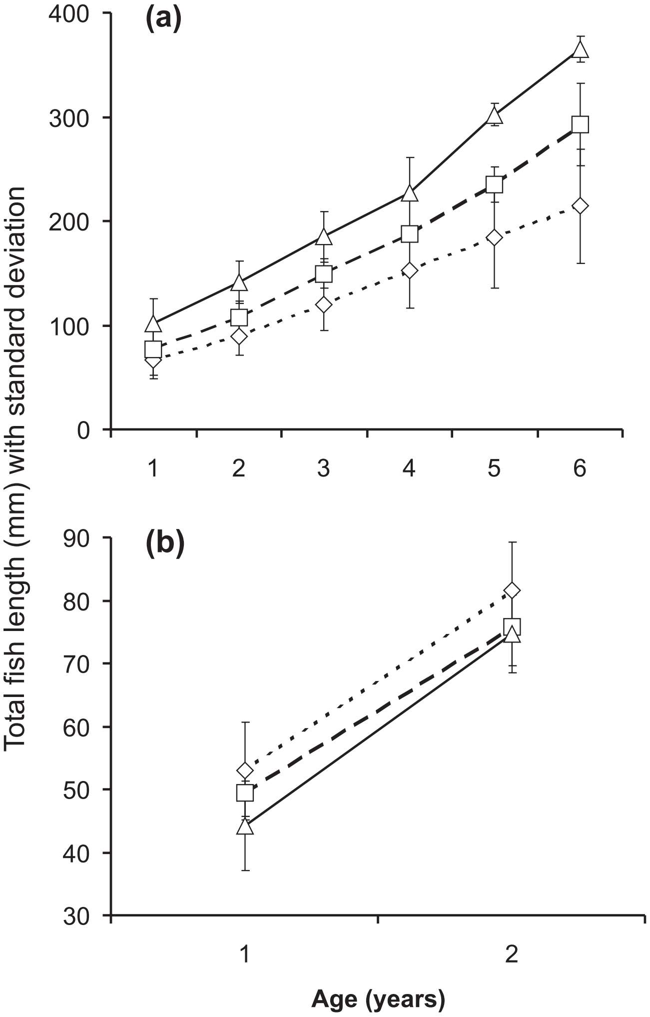
White sucker longevity showed no significant differences among lake groups (one-way ANOVA, $P = 0.27$) but tended to be higher in group I (10.7 ± 2.1 years (mean ± 1 SD), $n = 9$), intermediate in the group II (9.6 ± 2.7 years, $n = 5$), and lower in group III (7.7 ± 4.4 years, $n = 4$). Yellow perch also showed no significant differences in longevity among lake groups (one-way ANOVA, $P = 0.19$; group I, 4.0 ± 2.6 years, $n = 3$; group II, 3.8 ± 1.1 years, $n = 13$; group III, 2.9 ± 0.6 years, $n = 9$).

Feeding habits

Zoobenthic organisms were the main prey item in the diet of both size classes of white sucker and represented at least 85% of the gut content dry weight in all cases (Fig. 2). The fraction of zoobenthic organisms varied only among size classes (two-way ANOVA: model, $P = 0.0035$; size class, $P = 0.0004$; group, $P = 0.80$; $n = 22$), while the fraction of other prey items did not vary significantly either between size classes or among lake groups (Fig. 2).

The proportion of zooplankton in the diet of yellow perch was significantly related to both body size and lake group, decreasing from lake group I to lake groups II and III and

Fig. 1. (*a*) White sucker (*Catostomus commersoni*) and (*b*) yellow perch (*Perca flavescens*) growth trajectories. Lake groups: I, no piscivores (diamonds); II, with northern pike (*Esox lucius*) (squares); III, with northern pike and walleye (*Sander vitreus*) (triangles).



from small to large individuals (two-way ANOVA: model, $P = 0.0003$; size class, $P = 0.0004$; group, $P = 0.0078$; $n = 32$) (Fig. 2). The proportion of dipteran pupae decreased significantly with fish size but not among lake groups (two-way ANOVA: model, $P = 0.033$; size class, $P = 0.015$; group, $P = 0.19$; $n = 32$). The fraction of zoobenthos and prey fish did not show any significant difference among lake groups.

Discussion

This study shows that the abundance of piscivorous fish can have species-specific effects on the growth of white sucker and yellow perch. The growth of white sucker was higher in the presence of piscivorous fish, while that of yellow perch was not significantly different among lake groups and tended to be lower in the presence of piscivorous fish.

The relative abundance (CPUE) of white sucker was lower in the presence than in the absence of piscivorous fish. This result, coupled with the positive association between piscivory and both the growth and condition of white sucker, suggests that predation might have increased the mortality of white sucker, which in turn increased its growth by a release of intraspecific competition. The better growth and condition of white sucker from lake groups II and III compared with lake group I supports the hypothesis of an increased per capita availability of benthic resources with the increase of piscivory. The positive correlation between white sucker length-at-age 1–6 and the biomass of piscivorous fish gives complementary support to this interpretation.

Despite the apparent reduction in the levels of intra- and inter-specific competition by white sucker in lakes with northern pike and walleye, yellow perch growth was only slightly affected by piscivorous fish. Moreover, while white sucker growth and condition showed a positive response to piscivorous predation, only yellow perch condition showed a similar response. Yellow perch growth was negatively, although slightly, affected by the presence of piscivores during its first year. The superior competitive ability of white sucker over yellow perch could explain why yellow perch did not profit from its relatively low population density in lakes with piscivores and white sucker. Furthermore, yellow perch growth was inversely related to the biomass of piscivores in their first year of life. Stomach content data suggest that small yellow perch, which rely on zooplankton, might restrict their use of pelagic resources to reduce their predation risk by piscivores, thus reducing their growth. The lack of a significant relationship between piscivorous fish biomass and the length of age-2 yellow perch also suggests that the effects of piscivores were age specific, in contrast with what was observed for white sucker. Our results are in agreement with those of Olson et al. (2001), who suggested that stocking lakes with walleye could negatively affect the growth of small yellow perch if the competition levels are not reduced.

The growth of yellow perch can be considered as poor in our study lakes when compared with the observed growth range for the species in North America (Willis et al. 1991). In fact, such growth patterns are similar to those observed by Diana and Salz (1990) for stunted populations in the Great Lakes and by Hayes et al. (1992) for yellow perch populations in lakes dominated by white sucker. Hayes et al. (1992) suggested that competitive interactions between white sucker and yellow perch are strongly asymmetrical, with white sucker being a superior competitor on benthic invertebrates and eventually causing adult yellow perch to switch to alternative prey items such as zooplankton (Hayes et al. 1992). Magnan (1988) found such an asymmetrical competition between white sucker and brook trout, with the latter shifting from zoobenthos to zooplankton when living in sympatry with white sucker. As in the brook trout system (Magnan 1988; Tremblay and Magnan 1991), white sucker is better adapted to and thus more efficient than yellow perch in feeding on benthic organisms. Generally, fish having a ventrally oriented mouth, like white sucker, are more effective bottom feeders, whereas fish with a terminal mouth, like brook trout and yellow perch, are more effective in capturing surface and open-water prey (Webb 1984). Thus, it seems likely that the presence of piscivorous fish in our study lakes did not have a strong enough effect to ease the pressure on the yellow perch (populations were still stunted) because of the presence of a strong competition with white sucker. This

Table 4. Best models predicting the back-calculated length-at-age of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*).

Dependent variable	Independent variable	Standardized estimate	P	Partial R^2	Adjusted R^2	n	Model P
White sucker							
Length-at-age 1	PISC	0.58	0.002	0.37	0.60	18	0.0011
	CACO	0.35	0.042	0.16			
	PEFL	–0.38	0.028	0.14			
Length-at-age 2[a]	PISC	0.71	0.002	0.50	0.47	17	0.0001
Length-at-age 3	PISC	0.58	0.001	0.47	0.72	17	<0.0001
	CACO	0.36	0.018	0.10			
	COCL	0.46	0.004	0.20			
Length-at-age 4	PISC	0.64	0.006	0.40	0.37	17	0.0057
Length-at-age 5	PISC	0.66	0.007	0.44	0.39	15	0.0072
Length-at-age 6	PISC	0.68	0.005	0.47	0.43	15	0.0050
Yellow perch							
Length-at-age 1	PISC	–0.55	0.007	0.30	0.27	23	0.0067
Length-at-age 2	PEFL	0.63	0.004	0.39	0.36	19	0.0042

Note: Eight lake morphometric variables were used as independent variables in the analysis together with the relative biomass (BPUE) of piscivorous fish (PISC) and of five other major fish taxa: CACO, white sucker; COCL, white lakefish (*Coregonus clupeaformis*); PISC, northern pike (*Esox lucius*) plus walleye (*Sander vitreus*); PEFL, yellow perch. All stepwise regressions were significant after the sequential Bonferroni correction. Partial R^2 was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 2001).

[a] The dependent variable was transformed into ranks to homogenize the variance (Quinn and Keough 2002).

Table 5. Results of linear mixed models explaining variation in the log weight of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*).

(*a*) Type 3 test of fixed effects.

	White sucker			Yellow perch		
Effect	df	F	P	df	F	P
GROUP	2,14	47.7	<0.0001	2,21	25.7	<0.0001
log TL	1,14	93 998.4	<0.0001	1,21	148 844.0	<0.0001
log TL × GROUP	2,14	62.4	<0.0001	2,21	30.8	<0.0001

(*b*) Least square means log weight ± 1 SE.

Group	25th percentile[a]	50th percentile	75th percentile	25th percentile	50th percentile[b]	75th percentile[c]
I	1.74±0.01*a*	1.91±0.01*a*	2.35±0.01*a*	0.75±0.01*a*	0.87±0.01*a*	1.18±0.01*a*
II	1.79±0.01*b*	1.97±0.01*b*	2.43±0.01*b*	0.77±0.01*a*	0.89±0.01*a*	1.21±0.01*a*
III	1.79±0.01*b*	1.96±0.01*b*	2.42±0.01*b*	0.78±0.01*a*	0.91±0.01*a*	1.24±0.01*a*

Note: Adjusted weights (least square means) for the three lake groups were calculated at the 25th, 50th, and 75th percentiles of the independent variable (i.e., log TL, see text). The 25th, 50th, and 75th percentiles of log TL correspond to 180, 205, and 286 mm, respectively, for white sucker and 84, 92, and 117 mm, respectively, for yellow perch. Least square mean values with the same letter are not significantly different after the sequential Bonferroni correction. A total of 1270 white sucker and 2006 yellow perch were included in these statistical analyses.

[a] I versus III: $P = 0.012$.

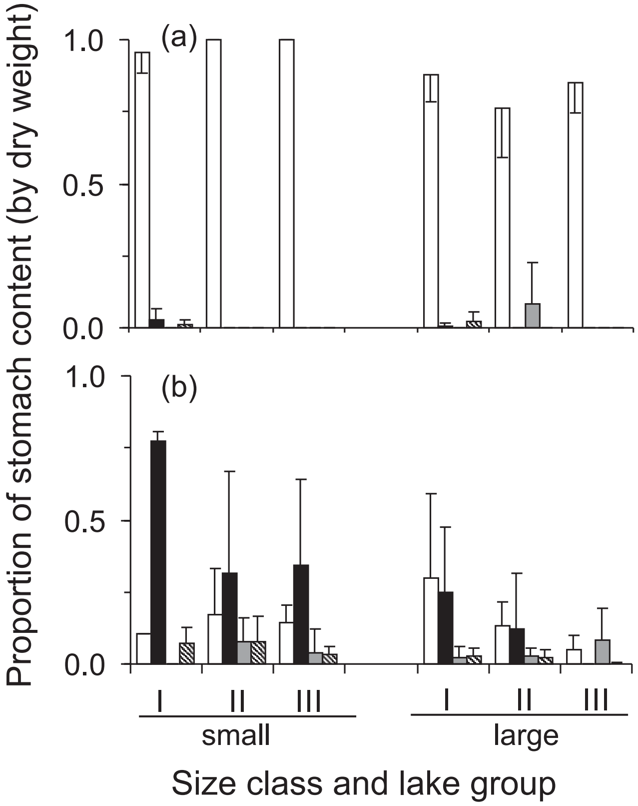
[b] I versus III: $P = 0.049$.

[c] I versus III: $P = 0.0069$.

might also be partially related to the mixed feeding regime of northern pike and walleye in our study lakes. The trophic positions of both walleye and northern pike are variable in the study lakes, suggesting that both species could include benthic invertebrates in their diet (Bertolo et al. 2005). However, stomach content analysis showed that piscivorous individuals were present in all group II and III lakes (A. Bertolo and P. Magnan, unpublished data). The higher growth of white sucker from lake group I compared with groups II and III corroborates the existence of a gradient of piscivory among our study lakes. Northern pike and walleye are in fact known to have strong effects on their prey and, given their different foraging behaviours (northern pike being a "lie-in-wait" predator, while walleye is a "rover" predator; sensu Moyle and Cech 1999), can have complementary effects on prey fish.

Despite the commonness of white sucker and yellow perch in the Canadian Shield, only a few studies have explicitly analyzed the interactions between these two species (e.g., Johnson 1977; Hayes et al. 1992). In contrast with our study, these studies showed that yellow perch responded in the short term to white sucker mass removal by an increase in growth. The differences in stability among these systems could explain this discrepancy, since these populations were

Fig. 2. Proportion of the four functional prey categories (by dry weight) in the stomach contents of two size classes (i.e., small and large) of (*a*) white sucker (*Catostomus commersoni*) (<200 and >200 mm) and (*b*) yellow perch (*Perca flavescens*) (<90 and >90 mm) in the three lake groups: I, no piscivores; II, with northern pike (*Esox lucius*); III, with northern pike and walleye (*Sander vitreus*). Open bars, zoobenthos; solid bars, zooplankton; shaded bars, fish; hatched bars, dipteran pupae.



probably not in a stable state compared with ours. A time lag in the compensatory response of white sucker might explain the short-term positive effects of its removal on yellow perch growth, as was observed by Johnson (1977), an effect likely to be dampened over the longer term. It has been shown that white sucker can rapidly recover to preremoval biomass levels by increasing its growth rate and fecundity after mass removal (i.e., within 3 years after mass removal; Brodeur et al. 2001). Thus, long-term improvement in the growth of stunted yellow perch populations by mass removal of competitors, as suggested by Johnson (1977) and Hayes et al. (1992), seems unlikely when this species cooccurs with white sucker.

In conclusion, our results suggest that the effects of piscivores on the growth of their prey can depend on species interactions and thus on community structure. By reducing the abundance of a prey, piscivores can favour a compensatory growth response of the prey (e.g., white sucker) by a release of intraspecific competition. However, while one of the prey species will profit from the competitive release (e.g., white sucker), the other will not (e.g., yellow perch), owing to interspecific competition with the first prey species. Moreover, differences in habitat use by juveniles of different species may be related to differences in vulnerability to piscivores. The piscivores can thus affect the growth of more vulnerable species (e.g., yellow perch) by restricting juveniles to a suboptimal diet. Given the large overlap in the distribution of these species, such interactions are likely to be common in Canadian Shield lakes and should be considered in the management of yellow perch populations as well as in studies testing the top-down effect of piscivores.

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