Spatial and temporal variation in abundance of *Diplostomum* spp. in walleye (*Stizostedion vitreum*) and white suckers (*Catostomus commersoni*) from the St. Lawrence River

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Abstract: Abundances of eye flukes (*Diplostomum* spp.) were compared between walleye (*Stizostedion vitreum*) and white suckers (*Catostomus commersoni*) collected in late summer 1997 from Lake St. Louis and Lake St. Pierre, two expansions of the St. Lawrence River in Quebec, Canada. The white sucker, a benthic consumer, was more heavily infected than the walleye, a pelagic piscivore, in both lakes. Infection levels increased significantly with host age and size. For both species, abundance of *Diplostomum* spp. within each age group and length class was higher in fish from Lake St. Louis than in those from Lake St. Pierre. Walleye of all ages and white suckers ≥7 years old from Lake St. Louis were also larger at age than those of corresponding age from Lake St. Pierre. Therefore, walleye and white suckers from Lake St. Louis are probably different populations from those in Lake St. Pierre. The higher infection levels in Lake St. Louis are most likely due to the larger number of ring-billed gulls (*Larus delawarensis*), an important definitive host of *Diplostomum* spp., in colonies in close proximity to that lake; there are >75 000 pairs within 40 km of Lake St. Louis and 16 000 pairs within 40 km of Lake St. Pierre. No detrimental effects of infection with *Diplostomum* spp. could be detected on fish fork length, body mass, condition index, or gonadosomatic index. Walleye from shallow lentic waters in Lake St. Louis were larger and possessed heavier infections of *Diplostomum* spp. than those from deeper lotic waters. Walleye collected from a fixed trap near Quebec City in July 1997 were smaller but more heavily infected with *Diplostomum* spp. than those collected in October, which implies that different populations of fish may be present seasonally at this location. A visual index developed to measure the degree of opacity of the lens of fishes does not appear to be a reliable indicator of levels of infection with eye flukes. Experimental infection of laboratory-raised juvenile ring-billed gulls with metacercariae from the lenses of various fish species collected in the St. Lawrence River demonstrated that metacercariae were primarily *Diplostomum indistinctum* (84–92%), the remainder being *Diplostomum huronense*, and this pattern is consistent across host species and localities.

Résumé : Nous avons comparé l'abondance des douves de l'œil (*Diplostomum* spp.) chez le Doré jaune (*Stizostedion vitreum*) et le Meunier noir (*Catostomus commersoni*), récoltés à la fin de l'été 1997 dans le lac Saint-Louis et le lac Saint-Pierre, deux élargissements du fleuve Saint-Laurent au Québec, Canada. Dans chacun des lacs, le Meunier noir, un poisson benthivore, était plus fortement infecté que le Doré jaune, un prédateur pélagique. La gravité des infections augmentait significativement avec la taille et l'âge du poisson hôte. Chez les deaux espèces, l'abondance de *Diplostomum* spp. dans chaque groupe d'âge et de taille était plus élevée au lac Saint-Louis qu'au lac Saint-Pierre. Au lac Saint-Louis, chez les dorés de tous âges et les meuniers de plus de 7 ans, la taille à un âge donné était plus élevée que celles des poissons capturés au lac Saint-Pierre. Ces résultats suggèrent que les Dorés jaunes et les Meuniers noirs du Lac Saint-Louis constituent des populations distinctes de celles du lac Saint-Pierre. Il est probable que la variation spatiale de la gravité des infections soit attribuable à la répartition des colonies du Goéland à bec cerclé (*Larus delawarensis*), un hôte terminal important de *Diplostomum* spp., alors que plus de 75 000 paires ont été dénombrées dans un rayon de 40 km autour du lac Saint-Louis contre seulement 16 000 paires dans le cas du lac Saint-Pierre. Aucun impact négatif de l'infection par la douve de l'œil sur la santé des poissons n'a pu être mis en évidence par l'examen de

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la taille, de la masse, du coefficient de condition ou du rapport gonado-somatique des poissons. Les dorés capturés aux stations lentiques du lac Saint-Louis avaient une taille supérieure et un plus grand nombre de *Diplostomum* spp. dans leurs yeux que ceux récoltés en milieu lotique. Les dorés échantillonnés en juillet à une station fixe près de la ville de Québec avaient une taille inférieure mais étaient davantage infectés que les individus capturés en juin et en octobre au même endroit, suggérant que des populations différentes fréquentent ce secteur du fleuve Saint-Laurent selon les saisons. Enfin, les indices visuels conçus pour évaluer le degré d'opacité des cristallins de poisson ne semblent pas être des indicateurs fiables de l'abondance des douves de l'œil. De jeunes Goélands à bec cerclé élevés en captivité ont été infectés par les métacercaires présentes dans les cristallins des poissons du fleuve Saint-Laurent. Ces infections expérimentales ont démontré que les métacercaires appartiennent essentiellement à deux espèces, l'une, majoritaire, est *Diplostomum indistinctum* (84–92 %), l'autre, minoritaire, est *Diplostomum huronense*. Cette tendence de l'abondance relative est constante, quels que soient l'espèce ou le lieu de capture.

Introduction

Eye flukes (*Diplostomum* spp.; Digenea: Diplostomatidae) are ubiquitous parasites of freshwater fishes. The most common species, *Diplostomum spathaceum*, has been found in over 100 species of fishes worldwide (Chappell 1995). Ninety-two fish species in Canada alone have been reported to be infected with *D. spathaceum* or unidentified *Diplostomum* spp. (Margolis and Arthur 1979; McDonald and Margolis 1995). These organisms are typically associated with blindness and cataracts in fish, and infection can lead to emaciation, deformities, and death (Shariff et al. 1980; Chappell et al. 1994; Chappell 1995).

The life cycle involves three hosts. Adult parasites are found in the intestine of piscivorous birds, with *D. spathaceum* being found in gulls and terns. Eggs are shed with the avian feces; a free-swimming miracidium hatches and penetrates a snail (of the family Lymnaeidae in the case of *D. spathaceum*). There the miracidium develops into a mother sporocyst, which reproduces asexually to produce daughter sporocysts. Each of these then reproduces asexually to produce a cercaria, a free-swimming infective stage that is released from the snail host. Tens to hundreds of thousands of cercariae may be released from a single snail (Chappell et al. 1994). The cercaria penetrates a fish and migrates to the eye, where it develops into a metacercaria, the stage that is infective to the avian definitive host, which acquires it by consuming an infected fish. The lens of the eye is the site of infection with *D. spathaceum*, but eye flukes can also occur in the vitreous humor and on the retina.

Blindness and cataracts are commonly observed among fishes, including commercial and recreational sport fishes, in the St. Lawrence River, a major waterway of high economic and social importance connecting the Great Lakes with the Gulf of St. Lawrence and the Atlantic Ocean (see Marcogliese and Compagna 1999 and references therein). Yet no quantitative data exist on recent eye-fluke infections in large fish, nor are there any historical data with which to make comparisons. Among smaller fishes, 12 of 16 species of young of the year and forage fish collected from the St. Lawrence River in 1997–1998 were infected with *Diplostomum* spp. (Marcogliese and Compagna 1999). Thus, the first goal of this study was to establish base-line data to correlate infections with *Diplostomum* spp. with size and age for fishes in the St. Lawrence River as a reference point for future comparisons. The second goal was to compare prevalence and abundance of *Diplostomum* spp. in the lens of a benthic consumer, the white sucker (*Catostomus commersoni*), and a pelagic piscivore, the walleye (*Stizostedion vitreum*). The third goal was to examine the spatial variation of infection in these fish by comparing samples collected from Lake St. Louis and Lake St. Pierre, two enlargements of the St. Lawrence River, during late summer 1997. The differences between host species, sites, and habitats are evaluated, and inferences are made concerning the population structure of these fishes in the St. Lawrence River, based on the numbers of *Diplostomum* spp. found in fish from each lake. Further inferences are made concerning the seasonal distributions of populations, based on fish collected during the summer and fall of 1997 from a third site, St. Nicolas. The fourth goal was to examine potential effects of *Diplostomum* spp. on host growth and condition. Lastly, the suitability of an opacity index used to measure the degree of cataract formation in the eyes of fish (Lair and Martineau 1997; Mikaelian and Martineau 1997) is evaluated as an indicator of current infections with eye flukes.

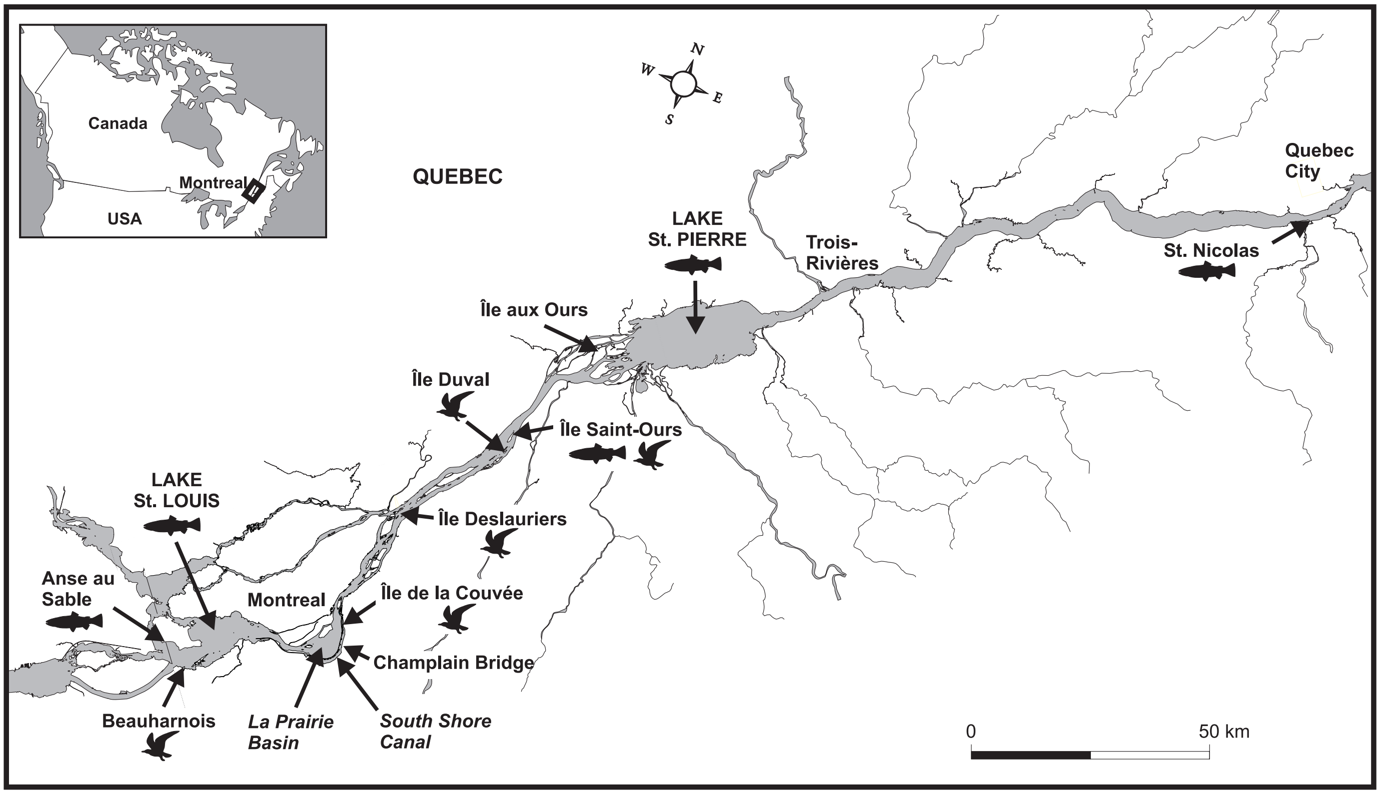
Materials and methods

Capture and sampling procedure

Walleye and white suckers were collected using experimental gill nets (60.8 m long, 1.8 m high; eight panels of increasing stretch mesh size from 25 to 152 mm). Sampling stations were systematically distributed among lentic (49 stations; one every km^2) and lotic (32 stations; one every 2 km^2) habitats of Lake St. Louis. Two nets were set at each station for 24 h between 15 September and 9 October 1997 (Fig. 1). Temperature decreased from 19 to 13°C during that time. Lentic habitats were characterized by abundant macrophytes to a depth of 2–6 m and water currents $<30\ cm\cdot s^{-1}$. Lotic habitats were characterized by depths of 6–13 m and currents of 20–70 $cm\cdot s^{-1}$. Fish from Lake St. Pierre were collected between 25 August and 1 October 1997 with the same multimesh gill nets at 25 stations systematically disposed in two channels without aquatic vegetation along the lake (water velocity ranged between 30 and 46 $cm\cdot s^{-1}$); additional captures were collected with four gill-net panels (32–76 mm) in 27 stations located in dense-vegetation habitats. Thus, samples were representative of the two lakes in their entirety. Further collections were made at a commercial-type fixed fish trap operated by the Quebec Aquarium at St. Nicolas, located 0.5 km west of Quebec City on the south shore of the St. Lawrence River (Fig. 1). Walleye and white suckers were captured during the first 2 weeks of June, July, and October 1997 for making temporal comparisons. Young-of-the-year (YOY) walleye (n = 32) were caught from Île Saint-Ours (Fig. 1) using a beach seine (22.6 × 1.15 m, 3-mm mesh) on 23 July 1999. This sample was utilized to characterize infection by *Diplostomum* spp. in early life stages. Twenty-one YOY walleye obtained from the Faune et Parcs Québec reference collection were examined for making a historical comparison of eyefluke infection in Lake St. Louis. These specimens were captured with a seine at Anse au Sable (Fig. 1) on 23 and 27 August 1968 (collection Nos. 12236 and 12235).

Fish were individually bagged and frozen for subsequent analysis. After thawing, specimens were measured to the nearest milli-

Fig. 1. Map of the St. Lawrence River depicting sampling sites (Lake St. Louis, Lake St. Pierre, St. Nicolas, Île St-Ours, Anse au Sable). Fish icons indicate areas where walleye (*Stizostedion vitreum*) and (or) white suckers (*Catostomus commersoni*) were collected and bird icons indicate major colonies of ring-billed gulls (*Larus delawarensis*). Inset: Map of northeastern North America showing the location of the sampling region.



metre (fork length; hereinafter referred to as length) and weighed to the nearest 0.1 g. Opercula were removed and used for aging individuals collected from Lake St. Louis; otoliths were used for fish from Lake St. Pierre. Gonads were dissected out and weighed. The fish condition index (*K*) was defined as

$$K = \text{body mass} \times \text{length}^{-3} \times 100\,000$$

The gonadosomatic index was determined as gonad mass as a percentage of body mass. Walleye, including their eyes, from the reference collection were in good condition. They were fixed in 10% formalin soon after capture and transferred after 2 weeks to 70% ethanol for storage. As viscera were partly missing from many of these specimens, only length was measured.

Eyes were removed and examined for *Diplostomum* spp. infection as described below.

Eye-fluke infection

The left and right eyes of all fish were dissected. The lens was separated from the vitreous humor and the parasites were removed from each tissue, identified, and counted. Only lens forms of *Diplostomum* spp. were used in the analysis. Parasites were rare in the vitreous humor. Although fixation in formalin and prolonged storage in alcohol hardened the lenses of preserved specimens in the 1968 sample, eyeflukes were still recognizable and as easy to count as in frozen individuals.

Three calculations of the level of eye-fluke infection were used: prevalence, abundance, and intensity. Prevalence is defined as the proportion of infected fish of a given species in a sample, expressed as a percentage, mean abundance as the mean number of parasites per host, infected and noninfected, in a sample, and mean intensity as the mean number of *Diplostomum* spp. per infected fish (Bush et al. 1997).

Parasite taxonomy

Metacercarial stages of diplostomatids are difficult to identify to species, and resolution of the group's taxonomy must be completed before individuals can be assigned to species (Chappell 1995; Gibson 1996). In North America, metacercariae found in the lens of fish are typically assigned to *D. spathaceum* and those in the vitreous humor to other species, but these identifications must be regarded with caution (Gibson 1996). To verify the identification of *Diplostomum* species, we experimentally infected ring-billed gulls (*Larus delawarensis*) raised in captivity with metacercariae from fresh-caught white suckers, walleye, redhorses (*Moxostoma* sp.), and spottail shiners (*Notropis hudsonius*) collected from various regions in the St. Lawrence River between Lake St. Louis and Quebec City. Lenses were dissected from the fish, thoroughly rinsed in Tyler sieves, and fed to juvenile gulls. After 2 weeks, birds were examined and the trematodes were removed, fixed in hot 70% ethanol, and stained in acetocarmine. Two morphologically different forms belonging to the *D. spathaceum* complex were found, one with a large symmetrical anterior testis and one with a smaller, slightly asymmetrical testis. These correspond to descriptions of *Diplostomum spathaceum huronense* and *Diplostomum spathaceum indistinctum*, respectively, as described in Dubois (1970), both of which were originally described from North America. As there is at present no evidence to support or refute Dubois' subspecies designations, in the interim we prefer to follow Sudarikov (1971), who considered each to be a separate species.

Between 84 and 92% of the worms recovered were *Diplostomum indistinctum* and the rest *Diplostomum huronense*, regardless of host species or locality (Table 1). Thus, *D. indistinctum* is the dominant

Table 1. Identification of *Diplostomum* spp. recovered from laboratory-reared juvenile ring-billed gulls (*Larus delawarensis*) experimentally fed washed lenses removed from fish collected from the St. Lawrence River between Lake St. Louis and Quebec City.

Host species	*D. indistinctum*	*D. huronense*	Total
Catostomus commersoni	39 (89)	5 (11)	44
	128 (84)	24 (16)	152
Stizostedion vitreum	134 (89)	17 (11)	151
Moxostoma sp.	112 (92)	10 (8)	122
Notropis hudsonius	81 (85)	14 (15)	95

Note: Numbers in parentheses are percentages. Specimens that could not be identified unequivocally as either *D. indistinctum* or *D. huronense* were assigned to the latter species. Hence, the percentage of *D. huronense* is overestimated and that of *D. indistinctum* underestimated. Despite this conservative approach, the majority of specimens were *D. indistinctum*.

species, with background levels of *D. huronense*. As there is no way to distinguish the metacercariae from fish and there are no data at present which suggest that the two species differ in ecology and transmission, we have designated all metacercariae in the lens *Diplostomum* spp. for the purposes of analysis, while fully cognizant of the fact that two species are present, albeit disproportionately, in the fish populations in the St. Lawrence River.

Opacity index

Immediately after capture, the eyes of live fish collected at St. Nicolas were individually classified according to the degree of opacity. The opacity index ranges from 0 to 4, as follows: 0, clear eyes; 1, some white spots on the lens; 2, lens partially opaque, with numerous white spots; 3, lens completely cloudy; and 4, eye completely white and lens damaged (Lair and Martineau 1997; Mikaelian and Martineau 1997). This opacity index has been used in previous surveys to describe the extent of blindness and cataract formation in a population (Lair and Martineau 1997; Mikaelian and Martineau 1997). A three-level opacity index was used to classify the eyes of walleye and white sucker collected from Lake St. Louis. In this case, one score was assigned to both eyes of a specimen, ranging from clear eyes (level 0) to partial (level 1) and severe opacity of the lens (level 2). This scale was used in previous surveys undertaken by Faune et Parcs Québec (e.g., Fournier et al. 1998).

Statistical analyses

Eye-fluke counts were not normally distributed and were generally not sufficiently normalized by transformations. Thus, abundances of *Diplostomum* spp. were compared between fish sexes, lakes, and habitats and among fish length classes, age groups, and opacity-index levels using nonparametric analyses, including Mann–Whitney *U* tests (two levels) and Kruskal–Wallis tests (more than two levels). Length-class intervals and midpoints were determined as described in Sokal and Rohlf (1981). Wilcoxon's signed-ranks test for paired data was used to assess the asymmetry of *Diplostomum* spp. distributions between the left and right eyes. Infection prevalences were compared between lakes and hosts with χ^2 tests. Relations between abundance of *Diplostomum* spp. and host age, size, mass, condition index, and gonadosomatic index were first examined through nonparametric Spearman's coefficents of rank correlations. Linear regression analyses were performed on transformed variables when the assumptions of linearity, normality, and homoscedasticity could be satisfied. In these cases, regression lines were compared between habitats and lakes by means of analyses of covariance (ANCOVAs) to take into account the confounding effects of fish age or length on *Diplostomum* spp. abundance. Differences in fish size or mass among age groups, months, habitats, or sampling sites were examined with one-way analysis of variance (ANOVA) followed by a Tukey–Kramer HSD multiple-range test for classes comprising more than two levels. The Shapiro–Wilk *W* statistic was used to test normality of distributions. Statistical significance was set at $P < 0.05$. Data were analyzed using the JMP® version 3.2.1 statistical package (SAS Institute Inc. 1997).

Results

In total, 229 and 86 walleye and 99 and 73 white suckers from Lake St. Louis and Lake St. Pierre, respectively, were examined. *Diplostomum* spp. distributions were aggregated, as indicated by the variance/mean ratios. There were no differences in mean abundance of infection between the right and left eyes for both host species, with the exception of walleye from Lake St. Pierre (Wilcoxon's signed-ranks test, $P = 0.016$), nor were there any differences in parasite mean abundance between the sexes for either fish species. Summary statistics for mean length and mass of hosts and prevalence, mean abundance, and variance/mean ratio of *Diplostomum* spp. are presented in Table 2.

Mean abundance of *Diplostomum* spp. was significantly higher in white suckers than in walleye from Lake St. Louis (Mann–Whitney *U* test, $P \leq 0.0001$) and Lake St. Pierre (Mann–Whitney *U* test, $P \leq 0.0001$). Prevalence was significantly higher in white suckers than in walleye from Lake St. Pierre (χ^2 test, $P \leq 0.0001$), but not in Lake St. Louis (χ^2 test, $P = 0.5565$). The maximum number of metacercariae was higher in Lake St. Louis than in Lake St. Pierre for both species of fish (Table 2).

YOY walleye <12 cm in length from Île Saint-Ours were infected with *Diplostomum* spp. in the lens. Parasite abundance was 0.9 ± 0.3 and intensity 2.6 ± 0.5 (mean ± SE), and prevalence was 34.4%. Metacercariae of *Diplostomum* spp. were found in the preserved sample of YOY walleye ≤13 cm in length collected from Lake St. Louis in 1968 at a prevalence of 100% and an abundance of 6.9 ± 0.9, which was greater, though not significantly different from, the abundance in similar-sized YOY walleye from Lake St. Louis in 1997 (Mann–Whitney *U* test, $P > 0.1$).

Variation in parasite abundance with size and age between lakes

For both fish hosts, infection levels of *Diplostomum* spp. were higher in Lake St. Louis than in Lake St. Pierre (Mann–Whitney *U* test, $P \leq 0.0001$). Parasite abundance also increased with host age and size in each species (Figs. 2, 3). To test for a potential confounding effect of these covariates,

Table 2. Fork length and body mass of hosts and prevalence, abundance, intensity, and variance/mean ratio of *Diplostomum* spp. in walleye (*Stizostedion vitreum*) and white suckers (*Catostomus commersoni*) collected from Lake St. Louis, Lake St. Pierre, and St. Nicolas in the St. Lawrence River in 1997.

	Site	*n*	Fork length[a] (cm)	Body mass[a] (g)	Prevalence (%)	Abundance[a]	Intensity[a]	Variance/ mean ratio
Walleye	Lake St. Louis	229	33.0±0.6	465.6±29.5	98.7	17.6±1.4	17.9±1.4 (1–116)	24.8
	Lake St. Pierre	86	32.1±1.0	450.4±51.0	67.4	3.2±0.5	4.7±0.6 (1–21)	5.9
	St. Nicolas	122	31.7±0.6	382.9±25.8	69.7	4.4±0.5	6.3±0.6 (1–29)	6.9
White sucker	Lake St. Louis	99	41.6±0.8	1230.5±53.4	100	151.3±8.6	151.3±8.6 (7–385)	48.9
	Lake St. Pierre	73	32.5±0.8	616.9±43.1	98.6	45.3±5.0	45.9±5.1 (1–154)	41.1
	St. Nicolas	103	30.9±0.6	469.1±25.3	95.1	40.3±4.7	42.4±4.8 (1–248)	56

[a] Values are given as the mean ± SE. Values in parentheses are ranges.

the relationship between *Diplostomum* spp. abundance and host age and length was compared between sampling locations.

Infection level was positively associated with age (r^2 = 0.18, $P \leq 0.0001$) and length (r^2 = 0.17, $P \leq 0.0001$) in walleye from Lake St. Louis but not in those from Lake St. Pierre, where these relationships were weak and not significant (Spearman's ρ = 0.05, P = 0.6416) (Fig. 2). When walleye of the same age group or length class were compared, differences in infection levels between lakes remained significant. Thus, specimens from Lake St. Louis aged 3–5 years had 6–24 times more *Diplostomum* spp. in their eyes than their counterparts from Lake St. Pierre (Mann–Whitney *U* test, $P < 0.003$). Similarly, eye flukes were 3–40 times more abundant in walleye of length classes ranging from 15 to 50 cm from Lake St. Louis than in those from Lake St. Pierre (Mann–Whitney *U* test, $P < 0.02$).

In both lakes, white suckers were also increasingly infected by *Diplostomum* spp. with increasing age and length. Linear regression analyses on logarithmically transformed data showed the infection level to be more closely related to length than to age of fish, irrespective of sampling location (Fig. 3). A visual comparison of regression lines suggests between-lake variation in the pattern of eye-fluke accumulation. This is also indicated by the ANCOVA, which revealed a significant effect of lake on both the slope ($P \leq 0.0001$) and the intercept ($P \leq 0.0001$) of the relationship between eye-fluke abundance and both covariates (length: r^2 = 0.68, $P \leq 0.0001$; age: r^2 = 0.61, $P \leq 0.0001$). Whereas large white suckers (length class 35 cm and above) in Lake St. Louis were up to 2 times more infected than those in Lake St. Pierre, between-lake differences in parasite abundance were 3–11 times greater in smaller individuals (length classes 15–30 cm). Differences in infection level between lakes were also 2–34 times greater in white suckers aged 2–6 years from Lake St. Louis, but only up to 6 times greater in those aged 7 years and older. When comparisons were done by age group and length class, between-lake differences in infection level remained significant (Mann–Whitney *U* test, $P < 0.001$).

Growth rates of walleye and white suckers were compared between lakes. Mean lengths of walleye aged 2–6 years from Lake St. Louis were significantly greater than those of walleye from Lake St. Pierre (ANOVA, P = 0.0031) (Table 3). Mean lengths of white suckers aged 4–6 years from Lake St. Louis were not significantly different from those of their counterparts from Lake St. Pierre (ANOVA, $P > 0.05$), whereas those of white suckers aged 7+ years were significantly greater when combined (ANOVA, $P \leq 0.0001$) and when examined by age group (Table 4).

Parasite abundance in relation to fish condition

Negative relationships between parasite abundance and measures of fish health or condition can be indicative of a detrimental impact of infection on the host. In general, there were no negative relationships between abundance of *Diplostomum* spp. and fish length, mass, gonad mass, condition index, and gonadosomatic index for walleye or white suckers in each lake. Moreover, within each age group, there was no significant relationship between *Diplostomum* spp. abundance and fish length, mass, condition index, or gonadosomatic index, or the relationship was positive, as with length of age 3 walleye (r^2 = 0.1095, P = 0.0454) and mass of age 4 walleye in Lake St. Louis (r^2 = 0.4154, P = 0.0128).

Parasite abundance and habitat

Samples collected in Lake St. Louis could be subdivided according to habitat (lentic or lotic). Walleye from lentic habitats were significantly older, longer, and heavier, with more *Diplostomum* spp., than those from lotic habitats (Mann–Whitney *U* test, $P < 0.0007$). Since infection with *Diplostomum* spp. increases with age and size of fish, parasite abundance was plotted against host age (Fig. 4) and length (data not shown) and regression analyses were performed on logarithmically transformed data. The relationship between eye-fluke abundance and fish age is considerably weaker in lotic than in lentic habitats (r^2 ratio = 4.17; Fig. 4), an observation that holds for the relation between infection level and fish length (lentic habitats: r^2 = 0.26, $P < 0.0001$; lotic habitats: r^2 = 0.06, P = 0.0046). An ANCOVA was used to test the influence of habitat on *Diplostomum* spp. infection while adjusting for the covariate age or length. The ANCOVA detected a slight but significant effect of habitat on the slope of the relationship between *Diplostomum* sp. abundance and fish age (P = 0.0006) and length (P = 0.0031), but no effect was found on the intercept of the relations ($P > 0.05$). Whereas young fish (<3 years old) were similarly infected irrespective of their habitat of origin, individuals aged 3–5 years captured in lentic areas had 2.6–3.3 times more *Diplostomum* spp. in their lenses than those collected at lotic sites.

Temporal changes in parasite abundance

Walleye collected at the fish trap at St. Nicolas were significantly longer and heavier in June and October than those

Fig. 2. Abundances of *Diplostomum* spp. plotted against age (A) and fork length (B) for walleye collected from Lake St. Louis and Lake St. Pierre in late summer and early fall of 1997. Linear regressions were performed on logarithmically transformed data. Parameter estimates of regression equations, along with the significance probability (*P*) and r^2 values from the model, are shown for Lake St. Louis. In spite of data transformation, some assumptions of the linear regression were not fulfilled for Lake St. Pierre.

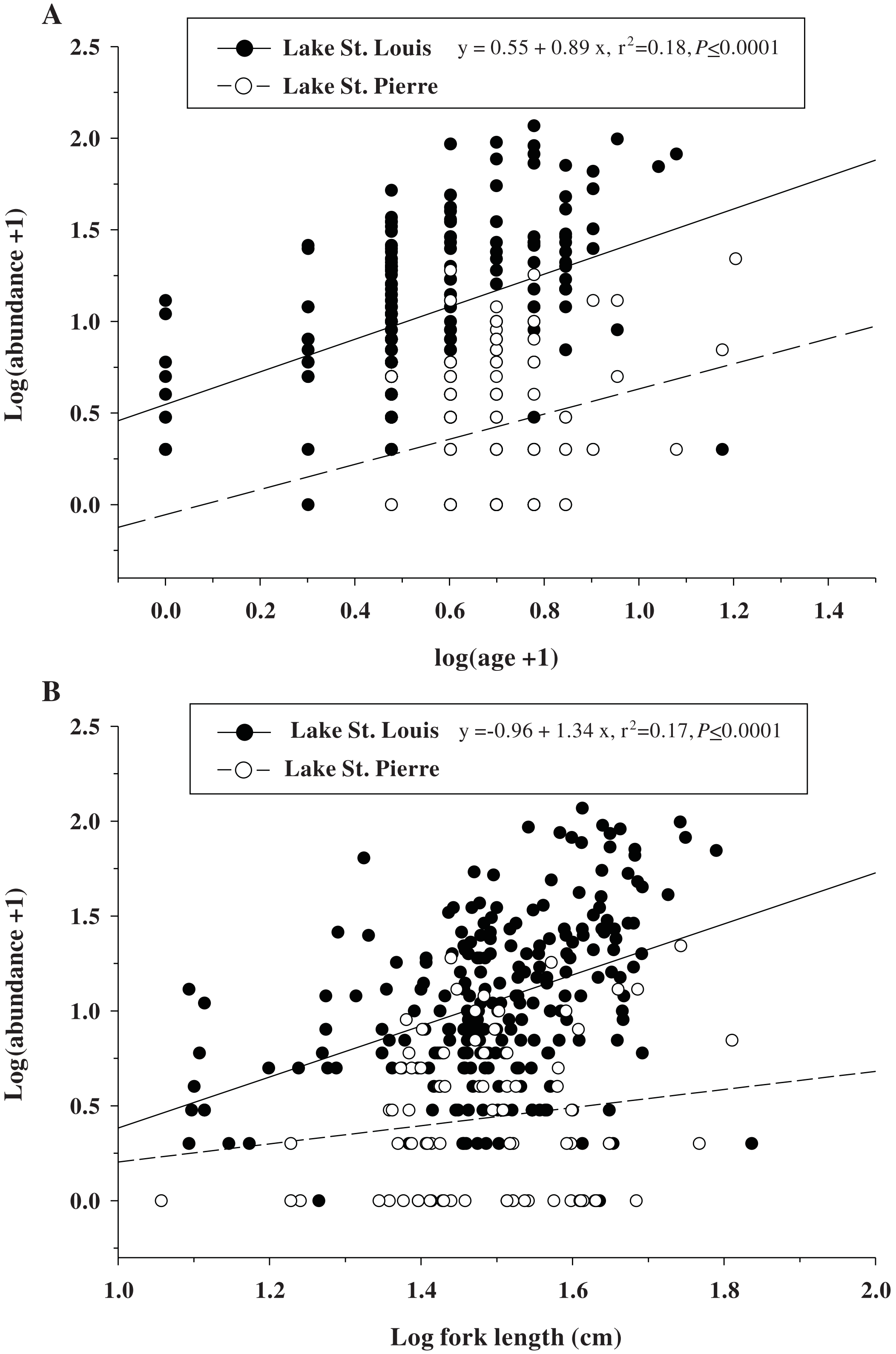
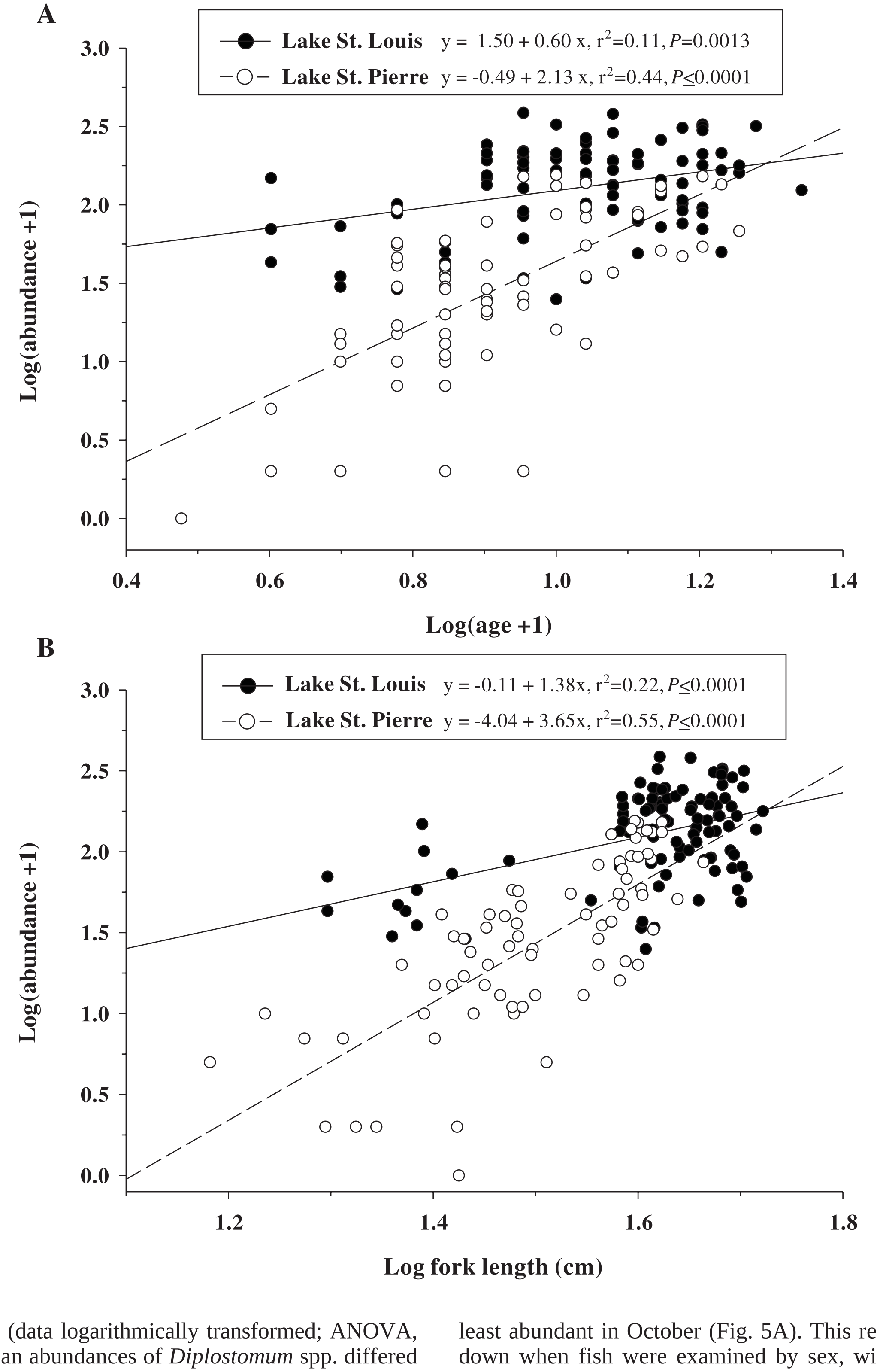


Fig. 3. Abundances of *Diplostomum* spp. plotted against age (A) and fork length (B) for white suckers collected from Lake St. Louis and Lake St. Pierre in late summer and early fall of 1997. Linear regressions were performed on logarithmically transformed data. Parameter estimates of regression equations, along with the significance probability (*P*) and r^2 values from the model, are presented for each plot.



collected in July (data logarithmically transformed; ANOVA, $P \leq 0.0001$). Mean abundances of *Diplostomum* spp. differed significantly among the 3 months (Kruskal–Wallis test, $P \leq 0.0001$), *Diplostomum* spp. being most abundant in July and least abundant in October (Fig. 5A). This relationship broke down when fish were examined by sex, with *Diplostomum* spp. abundance in June low in females but high in males (Fig. 5A). Abundance of *Diplostomum* spp. was significantly

Table 3. Fork lengths at age in walleye collected from Lake St. Pierre and Lake St. Louis in late summer.

Age group (years)	Fork length[a] (cm) Lake St. Louis	Lake St. Pierre	P (ANOVA)
0	13.5±0.5 (10)	—	—
1	20.5±0.5 (13)	—	—
2	29.6±0.3 (90)	20.0±1.7 (3)	<0.0001
3	34.8±0.5 (36)	26.4±0.7 (22)	<0.0001
4	40.1±1.6 (14)	31.6±1.1 (33)	<0.0001
5	42.7±1.6 (16)	36.2±1.6 (15)	0.0076
6	44.7±1.4 (16)	35.1±2.5 (5)	0.0031
7	44.7±1.7 (4)	31.8±8.3 (3)	0.1312
8	50.8 (2)	43.3 (2)	—
10	61.6 (1)	—	—
11	56.1 (1)	58.5 (1)	—
14	68.6 (1)	64.6 (1)	—
15	—	55.3 (1)	—

[a] Values are given as the mean ± SE. Numbers in parentheses are sample sizes.

higher (Kruskal–Wallis test, $P = 0.0004$), but length lower (ANOVA on logarithmically transformed data, $P = 0.0007$), in females collected in July than in those collected in June or October (Fig. 5). Similarly, the abundance of *Diplostomum* spp. was significantly lower (Kruskal–Wallis test, $P = 0.0003$), but the length higher (ANOVA on logarithmically transformed data, $P = 0.0111$), in males collected in October than in those collected in June or July (Fig. 5). The same relationship held for mass as for length when males and females were considered separately (data not shown). Mean abundance of *Diplostomum* spp. followed the same general pattern in white suckers over time, with abundance higher in July than in June or October, but the differences were not significant (Kruskal–Wallis test, $P > 0.05$). Summary statistics for levels of infection with *Diplostomum* spp. in walleye and white sucker from St. Nicolas are presented in Table 2.

Test of opacity indices

Mean abundance of *Diplostomum* spp. varied among opacity-index levels (scale 0–4): in white suckers from St. Nicolas, eyes with levels 0, 1, and 2 had significantly fewer metacercariae than those with levels 3 and 4 (Kruskal–Wallis test, $P \leq 0.0001$) (Fig. 6A). However, parasite abundances did not differ significantly among levels 0, 1, and 2, nor between levels 3 and 4. Among walleye from St. Nicolas, there was no significant difference in *Diplostomum* spp. abundance among levels 0, 1, and 2 (Fig. 6A). No walleye eyes were classified as level 3 or 4.

White suckers from Lake St. Louis classified with severe opacity of the lens (level 2, scale 0–2) had significantly higher numbers of *Diplostomum* spp. than those classified as level 0 (Kruskal–Wallis test, $P = 0.0244$) or level 1 (Kruskal–Wallis test, $P = 0.0139$) (Fig. 6B). White suckers classified as level 1 had a tendency to have more eye flukes than those classified as level 0, but the difference was minimal and not significant (Kruskal–Wallis test, $P = 0.5576$). None of the walleye examined from Lake St. Louis showed severe lens opacity (level 2). There were no differences in numbers of *Diplostomum* spp. between those with partial opacity of the lens (level 1) and those with clear eyes (level 0) (Kruskal–Wallis test, $P = 0.9065$) (Fig. 6B).

Table 4. Fork lengths at age in white suckers collected from Lake St. Pierre and Lake St. Louis in late summer.

Age group (years)	Fork length[a] (cm) Lake St. Louis	Lake St. Pierre	P (ANOVA)
2	—	26.6 (1)	—
3	21.4±1.6 (3)	18.2±3.0 (2)	—
4	24.4±1.0 (3)	26.9±2.7 (4)	0.4813
5	27.1±1.5 (3)	28.9±1.6 (10)	0.5760
6	27.9±4.0 (3)	28.1±1.2; 16)	0.9461
7	39.6±0.6 (7)	34.9±1.4 (9)	0.0154
8	42.2±0.7 (14)	33.7±2.9 (5)	0.0006
9	42.6±1.3 (5)	39.2±0.7 (4)	0.0372
10	43.1±0.7 (11)	37.9±0.7 (7)	0.0002
11	45.8±0.8 (10)	37.5 (1)	—
12	44.9±1.9 (7)	43.6±2.6 (2)	—
13	45.7±1.6 (4)	40.7±1.3 (4)	$P = 0.0531$
14	45.9±1.0 (7)	38.5 (1)	—
15	47.4±1.2 (8)	41.1±0.9 (2)	—
16	47.9±1.2 (3)	40.6 (1)	—
17	49.1±3.6 (2)	38.8 (1)	—
18	48.1 (1)		—
21	41.2 (1)		—

[a] Values are given as the mean ± SE. Numbers in parentheses are sample sizes.

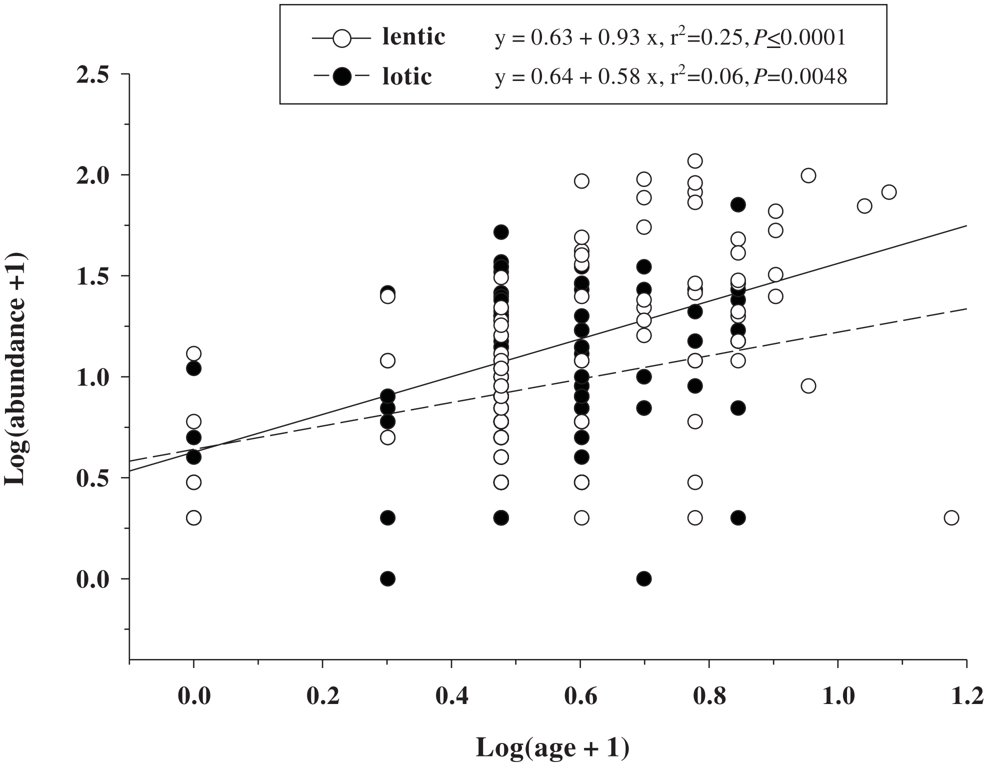
Discussion

Experimental infections of juvenile ring-billed gulls demonstrated that metacercariae belong primarily to one species, *D. indistinctum*, with comparatively low levels of background infection with *D. huronense*, regardless of which fish hosts were used as the source of metacercariae. Both parasites use gulls as definitive hosts; other fish-eating birds such as loons and mergansers are rare. Herons are common in Lake St. Pierre, but were not infected with *Diplostomum* spp. (J.D. McLaughlin and D.J. Marcogliese, unpublished data). No colonies of cormorants are listed between Lake St. Louis and Quebec City (see data in Environment Canada (2000)). Thus, results suggest that metacercariae from the lenses of fish in the St. Lawrence River belong primarily to a single species, with low rates of infection by a second species; both species use gulls as definitive hosts.

Levels of infection with *Dipostomum* spp.

The results demonstrate significant spatial variation in mean abundance of *Diplostomum* spp. along the St. Lawrence River. However, there are no published historical data with which infections in walleye and white suckers may be compared to determine annual trends. Infection levels in the St. Lawrence River are distinctly higher than those recorded in earlier surveys carried out in the Great Lakes. Prevalence of *Diplostomum* sp. or *Dipostomulum* sp. in white suckers in the Great Lakes and surrounding areas ranged from 10 to 68% between 1961 and 1975 (Dechtiar 1972*a*, 1972*b*;

Fig. 4. Relationship between abundances of *Diplostomum* spp. and ages of walleye caught in lentic and lotic habitats in Lake St. Louis in late summer and early fall of 1997. Linear regressions were performed on logarithmically transformed data. Parameter estimates of regression equations, along with the significance probability (*P*) and r^2 values from the model, are shown for lentic and lotic habitats separately.



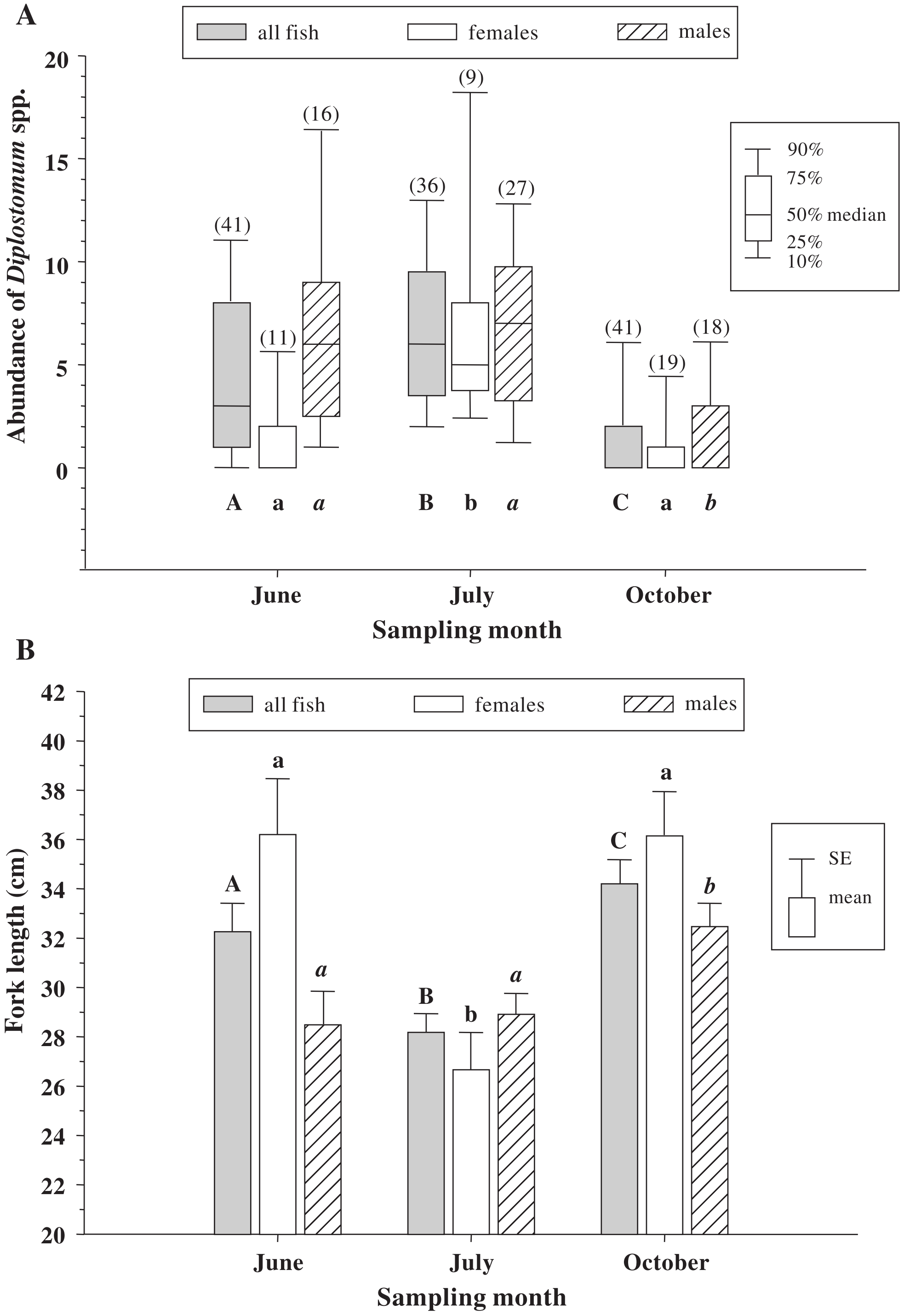
Nepszy 1988), though Bangham (1955) found that 82% in Lake Huron were infected in 1951. In walleye, prevalences in the Great Lakes and vicinity ranged from 2 to 27% between 1961 and 1975 (Dechtiar 1972*a*, 1972*b*; Nepszy 1988) but reached 68% in Lake Huron in 1951 (Bangham 1955). In smaller systems, where parasite transmission may be enhanced as a result of increased spatial overlap of hosts involved in the life cycle, infection levels can be quite high. Prevalences of 94 and 100% in white suckers >10 cm were observed in Douglas Lake, Michigan, and the Big Laramie River, Wyoming, respectively (La Rue et al. 1926; Hendrickson 1978). In the most recent survey carried out in the Great Lakes, only 2% of walleye in Lake Huron were found to be infected (Muzzall and Haas 1998).

Given that the numbers of ring-billed gulls are increasing, having approximately doubled between 1982 and 1994 (see data in Environment Canada (2000)), we originally suspected that levels of infection with *Diplostomum* spp. in fish are also increasing. The first record of ring-billed gulls breeding on the St. Lawrence River was obtained in 1953, and by 1981–1982, 30 233 pairs were ennumerated in the vicinity of Montréal (Mousseau 1984). In 1997 there were 6156 pairs near Beauharnois, 20 870 on Île de la Couvée, 48 767 on Île Deslauriers, 14 099 on Île Saint-Ours, and 1783 on Île Duval (Fig. 1) (P. Brousseau, Canadian Wildlife Service, 1141 route de l'Église, Ste-Foy, QC G1V 4H5, Canada, personal communication), for a total of 91 675 pairs along the St. Lawrence River in Quebec between Lake St. François and Lake St. Pierre.

However, *Diplostomum* spp. abundances measured in a small sample of YOY walleye collected from Lake St. Louis in 1968 demonstrate that infection levels were high and comparable to those in YOY fish collected in the same vicinity in 1997. It is known that ring-billed gulls colonized Île de la Couvée between 1967 and 1971, numbering 4000 pairs by 1974, and colonies have occupied numerous nesting sites in the vicinity of Montréal since 1953, including 10 000 pairs on Île Verte, south of the city, in 1967 (Mousseau 1984). The high abundance of *Diplostomum* spp. in 1968 may have resulted from a combination of high lymnaeid snail densities in Lake St. Louis (85/m in the littoral zone in 1967–1969; Magnin 1970) and large numbers of gulls. More recent surveys of snails report much lower densities of lymnaeids in the lake (Lepitzki 1993). In terms of *Diplostomum* spp. populations, the decrease in density of the snail first intermediate host may be compensated for by the much higher number of gulls in the area. However, it cannot be overlooked that there were high numbers of gulls in the immediate vicinity of Lake St. Louis as early as 1967.

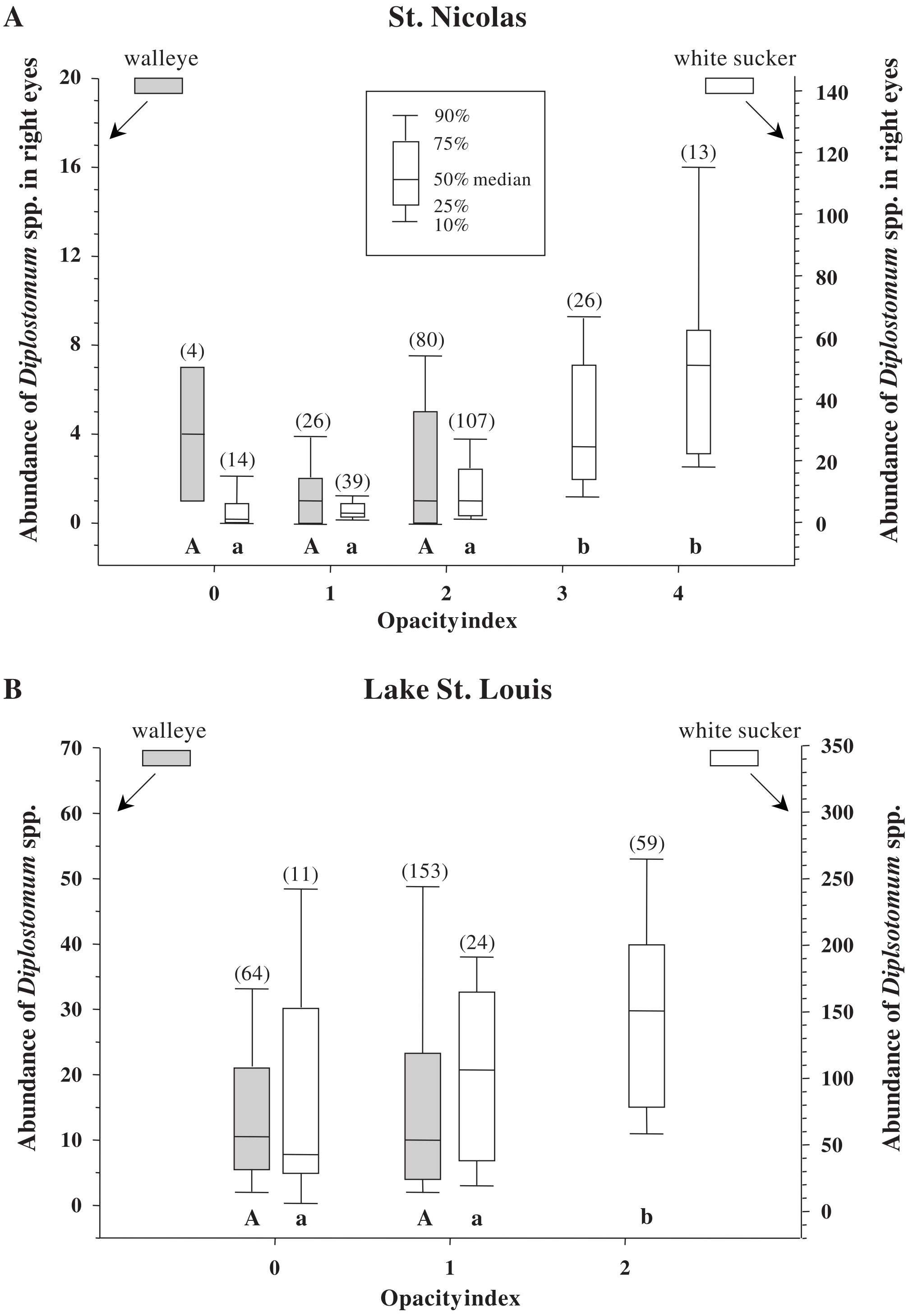
The higher abundance of *Diplostomum* sp. in Lake St. Louis than in Lake St. Pierre cannot be a result of differences in productivity between the lakes, as productivity is higher in Lake St. Pierre (Langlois et al. 1992; Armellin et al. 1994). Nor is it likely to be due to differences in densities of snail intermediate hosts, as recent surveys report higher densities of lymnaeid snails in the vicinity of Lake St. Pierre than in Lake St. Louis (Lepitzki 1993). Moreover, high densities of lymnaeid snails were also observed in Lake

Fig. 5. Temporal variation in *Diplostomum* spp. abundances (A) and fork lengths (B) of walleye captured at St. Nicolas in 1997. (A) Comparison of *Diplostomum* spp. counts among sampling months, using the nonparametric Kruskal–Wallis test. Within each subgroup (all fish, males, and females), different upper- and lower-case letters below the box plots indicate that they are significantly different from each other. Numbers in parentheses are sample sizes. (B) Comparison of logarithmically transformed mean lengths among sampling months, using ANOVA. Within each subgroup (all fish, males, and females), different upper- and lower-case letters above the box plots indicate that they are significantly different from each other as determined by the post-hoc multiple-range (Tukey–Kramer HSD) test.



St. Pierre in 1997 (D.J. Marcogliese, personal observation). Rather, the difference in abundance may be attributable to the distribution of ring-billed gulls along the St. Lawrence River. Given that gulls can feed as far as 40 km from a colony (Erwins et al. 1994), there are more than 75 000 pairs within foraging distance of Lake St. Louis, but about 16 000 within a day’s travel of Lake St. Pierre. The abundance of *Diplostomum* spp. was also twice as high in mudpuppies

Fig. 6. Comparison of *Diplostomum* spp. counts with opacity-index levels for different sites in the St. Lawrence River in 1997 for walleye and white sucker. Abundances of *Diplostomum* spp. were statistically compared among opacity-index levels using the nonparametric Kruskal–Wallis test. In both plots, walleye abundance is measured on the left axis with shaded box plots and white sucker abundance on the right axis with open box plots. Within each subgroup (walleye, white sucker), different upper- and lower-case letters below the box plots indicate that they are significantly different from each other. Numbers in parentheses are sample sizes. (A) Comparison of *Diplostomum* spp. abundances among opacity-index levels measured using theopacity-index scale at St. Nicolas, which ranges from 0 (clear eyes) to 5 (completely opaque and damaged). Data are shown for right eyes only. (B) Comparison of *Diplostomum* spp. abundances among opacity-index levels measured using the opacity-index scale at Lake St. Louis, which ranges from 0 (clear eyes) to 2 (severe opacity). Data are shown for the two eyes together.



(*Necturus maculosus*) from Lake St. Louis than in those from Lake St. Pierre (Marcogliese et al. 2000). However, a potentially important impact of lymnaeid population densities on the distribution of *Diplostomum* spp. between the two fluvial lakes cannot be ruled out, and an extensive gastropod survey of the two lakes is required to further examine this question.

In both lakes, white suckers were more heavily infected than walleye. Numerous other studies showed *Diplostomum* spp. to be more common in benthic than in pelagic species of fish (Heckmann 1983; Marcogliese and Compagna 1999). As a result of the distribution of infective cercariae in the water, pelagic fish are less likely to become infected than benthic or littoral fish (Sweeting 1974).

Within Lake St. Louis, differences were observed between size and infection levels in walleye from lotic and lentic habitats, those from lentic habitats being larger, older, and more heavily infected. However, statistical analyses indicated that some of the differences in infection level could not be explained by age or size alone. Lentic habitats are characterized by extensive macrophyte growth and slower currents. The macrophytes provide suitable habitat for the gastropod intermediate hosts. In addition, slower currents likely permit greater retention of both snails and free-swimming cercariae. Greater abundances of trematode metacercariae in fish, including *D. spathaceum*, have been observed in slow as opposed to faster currents elsewhere (Berra and Au 1978; Stables and Chappell 1986; Steedman 1991; Janovy et al. 1997). Styczynska-Jurewicz (1959) found that the abundance of *D. spathaceum* decreased with distance from shore, and that the highest levels occurred in association with the vegetated zone.

The results for walleye from Île Saint-Ours and Lake St. Louis and white suckers from Marcogliese and Compagna (1999) demonstrate that these fish begin acquiring *Diplostomum* spp. in their first year of life. Infection levels in YOY walleye are particularly high, being surpassed only by those in YOY brown bullheads (*Ameiurus nebulosus*) (Marcogliese and Compagna 1999) and quillback (*Carpiodes cyprinus*) (prevalence 93%, mean abundance 16.0; D.J. Marcogliese, unpublished data) in the St. Lawrence River. These levels of infection in a small visual predator may impede the foraging ability of YOY walleye, as low-intensity infections affect vision in other small fish (Owen et al. 1993).

Diplostomum spp. abundance as an indicator of fish stocks

The differences in size at age and the higher mean abundance of *Diplostomum* spp. in Lake St. Louis suggest that separate populations of both walleye and white suckers are present in Lake St. Louis and Lake St. Pierre. Parasites are useful and appropriate as biological indicators of fish stocks (Kabata 1963; Sindermann 1963; MacKenzie 1987, 1993; Williams et al. 1992; MacKenzie and Abaunza 1998). Individual species may be used as biological tags, or the entire parasite assemblage can be examined (MacKenzie and Abaunza 1998). According to Kabata (1963) and Sindermann (1963), the most important selection criteria, to be used as guidelines rather than fixed rules, for parasite species are that (*i*) the parasite should have significantly different levels of prevalence, abundance, or intensity in different areas; (*ii*) the parasite should be long-lived in the fish; (*iii*) the parasite should be easily detected and identified; (*iv*) minimal dissection or manipulation should be required, i.e., the parasite should display some degree of site specificity in the host; (*v*) the parasite should not have noticeable pathological effects on the fish, since such effects could impact host behavior; (*vi*) the life cycle should be relatively simple; (*vii*) the parasite populations should be relatively stable from year to year, or among seasons; and (*viii*) environmental conditions throughout the geographic range of the study should be within the limits of physiological tolerance of the parasite. It should be emphasized that these are guidelines, not strict rules (Williams et al. 1992; MacKenzie 1993). *Diplostomum* spp. meet many of the above conditions. Infection levels vary among areas. The parasites are considered long-lived, up to 4 years (Shigin 1964, in Burrough 1978). Longevity is considered the most important qualification for a parasite to be suitable as a biological tag (Lester 1990). The parasites are site specific and are detected and identified with relatively little effort. The parasites do have marked pathological effects in that they cause blindness and cataracts, but no detrimental effects on condition or growth were observed on host fishes in this study. Furthermore, pathogenic parasites may make good tags in certain circumstances (Lester 1990). The life cycle is not simple, but this is one of the most difficult conditions for parasites to meet. Many effective tags, such as anisakid nematodes (McClelland and Marcogliese 1994), have more complex life cycles than *Diplostomum* spp. No information is available on the stability of *Diplostomum* spp., either seasonally or annually, in these lakes, but this criterion can be overcome by examining infections in individual year classes (Williams et al. 1992), as was done in this study. Given the ubiquitous distribution of *Diplostomum* spp. in the northern hemisphere, there is no doubt that environmental conditions in the St. Lawrence River fall within the limits of physiological tolerance of these parasites. While our samples consist of two species, one is rare and the analyses remain valid. Moreover, the two parasites have the same life cycle and occur in the same proportion among fish species and localities along the river; thus, they can be regarded as one for tagging purposes. Therefore, given the suitability of *Diplostomum* spp. as a biological tag, the evidence is strong that spatially distinct populations of both walleye and white suckers are present in Lake St. Louis and Lake St. Pierre. However, it is not known if fishes from the two lakes share spawning areas, thus promoting genetic exchange between populations. This possibility could be tested by examining infection levels in fish on the spawning grounds. Unequivocal stock discrimination may require the use of genetic techniques (Lester 1990).

Walleye collected at St. Nicolas appear to be from two populations, one with lightly infected large fish and the other with more heavily infected small fish. These fish may represent different stocks or populations, but the data must be interpreted with caution, given the small sample sizes. Females and males from different stocks may mix, possibly accounting for the differences in abundance between the sexes in June, but again, this must be interpreted cautiously given the small sample sizes.

Most studies utilizing parasites as biological tags to discriminate among fish stocks are marine; however, there are some in freshwater systems. Differences in levels of infection with the eye flukes *D. spathaceum* and *Tylodelphis clavata* permitted the separation of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) into distinct populations in Lake Constance in Europe (Balling and Pfeiffer 1997). Within the Great Lakes drainage basin, the parasitic copepod *Salmincola corpulentus* could be used to discriminate between stocks of bloaters (*Coregonus hoyi*) in Lake Huron (Bowen and Stedman 1990). Parasite communities were also used to distinguish stocks of lake herring (*Coregonus artedi*) in Lake Superior (Hoff et al. 1997).

It is not surprising that fish species in the St. Lawrence River may be present as different populations. In tagging studies of walleye in the lower part of the St Lawrence River, the fish showed little tendency towards long-distance movements (Magnin and Beaulieu 1968). Furthermore, multiple stocks of yellow perch (*Perca flavescens*) exist in Lake St. Louis (Dumont 1996). Growth rates of various fishes are also known to vary along the St. Lawrence River. Yellow perch are known to grow at a lower rate, reach a larger size, attain a greater age at first reproduction, and have lower relative fecundity in Lake St. Louis than in Lake St. Pierre (Dumont 1996). Even if Lac Des Deux Montagnes connects directly with the St. Lawrence River, its lake sturgeon (*Acipenser fulvescens*) population has a slower growth rate, a lower condition index, and higher degree of site fidelity than the St. Lawrence population (Fortin et al. 1993). Morphological and genetic differences had also been observed between the two stocks (Guénette et al. 1992, 1993). In this study, both walleye and white suckers >6 years old attained larger sizes at age in Lake St. Louis than in Lake St. Pierre. These results, together with those on abundance of *Diplostomum* spp., suggest that walleye, which are sport fish, should be managed as separate stocks. This hypothesis could be examined further using meristic and genetic techniques.

Diplostomiasis and fish health

Eye flukes are known to cause emaciation, deformities, blindness, and death in fish (Shariff et al. 1980; Chappell 1995). Disruption of vision by metacercariae in the eyes may reduce feeding efficiency, as was observed in dace (*Leuciscus leuciscus*) and threespine sticklebacks (*Gasterosteus aculeatus*) (Crowden and Broom 1980; Owen et al. 1993). However, using the data reported herein, we could detect no effect of *Diplostomum* spp. on growth or condition, as measured by condition index or gonadosomatic index, in either walleye or white sucker. Walleye is a visual predator (Ryder 1977), yet it does not seem to be affected by the intensity of infection observed in the study area. White suckers probably do not need good vision for food collection; the eyes are in a dorsolateral position and the mouth is ventral, and this catostomid is known as a mouth taster (Miller and Evans 1965) that can live in a large diversity of habitats, including deep and turbid waters. Another possible consequence of infection is that it renders the fish more susceptible to predation (Crowden and Broom 1980; Brassard et al. 1982); however, we lack the information required to address this question.

The different visual opacity index levels are not a good measure of current infection with *Diplostomum* spp. Abundances of the parasite at St. Nicolas did not differ significantly between levels 0 and 2 for walleye and white suckers and between levels 3 and 4 for white suckers, using the scale 0–4. Comparable results were obtained by Mikaelian and Martineau (1997) for *Diplostomum* spp. in longnose suckers (*Catostomus catostomus*). Similarly, using the scale 0–2 in Lake St. Louis, abundances of *Diplostomum* spp. did not differ significantly among walleye or white suckers classified as level 0 or 1. Mikaelian and Martineau (1997) found that the absence of cataracts did not reflect the absence of eye flukes in five species of fish, while the presence of cataracts was not necessarily indicative of the presence of *Diplostomum* spp. in at least three species of fish. The index levels may reflect past infections with eye flukes and subsequent permanent damage. However, caution should be exercised because cataracts may have other causes, such as nutrient deficiency (Ferguson 1989).

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