

Decoupling of pelagic and littoral food webs in oligotrophic Canadian Shield lakes

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The importance of top-down effects of piscivorous fish on phytoplankton in natural oligotrophic lakes is still debated. In this study, we analyzed patterns in phytoplankton and zooplankton abundance in 37 oligotrophic Canadian Shield lakes in relation to variations in both piscivorous fish predation and resources (total phosphorus; TP). Zooplankton community structure (but not total biomass) was partially affected by the variation in fish predation while the phytoplankton community structure and total biomass showed no response. Carbon isotope analyses revealed that the lack of top-down effects is due to the uncoupling of the littoral and the pelagic food webs. We found that the fish community depends mostly on benthic resources, suggesting that only low planktivory occurred in our study lakes. Due to the absence of specialized zooplanktivorous fish, zooplankton is poorly exploited in these lakes and thus able to control phytoplankton by grazing. A comparison of our data with published studies on the TP–chlorophyll *a* relationships in both natural and manipulated systems shows that the phytoplankton biomass per unit of TP is relatively low in Canadian Shield lakes.

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Since the seminal papers by Hrbáček (1962) and Brooks and Dodson (1965) on the trophic effects of fish on zooplankton communities, there has been a long-lasting debate on the strength of top-down interactions in lake ecosystems (Brett and Goldman 1996). Different factors, including trophic bottlenecks, food web complexity, and ontogenetic omnivory, have been suggested to dampen the transmission of the effects of predators on organisms with lower trophic positions (Pinel-Alloul et al. 1998, Persson 1999). Although zooplanktivorous fish can have a strong positive impact on phytoplankton through a reduction of zooplankton grazing in experimental ecosystems (Carpenter and Kitchell 1993) and in natural eutrophic lakes (Jeppesen et al. 2003), the existence of

such “trophic cascades” in unmanipulated oligotrophic lakes has recently been questioned. By using fish presence–absence data, Currie et al. (1999) have shown that fish predation has no detectable impact on phytoplankton biomass in oligo-mesotrophic Canadian Shield lakes. Furthermore, in an analysis of 466 lakes representing a wide range of nutrient conditions, Jeppesen et al. (2003) showed that trophic cascades affecting phytoplankton are more likely to occur in eutrophic than in oligotrophic lakes. These empirical results corroborate the predictions of Sarnelle (1992), who suggested that the strength of top-down effects of planktivorous fish should be a positive function of nutrient concentration, and of Elser and Goldman

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(1991), who stated that the effects of zooplankton on phytoplankton would be low in oligotrophic lakes because of the dominance of inefficient grazers such as copepods. In contrast, the “bottom-up/top-down” model of McQueen et al. (1986) predicts that the strength of trophic cascades is a negative function of enrichment because of the increasing importance of inedible algae along the nutrient gradient and the consequent increasing likelihood of a trophic bottleneck between grazers and algae. It thus seems important to take into account nutrient status when analyzing trophic cascades in lakes.

It has been shown that the benthic pathway is particularly important in nutrient-poor lakes, where low phytoplankton biomass and high transparency favour benthic production (Vadeboncoeur et al. 2003). These conditions should facilitate trophic cascades in oligotrophic lakes because zooplanktivorous fish can be subsidized from the littoral food web (Schindler and Scheuerell 2002). However, this paradigm of seeing fish as integrators of benthic and pelagic habitats (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002) is not fully supported by studies conducted in oligotrophic lakes (Currie et al. 1999, Jeppesen et al. 2003). Thus the strength of the pelagic–littoral coupling is not still fully understood in these systems.

The objective of our study was to test the trophic cascade hypothesis by analyzing variations in the phyto- and zooplankton communities in Canadian Shield lakes with different degrees of piscivory (hypothesis 1). Furthermore, we tested two other hypotheses to explain the expected lack of trophic cascades in these systems: i) the effects of piscivorous predation are not transmitted to the base of the food web because of a trophic bottleneck caused by inedible algae (hypothesis 2), and ii) there is no trophic link between piscivorous fish and pelagic algae (i.e. a decoupling of pelagic and littoral food webs; hypothesis 3). Hypothesis 2 was tested by comparing the proportion of grazing-resistant algae among systems with different piscivory levels while hypothesis 3 was tested by determining the ^{13}C isotopic signature in fish, benthic invertebrates and zooplankton.

It has been predicted that lakes with piscivores will have lower chlorophyll *a* for a given amount of total phosphorus compared with lakes without piscivores (Drenner and Hambright 2002). Accordingly, the importance of trophic cascades has been tested in several studies by comparing the relationships between total phosphorus and chlorophyll *a* (hereafter referred to as TP–Chl) in lakes with different food webs. Therefore, we compared the TP–Chl relationships in our study lakes with similar relationships from the literature (Mazumder 1994, Currie et al. 1999) to estimate the importance of phytoplankton control in our system. We thus avoided confounding the effects of piscivory and productivity. This approach is particularly useful in comparative

studies where fish communities were not manipulated and therefore where it is not possible to assess the variation of Chl for a given lake in conditions of low and high piscivory.

Methods

Study area

Thirty-seven thermally stratified, unperturbed head-water lakes were selected on the basis of comparable size, basin morphometry, and catchment properties to test hypotheses 1 and 2. The lakes were oligotrophic, slightly acidic, and had a moderate humic content (Table 1). All the lakes were located within a 50 000 km² area around Réservoir Gouin in Haute-Mauricie, Québec, Canada (48°50' N, 75°00' W). The bedrock, covered by thin glacial tills, consists mainly of granite and gneiss. This area overlaps the transition zone of the boreal mixed and coniferous forests. Wetlands are sometimes present, but their area does not exceed 5% of the drainage area of the study lakes. Lake morphometry and catchment properties were determined from 1:20000 topographic maps, aerial photographs, and 15–25 echo-sounder transects. More detailed information about the study area can be found in Carignan et al. (2000).

Fish sampling

Eleven lakes were sampled in 1996, nine in 1997, nine in 2000, and eight in 2001. Fish data obtained in 1996 and 1997 were related to limnological analyses conducted in 1996 while fish data collected in 2000 and 2001 were related to limnological analyses conducted in 2000. Fish communities were sampled once between June and August using 102.3 × 2.7 m experimental monofilament gill nets 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, 0.32, 0.32, 0.32 and 0.32 mm, respectively). The nets were set perpendicular to the shore, with small and large meshes alternating from the shore among gill nets, and at regular intervals around the lake, with the first net location having been randomly selected. The fishing effort was six nets per night for lakes < 50 ha, eight nets per night for lakes 50–100 ha, 10 nets per night for lakes 100–150 ha and 12 nets per night for lakes > 150 ha. The nets fished for 18–19 h, covering the period between 16:00 and 10:30 h.

We considered only those species representing at least 1% of the average total fish biomass (biomass per unit effort [BPUE]; g of fresh weight per gill net per night) in our statistical analyses (below). Of the 25 taxa found in this survey, we retained northern pike (*Esox lucius*), white sucker (*Catostomus commersoni*), lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*), yel-

Table 1. Selected watershed characteristics and morphometric variables and relative biomass (BPUE; g fresh weight net⁻¹ night⁻¹) of major fish taxa in the study lakes. The lakes were classified into three groups according to the structure of the fish community (group I: no large piscivores; group II: with northern pike; and group III: with northern pike and walleye). Zoo: phyto indicates the ratio between the biomass of zooplankton and phytoplankton. Prey fish: all small-bodied species (mainly cyprinids) pooled. The occurrence of each fish species is indicated in parentheses.

Variable	Lake group Mean ±SD			Additional lakes ¹ (n = 17)
	I (n = 7)	II (n = 15)	III (n = 15)	
Lake morphometry				
lake area (km ²)*	0.49 ± 0.24	0.28 ± 0.15	0.62 ± 0.32	0.49 ± 0.49
maximum depth (m)	13.0 ± 3.5	11.1 ± 4.2	12.0 ± 4.8	15.3 ± 7.6
mean depth (m)	5.0 ± 1.7	4.1 ± 2.0	4.1 ± 1.67	5.0 ± 1.9
watershed area (km ²)	2.89 ± 1.65	2.61 ± 1.62	3.41 ± 1.89	4.9 ± 5.3
shoreline development	2.0 ± 0.8	1.9 ± 0.3	1.8 ± 0.5	1.3 ± 0.7
Physico-chemical parameters				
TP (µg l ⁻¹)	6.6 ± 1.8	8.4 ± 1.9	9.1 ± 3.3	10.6 ± 3.1
TN (µg l ⁻¹)	229.5 ± 55.8	251.5 ± 36.1	235.6 ± 53.2	321.0 ± 131.4
Chl a (µg l ⁻¹)	2.0 ± 0.6	2.2 ± 0.5	2.3 ± 0.8	2.8 ± 0.8
pH	6.4 ± 0.2	6.5 ± 0.4	6.4 ± 0.4	6.5 ± 0.4
DOC (µg l ⁻¹)	4.9 ± 1.3	6.5 ± 2.2	6.7 ± 2.6	7.0 ± 3.2
Chl: TP	0.30 ± 0.04	0.27 ± 0.07	0.26 ± 0.07	
Zoo: phyto	0.30 ± 0.14	0.41 ± 0.28	0.51 ± 0.71	
Fish biomass (BPUE; g net⁻¹ night⁻¹)				
brook charr ^{nt}	656 ± 505 (4)	0 ± 0 (0)	0 ± 0 (0)	1738 ± 1761 (3)
yellow perch	704 ± 674 (3)	105 ± 138 (9)	257 ± 458 (15)	129 ± 60 (12)
white sucker	3224 ± 2113 (7)	1925 ± 2764 (11)	1828 ± 1549 (12)	2801 ± 2315 (12)
northern pike ^{nt}	0 ± 0 (0)	2398 ± 1387 (15)	2061 ± 1321 (15)	2750 ± 1139 (13)
walleye ^{nt}	0 ± 0 (0)	0 ± 0 (0)	3373 ± 2046 (15)	3294 ± 943 (5)
lake whitefish ^{nt}	0 ± 0 (0)	2884 ± 2080 (2)	2903 ± 2117 (12)	2344 ± 2719 (6)
fallfish ^{nt}	177 ± 0 (1)	74 ± 0 (1)	493 ± 429 (11)	229 ± 284 (5)
prey fish*	354 ± 203 (6)	37 ± 28 (10)	9 ± 14 (6)	150 ± 250 (12)
Total fish community*	4234 ± 2811 (7)	4295 ± 2797 (15)	9845 ± 3854 (15)	6564 ± 4173 (17)

¹: an additional set of lakes was used only for the stable isotope analyses.

*: significantly different among the three lake groups (ANOVA) after the sequential Bonferroni correction.

^{nt}: not tested due to low sample size. Note that the means do not include lakes where a given species was missing.

low perch (*Perca flavescens*), fallfish (*Semotilus corporalis*), and brook charr (*Salvelinus fontinalis*). The BPUE of other small prey fish, which are potential planktivores (Scott and Crossman 1973), were pooled into a single “prey” category: pearl dace (*Margariscus margarita*), golden shiner (*Notemigonus crysoleucas*), rainbow smelt (*Osmerus mordax*), finescale dace (*Phoxinus neogaeus*), northern redbelly dace (*P. eos*), lake chub (*Couesius plumbeus*), trout perch (*Percopsis omiscomaycus*), spot-tail shiner (*Notropis hudsonius*), common shiner (*Luxilus cornutus*), logperch (*Percina caprodes*), blacknose shiner (*Notropis heterolepis*), brook stickleback (*Culaea inconstans*), ninespine stickleback (*Pungitius pungitius pungitius*), and mottled sculpin (*Cottus bairdi*). Burbot (*Lota lota*) was excluded from the analyses due to both low biomass and low occurrence (four lakes).

The study lakes were classified into three groups according to the presence/absence of northern pike and walleye: I) lakes without large piscivores, II) lakes with northern pike, and III) lakes with northern pike and walleye. These two species are 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), should have complementary and thus additive effects on the potential planktivores. We expected

piscivory to be different among these three groups of lakes. However, because some potential piscivores such as adult yellow perch, brook charr, burbot, and smelt are present in lake group I, we took them into account when computing the biomass of potential piscivores among the three lake groups. We considered all those individuals larger than a given threshold size, defined as the minimum size at which piscivory was observed for each given species, to be potential piscivores. The sizes of piscivory onset that we used were 100 mm for yellow perch, 35 mm for walleye, 45 mm for northern pike, and 103 mm for burbot (Mittelbach and Persson 1998); 200 mm for brook charr (East and Magnan 1991); and 65 mm for rainbow smelt (Evans and Loftus 1987). The trophic positions of the major fish taxa, estimated on the basis of stable isotope analysis (below), were compared among lake groups to give additional validation of our hypothesis about differences in the levels of piscivory among the lake groups.

Plankton and water chemistry analyses

Water for the analyses of zooplankton, phytoplankton, and chemical parameters was sampled in June, July, and September of 1996 (20 lakes) and in June and August of

2000 (17 lakes). We then used average summer values in statistical analyses. Zooplankton samples were taken over the entire water column with a 53- μm mesh cantilevering net, while phytoplankton and chemical parameters were sampled in the euphotic zone. To convert chlorophyll a ($\mu\text{g l}^{-1}$) into dry weight, we multiplied by 67 (Jeppesen et al. 1997). See Patoine et al. (2000), Planas et al. (2000), and Carignan et al. (2000) for details on the analytical methods.

The same sampling and analytical protocols were used in both 1996 and 2000, with the exception of the estimations of zooplankton biomass. In 1996, the different taxa (mostly species) were first counted and then measured to estimate specific biomass. The size of the first 30 specimens of each crustacean (length) and rotifer (length and width) species was measured and mean size estimates were converted into dry biomass using length–mass relationships (Patoine et al. 2000). Specific biomasses were aggregated into higher-level taxonomic units in order to work with functional groups rather than with species. In 2000, only a sub-sample of nine lakes was analyzed; the zooplankton samples were first counted, but specific biomasses were estimated by using the average biomass per species estimated in 1996. Therefore, to ensure that the two methods of estimating of zooplankton biomass did not bias our analyses, we always compared the results of these analyses with and without the 2000 data. The results for the pooled data always gave results similar to those without the 2000 data, so we will report only results of the pooled samples.

It is known that different features of phytoplankton, such as size (Cyr and Curtis 1999), the presence of protective structures (De Bernardi and Giussani 1990), or other taxon-specific features such as taste or cell mobility (Verity and Paffenhofer 1996), can influence zooplankton grazing. Therefore, to explore the response of the phytoplankton community to zooplankton grazing pressure, we classified the phytoplankton both on the basis of cell size and edibility. Algae were classified into nine groups based on cell size (μm^3) following Margalef (1995): a) $x < 12.5$; b) $12.5 \leq x < 50$; c) $50 \leq x < 200$; d) $200 \leq x < 800$; e) $800 \leq x < 3200$; f) $3200 \leq x < 12800$; g) $12800 \leq x < 51200$; h) $51200 \leq x < 204800$; and i) $204800 \leq x < 819200$. Finally, algae were classified as inedible if one or more of the following features were encountered: i) greatest axial length dimension of single cells or colonies $> 20 \mu\text{m}$; ii) known potential production of toxic compounds; or iii) presence of spines or of a rigid lorica.

Comparison of TP–Chl relationships with published data

To assess the strength of top-down control in lakes with different trophic levels, we compared TP–Chl relation-

ships in our study lakes to those of Currie et al. (1999) and Mazumder (1994) for similar ranges of TP. We obtained the data set of Currie et al. (1999) directly from the first author (D. Currie, Ottawa Univ., pers. comm.) while the data published by Mazumder (1994) were obtained by digitalizing his Fig. 3a and by extracting the position of each point in the Cartesian axes using the tpsDig© software package (Rohlf 2001). As in our study, the Currie et al. (1999) data set is composed of data from natural Canadian Shield lakes, with and without piscivorous fish. The Mazumder (1994) data set is based on a literature survey including data from both natural and manipulated lakes and mesocosms from North America (USA and Canada) and Europe (e.g. Czech Republic, Denmark, Norway, the Netherlands). Because information on the composition of fish communities was not always available, Mazumder classified the systems by using different clues for the presence of piscivores, such as the biomass of planktivores, the presence of large *Daphnia*, or the mean cladoceran body size. He used the terms “even-link” and “odd-link” to characterize the supposed structure of the food web: the even-link systems should have high piscivory and low zooplanktivory and vice-versa for the odd-link systems.

Stable isotope analysis

We analyzed the stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in zooplankton, benthic organisms, and fish to determine the origin of the carbon (littoral or pelagic) consumed by fish (hypothesis 3) (Peterson and Fry 1987) and to determine their trophic position (Vander Zanden and Rasmussen 1999). Samples were collected in 1996 (zooplankton and fish), 1997 (fish), and 1999 (zoobenthos).

Since the isotopic data for a given lake were not always available for all three trophic groups (fish, 37 lakes; zooplankton, 1 lake; benthic organisms, 20 lakes), we included data from seventeen additional comparable lakes of the same area ($48^{\circ}50' \text{ N}$, $75^{\circ}00' \text{ W}$) (Table 1). The watershed of these lakes underwent some perturbations in 1995 (fire or logging). The $\delta^{13}\text{C}$ signature of benthic organisms was not affected by these perturbations, but their $\delta^{15}\text{N}$ signature was slightly affected (Garcia 2001). Despite this, we used the $\delta^{15}\text{N}$ signature of fish and primary consumers (zooplankton and benthic organisms) to estimate their trophic position, assuming that the effect of these perturbations would not change the estimation of the trophic position. Lake morphometry, catchment properties, and fish communities were determined as above. The physico-chemical properties of these lakes were also comparable to those of the above data set (Carignan et al. 2000, Garcia 2001).

Fish and zooplankton were sampled following the protocol described above, the exception being that zooplankton samples were collected with a 200- μm mesh net to avoid detritus and algae contamination. Zooplankton samples were collected three times during the ice-free season (June, July and September) in 1996, but only the averaged values were used in the analyses. Benthic invertebrates (trichoptera, ephemeroptera, amphipoda, and odonata) were collected in the littoral zone (<2 m deep) of each lake with hand-held dip nets. Carbon isotopic ratios were measured on 0.7-mg samples of freeze-dried benthic invertebrates, zooplankton and fish. For each lake, a bulk zooplankton sample, at least two individuals from each benthic invertebrate group and three individuals from each fish species were used for isotopic determinations. These analyses were performed on a continuous flow Isoprime mass spectrometer coupled to a CHN analyzer model NC 1500. Stable isotope values are expressed in δ notation as parts per thousand deviations from a standard:

$$\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 1000$$

where R is $^{13}\text{C}/^{12}\text{C}$. The standard reference for $\delta^{13}\text{C}$ was Pee Dee Belemnite limestone.

The trophic position of fish (TrP_{fish}) was estimated relative to a baseline $\delta^{15}\text{N}$ value as follows:

$$\text{TrP}_{\text{fish}} = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{base}})/3.4] + 2$$

where $\delta^{15}\text{N}_{\text{fish}} = \delta^{15}\text{N}$ of fish, $\delta^{15}\text{N}_{\text{base}} = \delta^{15}\text{N}$ of primary consumers (zooplankton or benthic organisms), and 3.4 = one trophic level increment in $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen 1999). $\delta^{15}\text{N}_{\text{base}}$ values were corrected for variations in baseline $\delta^{13}\text{C}$ as suggested by Vander Zanden and Rasmussen (1999).

Lake-averaged $\delta^{13}\text{C}$ signatures were compared graphically among fish species, bulk zooplankton and benthic invertebrates in order to assess the origin of the C consumed by fish. The $\delta^{13}\text{C}$ signatures of fish were first averaged by taxon and by lake before calculating lake averages. We also graphically analyzed the distribution of TrP_{fish} and $\delta^{13}\text{C}$ signatures separately for each individual fish species.

Statistical analyses

Hypothesis 1a: biomass variation by taxon

We used redundancy analysis (RDA; CANOCO program, version 4.02; ter Braak and Smilauer 2002) to relate (i) the variation in the zooplankton community structure (biomass of major functional groups) to the structure of the fish community (BPUE of dominant taxa and lake groups; see above) and (ii) the variation in the size structure of the phytoplankton community to the biomass of both zooplankton and fish taxa. RDA explicitly models multiple response variables against

multiple predictor variables and thus can be viewed as an extension of multiple linear regression. The fish matrix included the BPUEs of the eight selected taxa plus a dummy variable coding for the fish community type (lake groups I, II and III). The inclusion of the relative biomasses of the different fish taxa allowed a more accurate estimation of the potential top-down effect of fish. To control for the effects of sampling year, a dummy variable corresponding to the year was used as a covariable in the ordinations. For RDA (ii), TP was also used as a covariable to control for the effects of nutrients.

The variables that contributed most to explaining the variation in the dependent variables were selected using a forward selection procedure available in CANOCO with a cut-off point of $p=0.10$ (i.e. alpha-to-enter, as in multiple regression analysis) based on 1999 Monte Carlo permutations. This relatively liberal alpha level was chosen in order to let potential suppressor variables be included in the model (Draper and Smith 1998). However, in the final RDA model, we focussed only on those variables significant at the more conservative alpha level of 0.05. The statistical significance of both selected variables and ordination axes ($\alpha=0.05$) were tested by a Monte Carlo permutation test ($n=1999$). The collinearity between explanatory variables was reduced by eliminating those selected variables with a variation inflation factor (VIF) greater than 10 (ter Braak and Smilauer 2002).

Detrended correspondence analysis (DCA) was used to evaluate if data transformation was needed (Legendre and Gallagher 2001). If the range of the ordination sample scores obtained by correspondence analysis was greater than the threshold of 1.5 standard deviations, we transformed the data according to Legendre and Gallagher (2001) before running the RDAs. The data were transformed using the five suggested transformations (i.e. chord distance, chi-square metric, chi-square distance, distance between species profiles and Hellinger distance; Legendre and Gallagher 2001), and ordinations (RDA) were produced for each transformed species matrix. In the absence of theoretical criteria for the choice of the best transformation, we selected the transformation explaining the largest part of the variation in the ordinations for subsequent analyses (Legendre and Gallagher 2001). For our data sets, the "distance between species profiles" transformation gave the best results.

Hypothesis 1b: biomass variation by trophic level

We used stepwise multiple regressions to test the hypotheses (i) that variations in the total phytoplankton biomass (measured as chlorophyll a) were related to fish biomass and nutrient availability, (ii) that variations in the total zooplankton biomass were related to fish biomass and nutrient availability, and (iii) that the

percent of edible algae was related to the biomass of zooplankton and fish taxa. Residual scatter plots, normal probability plots, and partial residual plots were used to determine if the assumptions of the multiple regression were satisfied (i.e. normality, linearity and homoscedasticity of residuals). When these conditions were not fulfilled, the data were log or square-root transformed. Collinearity between the independent variables was evaluated by examination of the VIF (above).

Hypothesis 1c: TP–Chl relationship

ANCOVA was used to test the effect of fish community on the TP–Chl relationship in our data set. To improve the power of the test for the effect of piscivores, we pooled our data and those from Currie et al. (1999) into a single data set for the Canadian Shield lakes (hereafter referred to as CSL). ANCOVA was also used to compare the effects of the fish community structure between the CSL data set and the data from Mazumder (1994). Differences in the elevations of the four regression lines were tested by pair-wise comparisons of adjusted Chl values (Goodnight and Harvey 1978).

Hypothesis 2: trophic bottleneck

The proportions of grazing-resistant phytoplankton were compared among lake groups by using one-way ANOVA. Data were arcsin transformed to normalize the residuals. If this procedure was not successful, we transformed the data in ranks.

When needed, we applied a sequential Bonferroni correction to control for the table-wise inflation of type I error (see text and table captions). However, p-values that fall between the standard (0.05) and the corrected alpha level should be carefully considered given the conservativeness of the Bonferroni approach (Moran 2003).

Hypothesis 3: littoral–pelagic coupling

Comparisons among lake groups of the $\delta^{13}\text{C}$ signatures and the trophic position data for fish were conducted graphically.

Results

Levels of piscivory

The modal sizes of yellow perch, brook charr, and rainbow smelt in lake group I were respectively 87, 155 and 205 mm, while their 90th percentiles corresponded to 122, 329 and 215 mm. Only two burbot were caught in group I lakes (mean size = 259 mm). These data confirm the rarity of large piscivorous individuals in lake group I. In contrast, the modal sizes of northern pike (lake groups II and III) and walleye (lake group III) were 533 and 345 mm and their 90th percentiles were 708 and 458

mm, respectively. The combined BPUE of these large piscivores, which were absent from lake group I, was significantly lower in lake group II ($2398 \pm 1387 \text{ g net}^{-1} \text{ night}^{-1}$; mean \pm SD) than in lake group III ($5432 \pm 2788 \text{ g net}^{-1} \text{ night}^{-1}$; one-way ANOVA: $F_{1,28} = 15.6$, $p = 0.0005$), thus confirming the existence of a gradient of piscivory among lake groups. The BPUE of potential piscivores (Methods) followed a similar pattern, being relatively low in lake group I ($539 \pm 584 \text{ g net}^{-1} \text{ night}^{-1}$), intermediate in group II ($2420 \pm 1301 \text{ g net}^{-1} \text{ night}^{-1}$), and relatively high in group III ($5792 \pm 3027 \text{ g net}^{-1} \text{ night}^{-1}$) (ANOVA on rank-transformed data: $F_{2,34} = 30.1$, $p < 0.0001$; Tukey's test: $I < II < III$). The proportion of the BPUE of potential piscivores also differed among lake groups, being lower in lake group I ($9.1 \pm 9.5\%$; mean \pm SD) than in lake groups II ($69.3 \pm 29.8\%$) and III ($56.0 \pm 19.2\%$) (ANOVA on rank-transformed data: $F_{2,34} = 15.6$, $p < 0.0001$; Tukey's test: $I < II$, III).

Furthermore, the biomass of prey fish was negatively correlated to the BPUE of large piscivores (Pearson's $r = -0.43$, $p = 0.0001$, $n = 37$), decreasing from lake group I to lake groups II and III (Table 1). Among the other taxa, only the BPUEs of lake whitefish and fallfish were significantly correlated with the biomass of large piscivores (respectively, $r = 0.45$, $p = 0.005$ and $r = 0.43$, $p = 0.008$).

Effects of fish on zooplankton communities

The forward selection procedure of the RDA retained only the BPUE of northern pike and walleye to explain zooplankton biomass (Fig. 1). The overall ordination was significant, but the small eigenvalues and taxa–environmental correlations (Table 2) indicate that the overall relationship between zooplankton assemblage and fish biomass was not very strong and that only a small portion of the variation in zooplankton assemblage was explained by the independent variables. The first axis explained 14.6% of the variation of the zooplankton species biomass and was mostly related to variations in northern pike biomass. This axis was positively correlated with *Holopedium gibberum* and rotifers and negatively correlated with both calanoids and cyclopoids. The second axis summarized 8.6% of the variation of the zooplankton species biomass and was mostly related to variations in walleye biomass and correlated positively with daphnid biomass (Fig. 1). Results were similar when using only the 1996 data.

The biomass of zooplankton species did not differ among the three lake groups (Table 3). However, the biomasses of daphnidae (mainly *Daphnia* spp.), *H. gibberum*, and total zooplankton tended to decrease from piscivore to piscivore-free lakes (Table 3). No independent variable (biotic or abiotic) was selected by

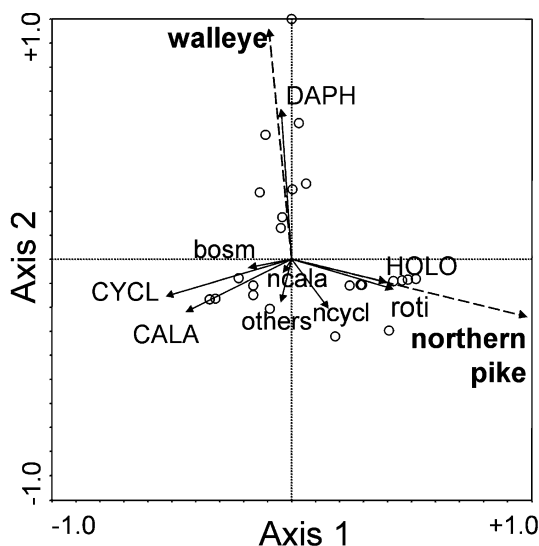


Fig. 1. RDA ordination diagram on the effects of fish (biomass of major taxa; dotted arrows) on zooplankton (biomass per group; solid arrows). The axes scaling is 1 for both fish and zooplankton variables and 0.29 for sites (open circles). Taxa are indicated as follows: DAPH: daphnids; bosm: bosminids; HOLO: holopedidae; others: other cladocerans (mostly benthic taxa); CALA: adult and copepodite calanoids; ncala: calanoid nauplia; CYCL: adult and copepodite cyclopoids; ncycl: calanoids nauplia; and roti: rotifers. Capitals are used to indicate those groups whose variability was best explained by the first two axes of the RDA.

the stepwise procedure of the multiple regression to explain variations in total zooplankton biomass.

Top-down effects of fish and zooplankton on phytoplankton

The RDA analyses showed no significant effects of zooplankton or fish on the phytoplankton community structure ($p > 0.05$). We obtained similar results when using only the 1996 data. The percent of edible algae was

Table 2. Results of the redundancy analysis for zooplankton communities in the study lakes explained by the biomass of major fish taxa ($n = 37$).

Variable	Axis 1	Axis 2
Canonical coefficients for environmental variables		
northern pike	1.054*	0.104
walleye	0.263	1.082*
Correlations of environmental variables with ordination axes		
northern pike	0.512*	-0.144
walleye	-0.052	0.608*
Summary statistics for ordination axes		
eigenvalue	0.14	0.08
species–environment correlation	0.53	0.61

Monte Carlo probabilities for significance of the first eigenvalue: 0.036; for the sum of all eigenvalues: <0.01 (1999 permutations).

*: significant values at $\alpha = 0.05$.

Table 3. Average zooplankton biomass ($\mu\text{g l}^{-1}$) per taxon in the three lake groups (see Table 1 for the definition of lake groups).

	Lake group Mean \pm SD		
	I (n=7)	II (n=11)	III (n=11)
Cladocerans			
bosminids	0.4 \pm 0.4	0.2 \pm 0.1	0.4 \pm 0.5
daphnids	2.9 \pm 2.3	5.3 \pm 5.2	15.0 \pm 31.8
holopedidae	7.6 \pm 6.3	28.6 \pm 37.7	18.6 \pm 18.8
others	0.4 \pm 0.5	0.4 \pm 0.6	0.17 \pm 0.14
Calanoids			
adults+copepodites	11.1 \pm 5.0	7.4 \pm 4.4	8.1 \pm 7.4
nauplii	0.5 \pm 0.3	0.9 \pm 0.9	0.7 \pm 0.5
Cyclopoids			
adults+copepodites	9.8 \pm 5.0	7.1 \pm 3.2	9.0 \pm 6.2
nauplii	0.7 \pm 0.5	1.1 \pm 0.7	0.8 \pm 0.5
rotifers	2.4 \pm 1.8	5.2 \pm 3.7	2.6 \pm 1.2
Total	35.8 \pm 11.0	56.3 \pm 41.4	55.3 \pm 47.9

Daphnids = mainly *Daphnia* spp.; holopedidae = *Holopedium gibberum*; others = other herbivorous cladocerans, mostly sidiidae and chydoridae.

not significantly different among the three lake groups (Fig. 2A) and was not correlated with any zooplankton or fish taxa (stepwise multiple regression analysis, $p > 0.05$).

The univariate approach (one-way ANOVA) revealed a significant among-group difference only for the smallest size fraction (a: $< 12.5 \mu\text{m}^3$) of the phytoplankton community ($F_{2,34} = 7.6$, $p = 0.002$), which decreased from lakes I to III and was intermediate in lake group II (Tukey's test: $p < 0.05$; Fig. 2B). No cells belonging to the largest size group were found ($i: 204800 \leq x < 819200 \mu\text{m}^3$).

The zooplankton:phytoplankton ratio was not significantly different among the three lake groups (Table 1).

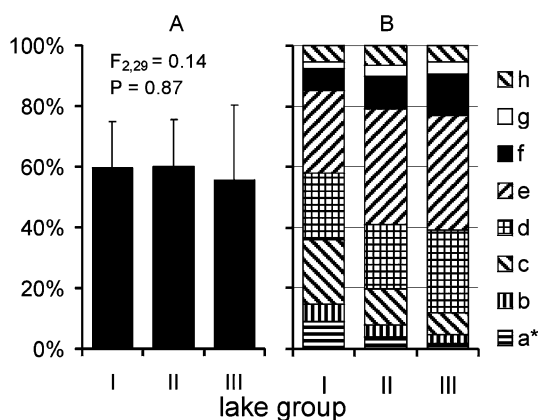


Fig. 2. Proportions of (A) edible and (B) different size classes of algae ($\mu\text{g fresh weight l}^{-1}$) in the three lake groups. Algae were classified into eight groups based on cell biovolume (μm^3): a) < 12.5 ; b) $12.5 \leq x < 50$; c) $50 \leq x < 200$; d) $200 \leq x < 800$; e) $800 \leq x < 3200$; f) $3200 \leq x < 12800$; g) $12800 \leq x < 51200$; and h) $51200 \leq x < 204800$. Significant among-group differences in the absolute values after the sequential Bonferroni correction are indicated by an asterisk ($\alpha = 0.05$).

TP–Chl relationships

We found a positive significant relationship between TP and Chl in our study lakes (Fig. 3), but no significant differences were found among the three lake groups (ANCOVA: $P=0.99$). Multiple regression analysis supported the conclusion of the ANCOVA: among nutrient, fish and zooplankton variables, only TP was selected and explained 52% of the total variation in Chl (Fig. 3). Pooling our data with the data of Currie et al. (1999) did not change these conclusions. Again, the ANCOVA showed no significant differences between lakes with and without piscivores ($p=0.49$; Fig. 4A).

The amount of Chl for a given TP concentration was lower in the CSL data set (both with and without piscivorous fish) than in Mazumder's odd-link systems (low piscivory and high zooplanktivory; Fig. 4B). In contrast, no significant differences were found for the adjusted concentrations of Chl between the CSL (both with and without piscivores) and the even-link systems (high piscivory and low zooplanktivory; Fig. 4B).

The Chl:TP ratio was not significantly different among lake groups (Table 1).

Stable isotopes

We found no correlation between the $\delta^{13}\text{C}$ of benthic invertebrates and zooplankton (Pearson's $r=0.37$, $p=0.13$, $n=18$). Furthermore, benthic invertebrates had significantly less negative $\delta^{13}\text{C}$ values than zooplankton (respectively -28.38 ± 1.92 and -32.38 ± 1.41 mean \pm SD; repeated-measures ANOVA: $F_{1,17}=82.5$, $p<0.0001$), and their respective mean values were similar to what has been found in other Canadian Shield lakes (France 1995). The existence of such a significant difference in the signatures of benthic and pelagic organisms allowed us to relate the isotopic signatures of fish ($\delta^{13}\text{C}_{\text{fish}}$) to these two potential carbon sources ($\delta^{13}\text{C}_{\text{zoo}}$ and $\delta^{13}\text{C}_{\text{benth}}$) (France 1995).

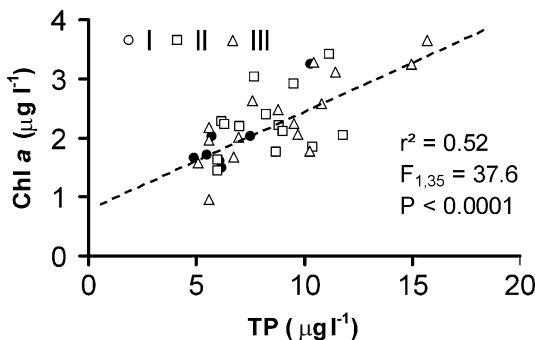


Fig. 3. The TP–Chl relationship in the study lakes. Since relationships for the three lake groups (I: filled circles; II: open squares, III: open triangles) were not significantly different (Table 1), only the regression for the pooled data is showed.

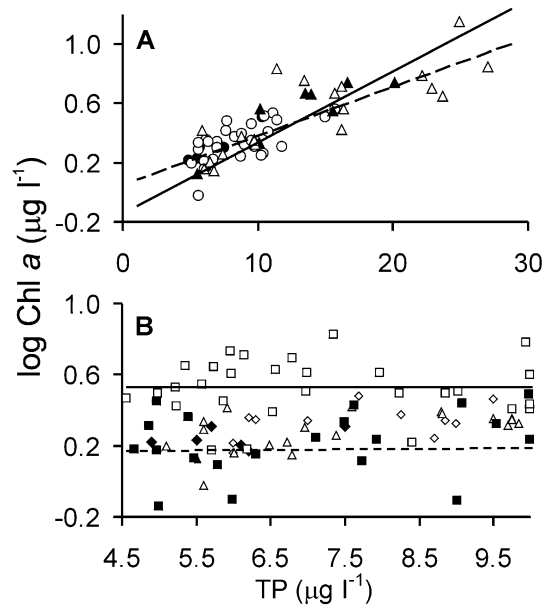


Fig. 4. (A) The TP–Chl relationship for Canadian Shield lakes with (open symbols; dotted line) and without (filled symbols; solid line) piscivores. Data are from this study (circles) and that of Currie et al. (1999) (triangles). (B) Comparison between the TP–Chl relationship for Canadian Shield lakes (present study and that of Currie et al. 1999) and the data of Mazumder (1994). Canadian Shield lakes: open diamonds indicate lakes with piscivores and filled diamonds indicate lakes without piscivores. Mazumder data: low piscivory (open squares; solid line) and high piscivory (filled squares; dotted line). Note the different scaling of axes.

The average $\delta^{13}\text{C}$ signature of the fish community (all taxa pooled) was strongly related to $\delta^{13}\text{C}_{\text{benth}}$ (Table 4) after the sequential Bonferroni correction was applied. Furthermore, $\delta^{13}\text{C}_{\text{fish}}$ and $\delta^{13}\text{C}_{\text{benth}}$ tended to be positively correlated in northern pike, white sucker and lake whitefish ($p<0.05$, but not significant when considering the Bonferroni correction; Table 4). The $\delta^{13}\text{C}$ signature of the fish community tended to be positively correlated with $\delta^{13}\text{C}_{\text{zoo}}$ ($p<0.05$, but not significant when considering the Bonferroni correction; Table 4). The correlation was not significant when single fish taxa were analyzed. Differences in the sample sizes between zooplankton and zoobenthos could explain the tendency for the lower p -values observed for the correlation between $\delta^{13}\text{C}_{\text{fish}}$ and $\delta^{13}\text{C}_{\text{benth}}$.

In addition, fish were more enriched in ^{13}C than zooplankton in almost all cases (Fig. 5A), whereas the $\delta^{13}\text{C}$ signatures of fish and benthic organisms were more similar (Fig. 5B). The graphical analysis of individual $\delta^{13}\text{C}_{\text{fish}}$ signatures revealed unimodal distributions for each taxa, overlapping almost perfectly with that of benthic invertebrates. Almost no overlap was observed with the distribution of $\delta^{13}\text{C}_{\text{zoo}}$ (Fig. 6). Based on these results, we used the $\delta^{15}\text{N}_{\text{benth}}$ as a baseline for the estimation of the fishes' trophic position (Fig. 7). The

Table 4. Pearson's correlations between $\delta^{13}\text{C}_{\text{fish}}$ vs $\delta^{13}\text{C}_{\text{zoo}}$ and $\delta^{13}\text{C}_{\text{fish}}$ vs $\delta^{13}\text{C}_{\text{benth}}$ for different fish taxa. $\delta^{13}\text{C}$ values represent lake averages. Results for brook charr and prey fish are not shown because they were analyzed in three lakes only.

	$\delta^{13}\text{C}_{\text{zoo}}$			$\delta^{13}\text{C}_{\text{benth}}$		
	r	P	n	r	P	n
n. pike	0.40	0.19	12	0.47	0.035	20
walleye	0.42	0.49	5	0.32	0.40	9
y. perch	0.67	0.14	6	-0.16	0.63	6
l. whitefish	-0.73	0.27	4	0.83	0.011	8
w. sucker	0.70	0.08	7	0.65	0.008	15
lake average	0.48	0.046	18	0.56	0.0003*	37

*: significant after the sequential Bonferroni correction.

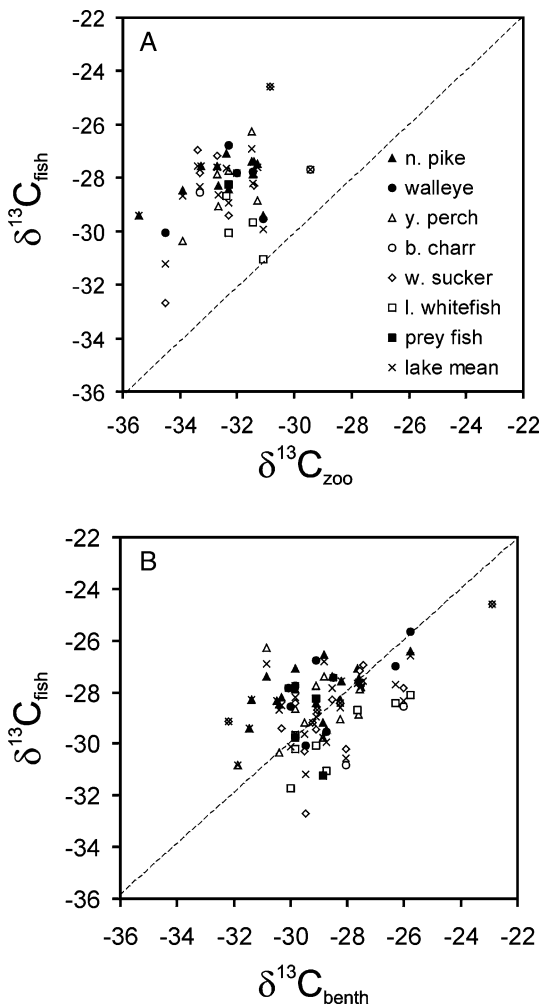


Fig. 5. Average $\delta^{13}\text{C}$ values for fish against (A) zooplankton $\delta^{13}\text{C}$ values (18 lakes) and (B) benthic invertebrate $\delta^{13}\text{C}$ values (38 lakes). Median numbers and ranges (in parentheses) of individuals analyzed per lake were as follows: northern pike = 5.5 (3–27); walleye = 3 (3–6); yellow perch = 3 (2–9); brook charr = 2.5 (2–4); white sucker = 3 (2–23); lake whitefish = 5.9 (3–20); prey fish = 3 (3–12). $\delta^{13}\text{C}_{\text{fish}}$ correspond to $\delta^{13}\text{C}_{\text{zoo}}$ or $\delta^{13}\text{C}_{\text{benth}}$ from the same lake, even though $\delta^{13}\text{C}_{\text{zoo}}$ were not always available.

graphical analysis revealed that potential piscivores present in some of the group I lakes (i.e. yellow perch and brook charr) had a lower trophic position than those in lake groups II and III (i.e. northern pike and walleye). The distribution of data also showed that yellow perch populations were more likely to include piscivorous individuals in lake groups II and III than in lake group I. However, there is some degree of piscivory in lake group I given that the average trophic position of yellow perch and brook charr was >3 . These data confirm the existence of a gradient in piscivory among the three lake groups. However, the data also show that the trophic position of both northern pike and walleye can be relatively variable and that populations of these

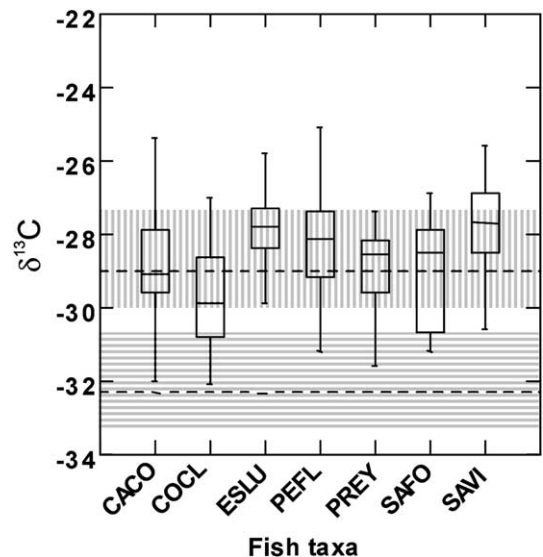
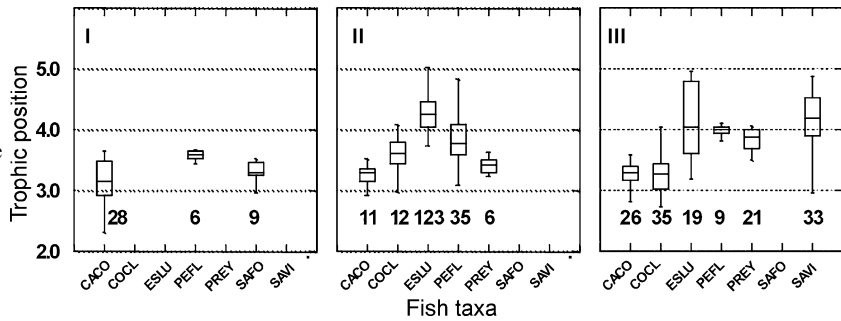


Fig. 6. Box plots showing median values with the 25th and 75th percentiles of individual $\delta^{13}\text{C}$ values for the seven fish taxa considered. The bars represent the range of observed values that fall within 1.5 times the inter-quartile range (25–50%). The horizontal dashed lines within the shaded areas represent the 50% percentile for zooplankton (horizontally shaded area) and benthic invertebrates (vertically shaded area). The width of the shaded zones represents the 25–75% range. CACO = w. sucker (n = 68); COCL = l. whitefish (n = 47); ESLU = n. pike (n = 142); PEFL = y. perch (n = 50); PREY = prey fish (n = 18); SAFO = b. charr (n = 11); SAVI = walleye (n = 33).

Fig. 7. Box plots showing median values with the 25th and 75th percentiles of the individual trophic position for the seven fish taxa considered. The bars represent the range of observed values that fall within 1.5 times the inter-quartile range (25–50%). Abbreviations for fish taxa as in Fig. 6. Sample sizes (individual fish) are indicated below each box plot. Trophic positions were derived from $\delta^{15}\text{N}$ data (Vander Zanden and Rasmussen 1999).



two piscivores probably included benthivorous individuals (Fig. 7).

Discussion

The results of our study showed that fish predation has no detectable impact on the phytoplankton biomass of Canadian Shield lakes and therefore does not support the prediction of McQueen et al. (1986) of strong cascading effects of piscivores on phytoplankton in oligotrophic lakes. However, the dominance of edible phytoplankton in oligotrophic systems, predicted by McQueen et al. (1986), was confirmed by our analysis. Thus, the lack of a trophic cascade in the pelagic zone cannot be ascribed to a trophic bottleneck at the phytoplankton–zooplankton level. By revealing that fish are strongly dependent on the littoral zone, our study suggests that there is a weak connection between the littoral and the pelagic food webs. This weak coupling does not seem to result from a scarcity of zooplankton (due to predation) that forces fish to feed on alternative prey (i.e. benthic organisms). It is more likely that, given its low capturability in our study lakes, zooplankton is simply not a very profitable prey for benthic–pelagic fish (i.e. fish potentially foraging in both zones). In contrast, we suggest that the absence of specialized zooplanktivores could explain the observed lack of a trophic cascade from piscivores to phytoplankton in these oligotrophic lakes.

The positive correlation between piscivores and relatively large zooplankton (i.e. daphnidae and *H. gibberum*) suggests a negative effect of facultative planktivores on herbivorous zooplankton. However, given the small amount of variability explained by the RDA and the absence of a significant difference in the abundance of cladocerans among lake groups, the cascading effect of piscivores on zooplankton, if any, is weak. Weak effects of fish on zooplankton were also found in other Canadian Shield lakes with functionally similar fish communities. In a survey of 43 oligotrophic lakes in the Canadian Shield, Rodriguez et al. (1993)

showed that brook charr affected the body size distribution of large *H. gibberum* by size-selective predation but found no effect on the size and biomass of similarly sized *Daphnia*. Furthermore, only a small amount of the variation in the zooplankton assemblage structure was accounted for by factors linked to fish predation. Pinel-Alloul et al. (1995) explained about 50% of the total variation in the zooplankton species density in 54 lakes of the Canadian Shield using data on fish, phytoplankton, and water chemistry, but fish accounted for only a small fraction of the explained variation in zooplankton community structure (15%). The small amount of variation in zooplankton biomass explained by the fish biomass could be related to a relatively small variation in the fish biomass among lakes due to the low TP gradient. The occurrence of some piscivory in lake group I might also have contributed to reducing the differences among the lake groups. However, the differences in the biomass of piscivores were relatively high among lake groups, thus it was surprising to find such a weak trophic cascade between piscivores and zooplankton.

The above results could be partly explained by the relatively low fish biomasses that can be sustained in oligotrophic systems (Hanson and Leggett 1982). It has been shown that benthic–pelagic particulate feeders can induce trophic cascades in North American eutrophic lakes only above a certain density threshold (Mills et al. 1987). However, these results contrast with the findings of Jeppesen et al. (2003) and Lauridsen et al. (2001), who found dramatic effects of salmonid predation on zooplankton in Greenland and New Zealand lakes, even at low fish densities, suggesting that the strength of the interactions between zooplankton and unspecialized zooplanktivores might vary over a broader scale. Lauridsen et al. (1999) suggested that such differences might be explained by a variation in the efficiency of particulate feeders. In a comparative analysis of zooplankton and fish communities in oligotrophic and mesotrophic lakes, they showed that sparse populations of relatively large salmonids in New Zealand had stronger effects on large zooplankton than more dense populations of small fish in North American lakes. They suggested that the discrepancy between the two systems might be due to

differences in water humic content and zooplankton pigmentation, respectively higher and lower in North American than in New Zealand lakes. These factors could in fact reduce the efficiency of particulate feeders (Sægvog et al. 1996), such as those found in our relatively humic lakes and in the North American lakes studied by Lauridsen et al. (1999). In contrast, specialized zooplanktivores such as clupeids can increase their foraging efficiency on zooplankton by switching from particulate to filter feeding in humic lakes (Janssen 1976). This behaviour probably explains their dramatic effects on the zooplankton in some North American lakes (Brooks and Dodson 1965, Scavia et al. 1986). The fact that specialized filter-feeders can invade oligotrophic systems already colonized by less specialized zooplanktivores (Böhn and Amundsen 2001, Harman et al. 2002) supports the idea that zooplankton is a relatively poorly exploited food source in many of these systems.

Thus, strong cascading effects of piscivores on zooplankton seem not to be the rule in oligotrophic Canadian Shield lakes, at least when truly pelagic zooplanktivores are absent. This weak predation pressure on zooplankton could partially explain the lack of an effect of piscivores on the phytoplankton. Furthermore, the pooled data sets on the Canadian Shield lakes (Currie et al. 1999 and our study) support that the TP–Chl relationship in both the presence or absence of piscivores is consistent with the relationship found by Mazumder (1994) in systems with large herbivorous zooplankton. This means that relatively high concentrations of Chl per unit TP are unlikely to be observed in the Canadian Shield lakes. Interestingly, Drenner and Hambright (2002) reached the same conclusion about Canadian Shield lakes when comparing the TP–Chl relationship of Currie et al. (1999) with other published data, even though the TP range used in their analysis (i.e. 0–800 $\mu\text{g TP l}^{-1}$) largely encompassed that of Currie et al. (1999). In contrast, the TP gradient observed in our study was very similar to that observed by Currie et al. (1999) (i.e. 4–30 $\mu\text{g l}^{-1}$). Relatively high zooplankton grazing in the presence of inefficient facultative zooplanktivores could explain the low Chl concentration in these lakes. Furthermore, there is increasing evidence that grazing by *H. gibberum* (Pérez-Fuentetaja et al. 2000) and copepods (Cyr 1998) could contribute substantially to controlling phytoplankton in oligotrophic lakes.

These conclusions are in agreement with our results on both the zooplankton:phytoplankton and the Chl:TP ratios. Neither ratio was significantly different among the three lake groups, and their ranges were similar to those reported by Jeppesen et al. (2003) for a number of oligotrophic lakes in the temperate zone. These authors found that the zooplankton:phytoplankton ratio decreased with increasing productivity, suggesting, as in our study, a relatively high potential for grazing in

oligotrophic systems. Accordingly, Jeppesen et al. (2003) showed that the Chl:TP ratio is directly related to productivity. The Chl:TP ratio was also relatively low in our study lakes and was found to be unrelated to fish abundance, as in the survey by Jeppesen et al. (2003). These authors found that the Chl:TP ratio increased with fish CPUE only in mesotrophic and eutrophic systems, suggesting that the top-down effects of fish occur only in highly productive systems.

The lack of specialized zooplanktivores could also explain why piscivores seem to depend mostly on the littoral food web in our study system. Specialized zooplanktivores are a key factor in determining the trophic pathways connecting piscivores to primary producers in lacustrine food webs, as shown by the results of Vander Zanden and Rasmussen (1996). These authors found that in the absence of truly pelagic prey (i.e. clupeids, coregonids or osmerids), lake trout (*Salvelinus namaycush*), generally considered as pelagic, shifted from a diet composed mainly of pelagic prey fish to a diet composed mainly of littoral prey (fish and benthic invertebrates). This suggests that the presence of specialized zooplanktivores might strengthen the link between piscivores and zooplankton, which is necessary to propagate top-down effects to phytoplankton. The presence in early summer of pelagic prey for piscivores, such as young-of-the-year perch, thus seems not to be sufficient to couple plankton and piscivore dynamics. Stable isotope analysis showed that the fish communities of our study lakes mainly depend on littoral resources, thus confirming the importance of the benthic pathway suggested by Schindler and Scheuerell (2002) and Vadeboncoeur et al. (2002). Stomach content analyses of yellow perch, white sucker, northern pike and walleye confirm the importance of littoral benthic prey in the diet of these fish (unpubl.). The benthic pathway could also be mediated by benthivorous fish that are prey for piscivorous fish, thus linking top piscivores to littoral zone. Our results also suggest that the presence of benthivorous northern pike and walleye individuals might have reduced the differences in the levels of piscivory among the lake groups, thus contributing to the low cascading effect on zooplankton.

In conclusion, our study confirms the importance of benthic sources of carbon for both benthic-pelagic and piscivorous fish in oligotrophic lakes (Vadeboncoeur et al. 2002), but at the same time suggests that the trophic cascades are not likely to happen in the pelagic zone of Canadian Shield lakes when specialized planktivores are absent. The emerging paradigm of piscivorous fish as integrators of pelagic and littoral food webs (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002) thus needs to integrate the role of functional fish diversity to fully explain the food-web dynamics in oligotrophic systems. Our results also suggest that the manipulation of fish communities

as a management strategy to improve water quality (Carpenter and Kitchell 1993) would probably not affect phytoplanktonic communities in oligotrophic lakes, This was also the conclusion reached earlier by Jeppesen et al. (2003) based on a multi-lake study of temperate lakes.

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