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Distinction of nektonic and benthic communities between fish-present (*Salvelinus fontinalis*) and natural fishless lakes

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Natural geographic barriers and escarpments inhibited the post-glacial colonisation of numerous lakes by fish on the eastern Canadian Boreal Shield. The aim of this study was to assess how different top-down control in lakes containing a single fish population of brook trout (*Salvelinus fontinalis*) and naturally fishless lakes affects the characteristics and structure of littoral macroinvertebrate communities throughout the ice-free season. Nektonic and zoobenthic communities were examined through univariate community characteristics [abundance, species density, species richness (D), evenness (J'), diversity, H')] and multivariate species assemblages. The total abundance of nektonic and zoobenthic communities and their univariate diversity indices were similar between fish-present and fishless lakes over the entire sampling period. However, species assemblages for both types of macroinvertebrate communities were significantly different between fish-present and fishless lakes throughout the season. Typically, the same invertebrate species occurred in the two lake types; but their relative abundance was different. The results of our study show that the top-down control in fish-present and fishless lakes leads to different littoral community structures, which were not perceptible through the studied univariate community characteristics. This study highlights the importance of selecting appropriate indicators for the assessment of invertebrate communities in lakes of the eastern Canadian Boreal Shield.

Introduction

Historically, mountain escarpments have limited the post-glacial colonisation of fish in some headwater lakes of the eastern Canadian Boreal Shield (Power *et al*. 1973). This natural geographic barrier for fish species distribution has resulted in the development of a distinct ecosystem, fishless lakes, and neighbouring fish-present lakes in the same area. Many of these fishless lakes, as many others throughout the world, have been successfully stocked with salmonids for the benefit of recreational fisheries (Knapp *et al*. 2001, Korsu *et al*. 2008). Assessing the consequences of these introductions through the study of natural fishless lakes is presently of

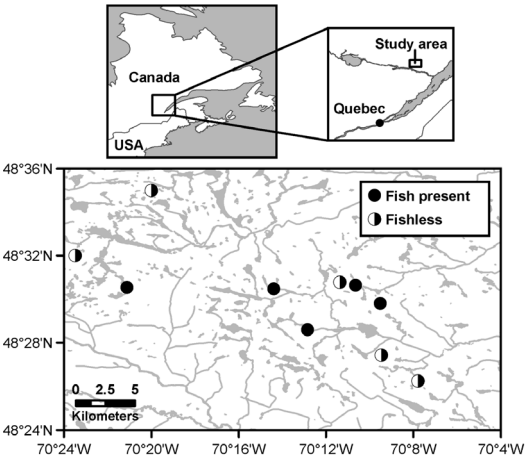

Fig. 1. Location of the 10 lakes within the study area.

great interest since a growing body of evidence suggests that the presence of non-native fish may alter the behaviour of native species, threaten prey populations, change community interactions and disrupt natural ecological processes (Simon and Townsend 2003, Dunham *et al*. 2004, Knapp 2005).

Different foraging characteristics of top predators may lead to distinct community structures. Fish are functionally distinct predators from amphibians or large aquatic insects, which are the main predators in fishless lakes (Kurzava and Morin 1998). For example, fish may attain a higher size than invertebrates or amphibians and can feed on larger prey than the latter (Zaret 1980, Pope 1989). As well, predation vulnerability depends on traits that permit coexistence with predators; thus, species having evolved in fishless communities may have developed anti-predator strategies ineffective against fish (McPeek 1990, 1998). Studying the effects of predation in a natural system, where species have co-evolved, may reveal important information about the fundamental role of predation in community organisation (Wellborn *et al*. 1996, Creed 2006).

From a concomitant study, we observed that a difference in predation pressure between fish-present and fishless lakes led to different zooplankton assemblages in the pelagic zone (Drouin *et al*. 2009). In that study, Chaoborid larvae had stronger predation effects than fish on daphnids and this appeared to be the key factor for structuring the zooplankton community in fishless lakes. Fish predation has also been shown to affect different littoral prey populations (Zimmer *et al*. 2001, Leppä *et al*. 2003, Tate and Hershey 2003); however knowledge concerning the role of predation on the overall diversity and structure of littoral invertebrate species assemblages is still scarce.

The main objective of this study was to assess how top-down control in littoral areas of fish-present and fishless lakes influences macroinvertebrate community characteristics and structure and if it differs between the two lake types. More specifically, our research hypotheses on the nektonic and benthic communities were that assemblage characteristics (abundance, species density, species richness, evenness and diversity), and structure (species assemblages) between fish-present and fishless lakes should differ, likely due to a different top-down control from predation by fish and/or invertebrates, respectively.

Methodology

Study area

The study was conducted during the summer of 2003 in small oligotrophic lakes on the Boreal Shield bedrock north of the Saguenay Fjord in Québec, Canada (Fig. 1). The current distribution of fish in this area has been modulated by postglacial colonisation, where natural barriers allowed the upriver invasion by salmonids only (Power *et al*. 1973). Fewer species occur upstream, where monospecific fish populations of brook trout (*Salvelinus fontinalis*) dominate while some lakes remain fishless above the escarpment marking the edge of the Laurentian Plateau (Power *et al*. 1973).

This study was conducted in 10 lakes, 5 that contained natural (unstocked) monospecific fish populations of brook trout and 5 fishless lakes. All lakes were located within 2 controlled harvested zones (ZEC Martin-Valin and ZEC Chauvin), territories where fishing is regulated and controlled by organisations mandated by the Government of Québec. The presence and absence of fish in the 10 selected lakes was determined by the Québec Ministry of Natural

Resources and Wildlife (MNRW) recreational fisheries statistics of brook trout between 1994 and 2003 (Table 1). Furthermore, the absence of fish was confirmed in 4 of the five selected fishless lakes (de la Foulque, de la Manne, aux Nénuphars and de la Perdrix) in June 2001 by experimental multifilament gill nets (22.9 m long × 1.8 m deep with stretched mesh panels of 25, 32, 38, 51, 64 and 76 mm) set perpendicular to the shore in the littoral zone (MNRW unpubl. data).

All lakes were sampled 4 times during the ice-free season of 2003, which lasts from the beginning of June to October in the area. The sampling periods were during the weeks of 23–29 June, 14–19 July, 11–16 August and 8–13 September, hereafter referred to as June, July, August and September, respectively. Near the deepest point of each lake, depth and transparency were estimated using a graduated cable and Secchi disk. Water temperature, dissolved oxygen concentration, pH and conductivity were measured (Table 1) with a YSI model 556 MPS (Yellow Springs Instrument Co., Yellow Springs, Ohio). Zooplankton samples were also collected in the pelagic zone of each lake as part of a related study (Drouin *et al*. 2009). We used a multivariate procedure to evaluate if fish-present and fishless lakes had similar geographical and limnological measure characteristics (altitude, surface area, maximum depth, mean Secchi depth, mean pH, mean temperature, mean conductivity, mean dissolved oxygen; Table 1; ANOSIM on normalised data using Euclidean distance matrix; $R = 0.056$, non-significant at the $p > 69\%$ level; ANOSIM procedure Primer ver. 6 statistical package, Clarke and Warwick 2001).

Sample collection

Nektonic (large-bodied zooplankton taxa and swimming organisms) and benthic invertebrates were sampled randomly at locations evenly distributed around lake margins, at about 1 m depth and 5 m away from the shoreline. Sampling was performed during the daytime. The habitat structure in all lake margins was homogenous, showing a rather scarce macrophyte presence. Thus, all samples are considered to have been taken from a comparable habitat, with respect to the presence and abundance of the macrophytes. Four nekton samples and three benthos samples were collected at each sampling time and in all lakes using a D-frame dip net measuring 30.5 cm × 27 cm and a 1 mm mesh size. For nekton and benthos, the dip net was manipulated using a standardized procedure in all lakes and on each date in order to obtain comparable data (Rabeni 1996). Nektonic organisms were sampled by sweeping the water column 10 times in a "figure 8" motion using the dip net. The size of the "figure 8" motion was approximated to the length of the dip net, and each haul filtered a similar quantity of water between samples. Benthic organisms were sampled using the same dip net and dragging it along the bottom over a 0.5 m distance, sampling a total surface area of approximately 0.15 m^2. Organisms were anaesthetized using carbonated water and preserved in 4% buffered formaldehyde.

In the laboratory, all nektonic organisms were identified except for samples with an estimated abundance over 200 organisms, which were sub-sampled using a 500 ml Folsom splitter. Benthic organisms were split into two size fractions of 1–6.3 mm and > 6.3 mm to optimize the identification of larger organisms that may have a sparse distribution. We sorted a minimum of 100 of all the organisms in the 1–6.3 mm fraction by a quantitative fixed-count method used by the U.S. Geological Surveys (Moulton *et al*. 2000). All invertebrates were identified to the lowest taxonomic level possible, depending on the group, the life-stage and the specimen condition (*see* Drouin *et al*. 2006 for the complete list). Insect taxa (Coleoptera, Diptera, Ephemeroptera, Hemiptera, Megaloptera, Neuroptera, Odonata, and Trichoptera) were identified to the genus, except for Hymenoptera, which were identified to the family. The annelids were identified to genus for Hirudinae and to species for Oligochaeta. Amphipoda, Cladocera, Copepoda, and Rotifera were identified to the species. Acariformes, Gastropoda and Porifera were identified to the genus and Tartigrada to the order. Nematoda and Nematomorpha were not identified further than the phylum. All *Chaoborus* larvae were identified to the species level, except in nekton samples where they were very abundant (29 of the 54 samples with *Chaoborus* larvae), where

Table 1. List of coordinates, morphological and physicochemical characteristics of the studied lakes. Parameters are expressed as the mean of the four sampling periods with the standard error of the mean in parentheses.

Parameters	Fish-present lakes					Fishless lakes				
	Beauvoir	Calumet	Des Castors Maigres	Cinquième lac de la Chaîne	Troisième lac Ciseau	De la Foulque	De la Manne	Aux Nénuphars	De la Perdrix	Zoël
Latitude	48°30´32´´	48°30´28´´	48°28´36´´	48°29´48´´	48°30´38´´	48°31´00´´	48°34´00´´	48°26´15´´	48°30´47´´	48°27´26´´
Longitude	70°21´07´´	70°14´23´´	70°12´50´´	70°09´30´´	70°10´38´´	70°23´28´´	70°20´00´´	70°07´47´´	70°11´21´´	70°09´27´´
Altitude (m)	754	712	655	688	713	775	804	621	726	729
Surface area (km^2)	0.067	0.039	0.086	0.020	0.051	0.049	0.054	0.063	0.033	0.039
Max. depth (m)	15	10	16	9	9	5	23	8	15	10
Secchi depth (m)	5.4 (0.8)	3.4 (0.5)	3.0 (0.5)	3.0 (0.4)	4.5 (0.5)	2.3 (0.9)	3.6 (0.5)	3.1 (0.8)	3.3 (0.3)	3.9 (0.6)
pH*	7.31	6.02	6.88	7.08	7.33	7.48	6.18	6.22	7.31	6.05
Temp. (°C)	18.28 (4.70)	18.02 (4.23)	18.73 (2.67)	19.52 (2.61)	17.64 (4.23)	19.04 (4.76)	18.20 (3.92)	19.25 (3.50)	18.67 (2.84)	18.58 (3.78)
Conductivity ($\mu S\ cm^{-1}$)	13.2 (2.3)	10.5 (1.3)	10.7 (2.3)	12.7 (3.1)	9.4 (2.5)	15.0 (1.5)	6.9 (2.2)	8.4 (1.4)	9.1 (0.9)	6.7 (1.1)
Dissolved oxygen ($mg\ l^{-1}$)	10.20 (2.13)	9.91 (2.02)	9.23 (1.63)	9.34 (1.47)	9.66 (2.15)	10.31 (1.91)	9.71 (1.74)	8.8 (1.78)	9.83 (1.90)	9.51 (1.97)
Mean annual brook trout yield 1994–2003 ($kg\ ha^{-1}\ yr^{-1}$)	4.48	4.66	5.06	5.60	4.39	0	0	0	0	0

* pH values for July only.

only 10 specimens were randomly selected and identified to the species level.

Statistical analyses

Data for the nekton and benthos were first analysed using a univariate approach. The total abundance of invertebrates was calculated for each sample. The abundance of particular insect groups was also compared in order to allow comparison with other studies. Species richness was evaluated considering the effects of the sampling volume/area, further identified as species density (number of species per volume/surface units) and the effect of the number of individuals collected, by using Margalef's richness index (D), which standardises the number of species with the number of individuals found in a replicate. In addition, rarefaction curves based on the number of individuals collected were also created using Estimate S (Colwell 2000, and *see* Gotelli and Colwell (2001) for more details about species density and species richness). Other community characteristics such as the evenness (Pielou's J') and diversity (Shannon's H') indices were also calculated for each sample. Differences among (1) lake type (fish-present lakes, fishless lakes), (2) individual lake nested within lake type (5 lakes), (3) Sampling time (June, July, August and September), (4) interactions among those factors, and (5) an error term, were statistically assessed using a three-way partly nested analysis of variance test (ANOVA). The assumptions of normality and homoscedasticity were verified by viewing the distribution of residuals *vs*. predicted values as suggested by Quinn and Keough (2002). Data were transformed to achieve normality and homoscedasticity when necessary (details given in Table 2 where appropriate). *A posteriori* comparisons were made using Tukey's test.

Species assemblages were also analysed via multivariate analysis based on Bray-Curtis dissimilarity distances and matrices calculated using the statistical package PRIMER ver. 6 (PRIMER-E© Ltd.). Species assemblages were calculated over fourth-root transformed data ($\sqrt[4]{x}$) as suggested by Clarke and Warwick (2001). This transformation has the propriety of assigning more importance to less common species by down-weighting the importance of very abundant ones while maintaining the original order of abundance (Thorne *et al*. 1999, Clarke and Warwick 2001). The taxa with a single occurrence were removed from the data set before computing the Bray-Curtis dissimilarity to reduce the noise in the matrix caused by very rare species (Clarke and Warwick 2001). Tests of significance were then sought using a permutational multivariate analysis of variance (PERMANOVA) to test variations of species assemblages among the studied factors and pairwise comparisons (PERMANOVA+ ver. 1.0.1; Anderson 2001, McArdle and Anderson 2001). Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the dissimilarities between samples. The discriminating species between the species assemblages from Bray-Curtis dissimilarity matrices were identified by the SIMPER procedure.

Results

Nektonic communities

A total of 128 taxa were identified during the 4 sampling months. From all the taxa identified, cladocerans dominated over other taxa in abundance by representing 76% and 77% of the abundance in fish present and fishless lakes, respectively. Chironomids were the most abundant insect taxa in fish-present lakes, with a mean of 17% of the sample abundances and *Chaoborus flavicans* larvae was the only Chaoboridae species identified and accounted for < 1% of the abundance. In comparison, chironomids accounted for only 5% of sample abundances whereas *Chaoborus* larvae for 15% of sample abundances in fishless lakes. From the 333 specimens of *Chaoborus* larvae identified to the species level in the fishless lake samples, 86% were *C. america*, 14% were *C. trivittatus*, while no *C. flavicans* were observed. Insects other than dipterans composed on average 3% and 2% of the fish-present and fishless lake samples, respectively.

The total abundance of nektonic organisms showed no significant difference between the

two lake types (Table 2), but varied between sampling periods to reach a higher maximum in August (Fig. 2). The abundance of *Chaoborus* larvae was significantly greater in fishless lakes at each sampling time (Table 2 and Fig. 2). In addition, there was lower species density and

Table 2. Results of a three-way partly nested ANOVA and nonparametric multivariate analysis of variance (PERMANOVA) testing the effect of lake type (fish-present, fishless), Lake nested within the lake type 'La(Type)', sampling time (June, July, August and September) and their interactions on total abundance, species abundance, community characteristics and species assemblages for nektonic and zoobenthic communities. The species assemblages were calculated on fourth-root transformed data ($\sqrt[4]{x}$).

Variables		Type	La(Type)	Time	Type × Time	La(Type) × Time	Residual
Nekton	df	1	8	3	3	24	120
Ln Total abundance + 1	MS	7.39	12.69	7.74	0.97	2.22	1.39
	p	0.47	< **0.001**	**0.03**	0.73	0.054	
Ln *Chaoborus* larve + 0.01	MS	879.73	117.04	4.94	1.52	6.41	3.13
	p	**0.03**	< **0.001**	0.52	0.87	**0.01**	
Species density	MS	87.02	36.31	207.78	7.68	12.46	38.51
	p	0.16	0.48	< **0.001**	0.61	1.00	
Species richness (*D*)	MS	9.36	1.98	3.73	0.80	0.77	1.06
	p	0.06	0.07	< **0.001**	0.39	0.82	
Evenness (*J'*)	MS	0.20	0.27	0.04	0.01	0.08	0.04
	p	0.42	< **0.001**	0.72	0.95	**0.01**	
Shannon diversity (*H'*)	MS	2.52	1.39	1.03	0.19	0.43	0.40
	p	0.21	< **0.001**	0.10	0.73	0.38	
Species assemblage	MS	47051.40	12776.86	11625.40	4628.03	3199.31	2508.02
	p (perm)	**0.04**	< **0.001**	< **0.001**	**0.02**	< **0.001**	
Benthos	df	1	8	3	3	24	80
Ln Total abundance + 1	MS	2.02	1.50	3.71	0.78	0.41	0.49
	p	0.28	< **0.001**	< **0.001**	0.16	0.69	
Ln Chironomidae + 1	MS	3.66	2.53	1.87	0.46	0.72	0.77
	p	0.26	**0.00**	0.08	0.60	0.56	
Ln Amphipoda + 0.01	MS	1.45	60.21	26.27	6.55	4.87	2.14
	p	0.88	< **0.001**	**0.01**	0.28	< **0.001**	
Ln Coleoptera + 0.01	MS	113.87	7.45	34.69	27.85	10.27	8.36
	p	**0.00**	0.53	**0.03**	0.07	0.24	
Ln Ephemeroptera + 0.01	MS	13.14	8.49	124.47	15.79	12.54	15.73
	p	0.25	0.82	< **0.001**	0.31	0.73	
Ln Hemiptera + 0.01	MS	484.20	8.56	57.06	57.06	4.34	5.18
	p	< **0.001**	0.12	< **0.001**	< **0.001**	0.68	
Ln Megaloptera + 0.01	MS	21.52	39.73	20.33	3.98	12.49	13.11
	p	0.48	**0.01**	0.21	0.81	0.53	
Ln Mollusca + 0.01	MS	257.21	36.16	5.83	3.80	5.70	5.92
	p	**0.03**	< **0.001**	0.40	0.58	0.52	
Ln Odonata + 0.01	MS	36.34	44.56	45.57	7.90	8.45	9.95
	p	0.39	< **0.001**	**0.01**	0.44	0.67	
Ln Trichoptera + 0.01	MS	65.00	12.55	59.73	12.52	11.87	8.38
	p	0.05	0.17	**0.01**	0.39	0.13	
Species density	MS	44.41	63.88	281.19	35.61	42.87	37.41
	p	0.43	0.11	< **0.001**	0.49	0.32	
Species richness (*D*)	MS	0.08	2.46	3.14	0.48	0.77	1.02
	p	0.86	**0.02**	**0.02**	0.61	0.77	
Evenness (*J'*)	MS	0.004	0.05	0.002	0.004	0.01	0.01
	p	0.78	< **0.001**	0.76	0.54	0.80	
Shannon diversity (*H'*)	MS	0.24	0.75	0.39	0.10	0.09	0.12
	p	0.59	< **0.001**	**0.01**	0.36	0.80	
Species assemblage	MS	8753.01	4892.14	7837.28	2701.66	2618.13	2717.32
	p (perm)	**0.02**	< **0.001**	< **0.001**	0.39	0.66	

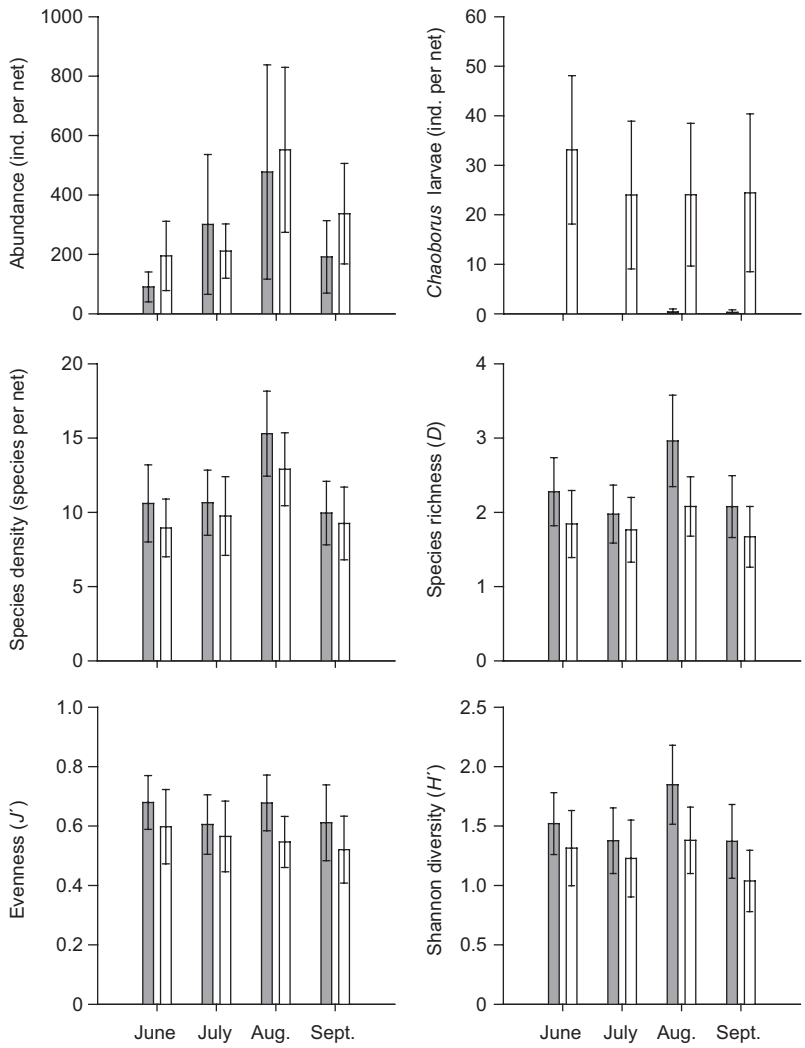

Fig. 2. Average (± 95% CI) abundance and community characteristics of nekton associated with Lake type [fish-present (grey), fishless lakes (white)] for each sampling time. Results for the corresponding ANOVA analysis are given in Table 2.

species richness in fishless lakes; although this trend was not significant in the case of species density while being marginally significant in the case of species richness (Table 2 and Fig. 2). The rarefaction curves show that the expected species richness for fishless lakes was lower than for fish-present lakes, but reach the 95% confidence interval of the fish-present curve at a higher number of individuals (Fig. 3). No significant difference between evenness and diversity indices were observed among the two lake types (Table 2). Both lake types followed the same temporal variations in community characteristics, with a significant higher number of species density in August than in other periods (Fig. 2).

The interaction between lake type and sampling period indicates that nektonic community structures (or species assemblages) varied differently among sampling times (Table 2). *A posteriori* pair-wise comparisons revealed that nekton community structure differed between fish-present and fishless lakes at each sampling period. The species assemblages did not vary between time periods within the fishless lakes group, but species assemblages within the fish-present lakes group varied significantly between August and September. This relation is visualised by a non-metric multidimensional scaling (nMDS) ordination, which shows distinct clusters for each lake type (Fig. 4). In addition,

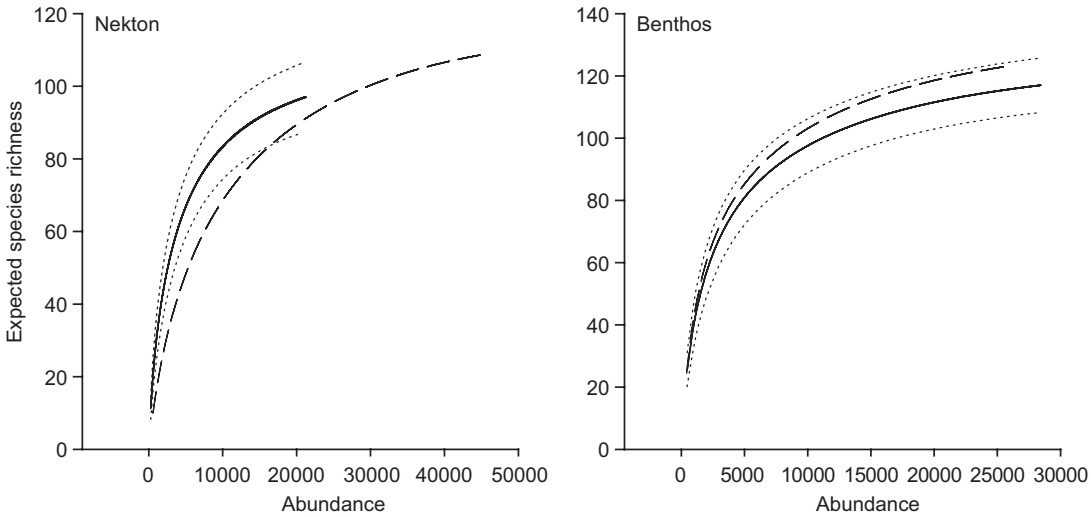

Fig. 3. Rarefaction curves of the pooled replicates of fish-present and fishless lakes for nektonic and benthic invertebrates. Solid lines indicate the fish-present lakes and dotted lines represent the 95% confidence limits of the fish-present curves. Dashed lines represent the fishless lakes.

the SIMPER procedure shows that average dissimilarity between the nekton assemblages of the two lake types was of 86.12%. Species contributing most to the dissimilarity in community structure between fish-present and fishless lakes were *Daphnia pulex* and *Holopedium gibberum*, which were associated with fish-present lakes while *Chaoborus* larvae, along with the cladocerans *Sida crystallina* and *Latona setifera*, were associated with fishless lakes (Fig. 4).

Zoobenthic communities

We identified a total of 131 zoobenthic taxa during the 4 sampling periods. Chironomids were the most abundant taxa identified in samples from fish-present and fishless lakes, representing respectively 54% and 51% of the mean abundance. Molluscs composed on average 21% of the fish-present and 9% of the fishless lake samples. Amphipods comprised on average 3% of the fish-present lake samples and 9% of the fishless lake samples. Non-dipteran insects accounted for at least 10% of the zoobenthic organisms in fish-present and fishless lakes samples.

The total abundance was not significantly different between lake types and there was no interaction between this factor and sampling periods (Table 2). However, the total abundance of zoobenthic organisms was significantly lower in June than in other periods (Fig. 5). The abundance of each non-dipteran insect group was analysed separately and results show that only the water boatmen (Corixidae, Hemiptera) and diving beetles (Dytiscidae, Coleoptera) were significantly more abundant in fishless lakes than in fish-present lakes (Table 2). Both species density and species richness were not statistically different between fish-present and fishless lakes (Table 2), but showed temporal variations between sampling periods, where values were higher in July (Fig. 5). The expected species richness in fishless lakes was higher than for the fish-present lakes, however the curve representing the fishless lakes fell inside the 95% confidence limit of the rarefaction curve for the fish-present lakes (Fig. 3). Evenness and diversity indices were not significantly different between lake types and there were no interactions between this factor and sampling periods (Table 2). The diversity index significantly increased between June and July in comparison to other sampling periods (Fig. 5).

Zoobenthic community structures were different between fish-present and fishless lakes and show similar temporal variations (Table 2). From the pair-wise *a posteriori* comparisons,

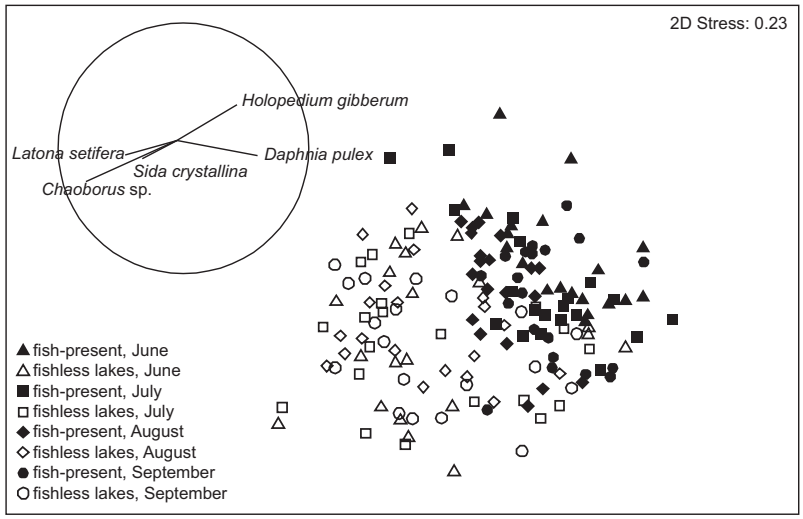

Fig. 4. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix (transformed abundance data) for nekton samples collected in fish-present and fishless lakes during the ice-free season. Discriminating species identified by the SIMPER procedure are illustrated as vectors from Pearson correlations and reflect the correlation of the individual species contribution to the community pattern.

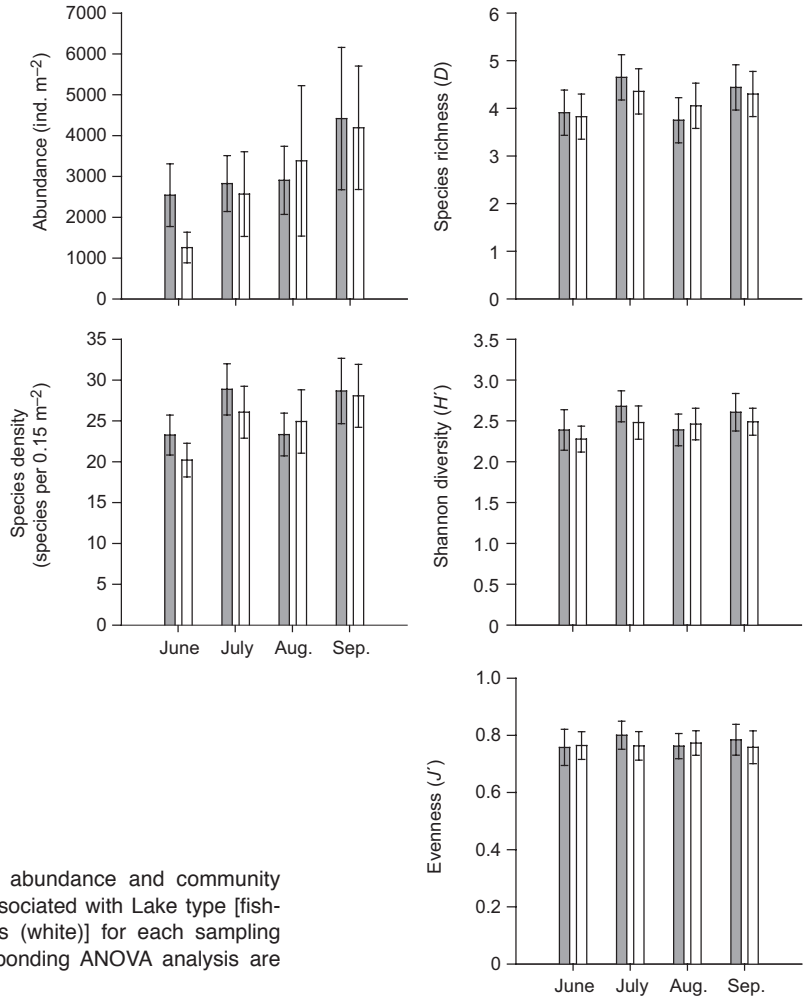

Fig. 5. Average (± 95% CI) abundance and community characteristics of benthos associated with Lake type [fish-present (grey), fishless lakes (white)] for each sampling time. Results for the corresponding ANOVA analysis are given in Table 2.

the benthos assemblages were similar, except for July and August. This relation is not graphically showed since its stress value was in the upper limit of the 0.20–0.30 range with 0.28; this might not be a relevant statistical result (Clarke and Warwick 2001). According to the SIMPER procedure, the average dissimilarity in benthos species assemblages between fish-present and fishless lakes was of 62.52%. The most discriminating taxa of this average dissimilarity were Pelecypoda (mollusc), the dipterans *Psectrocladius* sp. and *Cladotanytarsus* sp., which were associated with fish-present lakes, and the amphipod *Hyalella azteca*, which was associated with fishless lakes.

Discussion

This study demonstrates that a pattern exists in invertebrate communities between fish-present and fishless lakes, but that its revelation is dependent on the community indicators used. Upper littoral zones of fish-present and fishless lakes in the study area had a similar total abundance of organisms, species density, species richness, evenness and diversity, despite marked differences in multivariate species assemblages. The identified taxa were generally found in the two lake types, thus the distinctions between the nektonic and benthic communities from fish-present and fishless lakes were mainly related to differences in the abundance of specific taxa.

The observation of similar average total abundance and diversity indices between fish-present and fishless lakes contrasts with those of recent studies by Schilling *et al*. (2009a, 2009b), who reported that these characteristics were higher in fishless lakes than in fish-present lakes. We believe that some differences between the fish population composition and abundance could explain the diverging results. First, presence of baitfish populations were observed for certain lakes (Schilling *et al*. 2009b), a potentially influential factor on the total predation pressure exerted towards macroinvertebrates. Secondly, trout were repeatedly stocked in some lakes (Schilling *et al*. 2009a); something that possibly improved the predation pressure effects by fish on invertebrates since the effective fish population can exceed, at least temporarily, what normally occurs in a natural population.

In the present study, the number of samples collected per lake might have limited the characterisation of communities by univariate methods, although the sampling effort was comparable to that of other studies looking at littoral community patterns in boreal lakes (e.g. Scrimgeour *et al*. 2000). Our results likely underestimated the absolute species richness present in the studied communities since we did not attempt to catch an equal number of organisms from each fraction size in each lake. Furthermore, the taxonomic resolution reached for particular groups may not have revealed all possible distinctions. However, despite these limits, this study demonstrates that a distinction exists between invertebrate communities in fish-present and fishless lakes. We believe that this result further highlights the importance of selecting appropriate indicators for the assessment of communities, especially for the studied boreal area. Given that the regional number of species (gamma diversity) in boreal areas is rather low in comparison with that in southern regions, the potential number of species that could be found in a particular habitat inside these areas (alpha diversity) can be influenced. If most of the species in the regional pool are generalists, this could also contribute to a decrease in the rate of change in species composition across habitats (beta diversity), as we observed in both lake types sharing most of the identified taxa. Variability within space (individual lakes) due to natural lag between phenomenons has most certainly affected the demonstration of a general pattern for a type of lake. Nevertheless, this reflected the natural fluctuations in communities that are likely to occur in lake's littoral habitat.

Nektonic community

Contrary to many studies which reported that brook trout affect the abundance of large zooplankton forms (Brooks and Dodson 1965, Hutchinson 1971, Carpenter *et al*. 1985, Vanni 1987, Pace *et al*. 1999), we observed that larger

forms of zooplankton, such as *Daphnia pulex*, a known prey of brook trout (Lacasse and Magnan 1992), and *Holopedium gibberum*, were present in higher abundance in fish-present lakes. This observation was correlated with the high density of *Chaoborus americanus* larvae present within the water column during daytime in fishless lakes.

According to the literature, it is possible to relate this pattern to the effect of difference in top-down control between fish-present and fishless lakes. Monospecific populations of brook trout in Boreal Shield lakes have been observed to be selective on *Chaoborus* larvae, but not on *Daphnia* sp. and *Holopedium gibberum* (Tremblay-Rivard 2007). Thus, direct predation by fish can explain the absence of *Chaoborus* larvae from the nekton samples of the studied fish-present lakes. Moreover, studies have demonstrated the capacity of large Chaoborid larvae to regulate *Daphnia* populations (MacKay *et al*. 1990, Wissel and Benndorf 1998). Thus, the brook trout could indirectly regulate populations through its influence on a predacious invertebrate density, *Chaoborus americanus* larvae. The results of a study done at the same time in the pelagic zone of the studied fishless lakes have revealed a similar pattern in zooplankton community structure (Drouin *et al*. 2009). Other large cladocerans, *Sida crystallina*, and *Latona setifera*, also contributed to the dissimilarity between nekton assemblages, but by being more abundant in fishless lakes. Some microcrustaceans, such as *S. crystallina*, are known to develop an anti-predator behaviour in shallow lakes containing fish by aggregating at small scales, and using vegetation as refuge during the daytime (Fairchild 1981, Cerbin *et al*. 2003). Since vegetation cover was rare in our situation, these species could have been more affected by biotic interactions in fish-present lakes due to a lack of refuge habitat.

Benthos community

Predation by fish can decrease the abundance and species composition of larger invertebrates found in lakes (Evans 1989, Blois-Heulin *et al*. 1990, Bendell and McNicol 1995, McPeek 1998, Tate and Hershey 2003). In this study, large insect taxa represented a small proportion of the samples and were not present in all of them, and thus their overall weight in the dissimilarity between the species assemblages over the entire community was not important (*see* Clarke and Warwick 2001). When analysed separately, the total abundance of non-dipteran insects showed a significantly higher abundance of hemipterans and coleopterans in fishless lakes, as in other studies (Evans 1989, Bendell and McNicol 1995, Tate and Hershey 2003). By preying on insect predators, fish can indirectly control untargeted prey populations and thus affect the community structure. Studies have reported this type of population control by showing increased proportions of predacious invertebrates in fishless lakes (Gilinsky 1984, Evans 1989, Blois-Heulin *et al*. 1990, Goyke and Hershey 1992, Tate and Hershey 2003, Rennie and Jackson 2005).

Well structured patterns of the top-down control on the entire littoral benthic communities are more difficult to develop since they have not been studied as much as nekton or zooplankton communities. This is probably because of the structural complexity that can occur in this habitat as well as the complex life cycles of the organisms that inhabit this specific environment The low abundance of *H. azteca* in the fish-present assemblages could be associated with direct predation by fish, based on other studies that have noted their consumption by salmonids (Strong 1972, Luecke 1990, Lacasse and Magnan 1992). As for the nektonic communities, other biotic factors, such as competition with other taxa or invertebrate predation, must also be involved in the structuring of species assemblages. A number of studies have observed that fish can reduce the abundance of predacious chironomids (Gilinsky 1984, Goyke and Hershey 1992), and this could be explained by the fact that in general, these predators are more mobile and can be detected more efficiently by visual predators such as fish (Zaret 1980). The depletion of predacious chironomids could be advantageous to collector organisms such as *Psectrocladius* sp. and *Cladotanytarsus* sp., which could benefit from this reduction of predation pressure exerted on them by other chironomids.

Predation and diversity

The post-glacial colonization of previously fishless lakes by fish may have affected diversity through selective feeding or coevolution of predator–prey interactions, but predation is not necessarily a factor that regulates diversity in the current communities. According to Thorp (1986), to be the agent controlling diversity, a predator has to exclude some species (or at least reduce the rate of demographic expansion) and competitive exclusion has to occur in the absence of predation. By suppressing dominant competitive relationships, the predator could lead the community to experience an increase in diversity. In this study, no difference of diversity in littoral communities between fish-present and fishless lakes was observed. It can be expected that predation had no detectable effect on a dominant competitive relationship.

However, the results from a concomitant study done on the zooplankton community in the same fishless lakes suggest that predation could regulate community structure without influencing the diversity or being detectable over this variable (Drouin *et al*. 2009). These authors observed that the phantom midge fly larvae (*Chaoborus americanus)* may affect a well-known competitive relationship between daphnids and small herbivores, but this interaction had no effect on the species richness, evenness or diversity, when compared with that in fish present lakes where *C*. *americanus* was not dominant. It is possible that the predator did not preferentially consume prey that are competitively dominant in the system, which would not favour an increase in diversity. Prey species with efficient hiding strategies could find refuges in a complex spatial habitat and maintain population densities in presence of fish as high as in fishless lakes (e.g. Gilinsky 1984), however macrophytes were seemingly scarce (A. Drouin pers. obs.) in the studied lakes and refuge habitat not necessarily highly abundant. The food web complexity in the littoral zone of freshwater habitats can also be a factor which can buffer the effect of fish predation on invertebrate diversity (Thorp and Bergey 1981). There are many invertebrate predator taxa in the benthic communities with different feeding strategies, which could limit the control of resources by a single predator species.

Conclusion

Our results show that fishless lakes support a different littoral community structure, although this pattern might not be revealed via diversity indices (D, J', H'). The presence of such a distinct type of aquatic habitat can be of great importance to the regional pool of biodiversity in this boreal area. Many studies support a linkage between the emergence of aquatic insects and the terrestrial food webs. In the studied area, the presence of an endangered waterfowl species, Barrow's goldeneye (*Bucephala islandica*), on fishless lakes during its breeding period could be the result of competitive interactions for food with fish (Eriksson 1978, 1983, Einarsson 1987, Robert *et al*. 2000). Furthermore, evidence of different trophic cascades from lakes to the surrounding forest has been found (Murakami and Nakano 2002, Knight *et al*. 2005).

Fishless lakes are presently under stress by fish stocking activities, and it has been shown that their number has recently decreased in north-eastern America (Schilling *et al*. 2008). Since ecological evidence supports the hypothesis that fishless lakes play a role and have an importance in the Boreal ecoregion, we believe that preserving this habitat should be part of future conservation and wildlife management strategies. In this way, this study could contribute to further restoration programs, partly by giving evidence of the natural variability among lakes in the studied areas, but also by highlighting the importance of selecting appropriate indicators reflecting the community structure for the assessment of invertebrate communities in lakes from the eastern Canadian Boreal Shield.

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