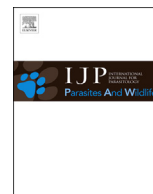




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Enigmatic decline of a common fish parasite (*Diplostomum* spp.) in the St. Lawrence River: Evidence for a dilution effect induced by the invasive round goby

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ABSTRACT

As they integrate into recipient food webs, invasive exotic species may influence the population dynamics of native parasites. Here we assess the potential impact of the Eurasian round goby (*Neogobius melanostomus*) on the abundance of eyefluques of the genus *Diplostomum*, which are common parasites in fishes of the St. Lawrence River (Canada). Analyses of data collected over nearly two decades revealed that the infection levels in three native fish [spottail shiner (*Notropis hudsonius*), golden shiner (*Notemigonus crysoleucas*) yellow perch (*Perca flavescens*)] declined sharply throughout the St. Lawrence River after the introduction of the goby. At two sites where data were collected at regular time intervals, declines of *Diplostomum* spp. in spottail shiners occurred within two years of the goby's first recorded appearance, with prevalence dropping as much as 77–80% between pre-invasion and post-invasion periods. Furthermore, in localities where gobies remained scarce, infection in native species did not change significantly over time. Altogether, these observations suggest that gobies play a role in the eyefluke collapse. The decline in populations of the main definitive host (ring-billed gulls, *Larus delawarensis*) and changes in hydrology during periods of parasite recruitment were not strongly supported as alternate explanations for this phenomenon. Since other snail-transmitted trematodes with similar life cycles to *Diplostomum* spp. did not show the same decreasing pattern, we conclude that eyefluques did not decline as a result of snail depletion due to goby predation. Rather, we suggest that gobies acted as decoys, diluting the infection. As *Diplostomum* spp. occurred at lower abundance in gobies than in native fish hosts, the replacement of native fish with exotic gobies in the diet of gulls might have played a part in reducing parasite transmission. In contrast to the typically negative impact of invasions, the goby-induced decline of this pathogen may have beneficial effects for native fishes.

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1. Introduction

When one considers the issue of exotic species and the risk they pose to ecosystem in terms of disease transmission, what generally spring to mind are the pathogens that these non-native species carry with them which could be introduced into the invaded habitats. Yet, despite numerous documented cases of co-introduced

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natural hosts, referred to as spillback (Kelly et al., 2009a) or, as a decoy, leading to an overall loss of infection, also called the dilution effect (Kopp and Jokela, 2007). Both of these response patterns – parasite amplification and dilution – have been documented following the introduction of invasive species in taxonomically and geographically diverse systems (Kelly et al., 2009b; Hershberger et al., 2010; Mastitsky and Veres, 2010; Litvintseva et al., 2011; Paterson et al., 2011; Nelson et al., 2015; Ondračková et al., 2015). However, host competence alone is not always a good predictor of the net effect of a non-native species in these systems, being edged out by demographic factors such as host density (Paterson et al., 2013b; Searle et al., 2016). When considering parasites with complex life cycles, the actual impact of an exotic host on infection dynamics is also likely to be driven by how different interspecific interactions (including competition and predation) develop over time between the exotic species and members of the recipient community. For instance, an invader could end up diluting a parasite, be it a competent host or not, if it downsizes the populations of its main first intermediate host by predation, or if it does not become a significant prey item in the diet of the main definitive host.

Most field evidence of parasite dilution or amplification induced by exotic species has been obtained by contrasting the abundance of parasites in natural hosts between invaded and non-invaded localities (Telfer et al., 2005; Kelly et al., 2009b; Lettoof et al., 2013), with limited knowledge of the pre-invasion levels of infection. In this study, a before-after approach was used to assess the influence of the Eurasian round goby (*Neogobius melanostomus*) on the transmission of parasites of the genus *Diplostomum* to native fish in the St. Lawrence River. These eye-dwelling digeneans, which commonly infected native fish in the St. Lawrence River before the introduction of the round goby (Marcogliese and Compagna, 1999; Marcogliese et al., 2001, 2006, 2010; Locke et al., 2013), were recently reported to have declined at localities where historic infection levels were previously very high (Désilets et al., 2013). To further document this apparent reduction in eyefluke abundance and clarify the role that the round goby may have played in it, infection levels in three native fish hosts, the spottail shiner (*Notropis hudsonius*), the golden shiner (*Notemigonus crysoleucas*) and the yellow perch (*Perca flavescens*), were compared before and after the goby's establishment at sites where historical data on the parasite fauna of these fish species were available. The potential influence of the non-native goby was assessed while considering other key biotic and abiotic factors likely to modulate the transmission of eyefluks from one host to the other. These include: (1) the hydrological conditions during the known periods of release of *Diplostomum* spp. cercariae and (2) the size of the populations of ring-billed gulls, which are the predominant definitive hosts for *Diplostomum* spp. in the St. Lawrence River.

Parasites of the genus *Diplostomum* have a three-host life cycle (Chappell, 1995). These digeneans use lymnaeid snails as first intermediate hosts, fish as second intermediate hosts, and gulls and terns as definitive hosts. Birds acquire the infection when they feed on infected fish. Worms mature and reproduce in their intestines and eggs are shed in feces. Miracidia hatch from eggs and infect the snails, which in turn release asexually-produced cercariae into the water. These free-living larvae penetrate the skin of fish and migrate to the eye, where they become metacercariae which are infective to the avian definitive hosts.

The genus *Diplostomum* is composed of numerous cryptic species (Locke et al., 2010, 2013), with at least fifteen occurring in the St. Lawrence River (Locke et al., 2015). Those establishing in the retina and vitreous humor of fish are more host-specific than lens forms (Locke et al., 2010; Blasco-Costa et al., 2014). Eyefluks found to date in the round goby belong to a few generalist lens-dwelling

species also common in the lens of the three native fishes considered herein (Désilets et al., 2013; Locke et al., 2015). The vast majority of non-lens forms in perch in the St. Lawrence River are *D. baeri* but other putative *Diplostomum* species also were found (Locke et al., 2010).

2. Material and methods

2.1. Sampling design

One-year old round gobies and spottail shiners were captured in June at two localities of the St. Lawrence River: Îles de la Paix (IPA: 4520.5740'N; 7350.9630'W) and Îlet Vert (IVT: 4542.4300'N; 7326.9600'W). The parasite load of one-year old fish collected in June reflects the infection acquired since the preceding fall and can thus be used unambiguously to follow year to year variations in parasite recruitment. At each sites, samples of both species were collected two years after the goby's first sighting, in 2007 at IVT and in 2009 at IPA, and thereafter in 2011, 2013 and 2016 at both sites. Pre-invasion samples of 1-year-old spottail shiners obtained in June 1998, 1999, 2000 and 2004 (Marcogliese et al., 2006; Thilakarathne et al., 2007) completed the chronological sequence.

Additional data on *Diplostomum* spp. infection levels in native species along the St. Lawrence River were mined from the database on fish parasites maintained by the Department of Environment and Climate Change, which were collected for other research studies and have been published in part (Marcogliese et al., 2010; Désilets et al., 2013; Locke et al., 2013; Giraud et al., 2016). Only samples comprising at least 15 fish of a given age class were considered for analyses. These include samples of 1 and 2-year-old perch and 1 year-old golden shiners collected between 1998 and 2016 from 6 sites situated within the three fluvial lakes of the St. Lawrence River: LSF-1 (45°09.770'N; 74°25.514'W) and LSF-2 (45°07.646'N; 74°24.273'W) in Lake St. Francis, LSL-1 (45°24.415'N; 73°53.989'W) and IPA in Lake St. Louis and LSP-1 (46°12.000'N; 72°59.000'W) and LSP2 (46°8.950'N; 72°47.950'W) in Lake St. Pierre.

2.2. Fish capture and examination

Most fish were collected with a beach seine (22.6 m × 1.15 m; 3 mm mesh) towed on foot or partially deployed from a boat, with the exception of 2-year-old perch from Lake St. Pierre which were captured with fyke nets (in 2004 and 2005) or hoop nets (in 2013). Upon capture, fish were euthanized by immersion in a 400 mg/L Eugenol (clove oil) solution (American Veterinary Medical Association, 2013), placed in bags and frozen for subsequent analyses. Morphometric measurements (total, fork or standard lengths, to the nearest mm) and total weight (to the nearest 0.1 g) were obtained on thawed specimens. Minnows and gobies were divided into age classes using length frequency distributions. Perch were aged by counting the number of year marks (annuli) on their opercular bones or scales [see detailed methodology in (Marcogliese et al., 2005)]. Individuals of *P. flavescens* for which age was not available were *a posteriori* assigned to a given age class based on age-length curves generated for the species in each fluvial lake.

Parasitological examination followed standard procedures for macroparasites (Gendron et al., 2012). Parasite search was comprehensive and extended to the whole body with the exceptions of perch in 2011, 2013, 2014 and 2016 and golden shiners in 2011 for which only specific target organs/tissues were examined. In all instances, the left and right eyes of each fish were dissected out and their contents inspected under a stereomicroscope. The lens was detached from the vitreous humor and the eyefluks were

identified to genus and counted. In spottail shiners, golden shiners and round gobies, eyeflukes were exclusively found in the lens whereas in perch they were primarily associated with the vitreous humor/retina, (less than 5% were lens dwelling forms). Subsamples of the parasites found were preserved in 95% ethanol for molecular analyses or fixed in ethanol 70% prior to being stained and mounted on slides. The taxonomic status of many species of eyeflukes being still unresolved (Locke et al., 2010, 2015), and in the absence of actual molecular data to ascertain the identification of each specimen, we refer to them collectively herein as *Diplostomum* spp.

2.3. Alternative explanatory variables

The effect of demographic changes in the predominant definitive hosts of *Diplostomum* spp. in the St. Lawrence River (Levy, 1997; Marcogliese et al., 2001) was evaluated using ring-billed gull counts in colonies along the St. Lawrence River from 1998 to 2012 that were accessed through the St. Lawrence Global Observatory-SLGO 2016 portal (www.ogsl.ca). More recent observations for Quebec populations (2016) and data relative to colonies in Ontario (west to Cornwall) were provided by the Canadian Wildlife Service.

To assess potential hydrological effects, mean daily water levels in the St. Lawrence River for the period ranging from January 1998 to September 2016 were extracted from the Department of Fisheries and Ocean archived hydrometric database (www.isdm-gdsi.gc.ca/isdm-gdsi/twl-mne/maps-cartes/inventory-inventaire-eng.asp). Data from Summerstown station were considered representative of Lake St. Francis where water levels are maintained stable throughout the year, whereas Montreal Jetty no 1 station was selected to represent the hydrological conditions of the river downstream from Lake St. Francis where water levels fluctuate.

2.4. Calculations and statistical analyses

To evaluate fish infection, the following parasitological descriptors were calculated (Bush et al., 1997): mean abundance, which is the mean number of parasites of a given taxon per fish in a sample, including uninfected fish; mean intensity, which is the mean number of individuals of a given parasite taxon in a sample, considering infected fish only; and prevalence, which is the proportion of parasitized fish in a given sample, expressed as a percent.

To account for overdispersion of data (variance being greater than the mean), a negative binomial model was fitted to the untransformed eyeflukes counts (using the GENMOD procedure of SAS). This model was used to test the effect of year and fish host for each sampling site. When more than two years were compared, differences between pairs were computed and a Tukey–Kramer adjustment of the p value was applied. For a number of historic perch samples (LSP-1 and LSP-2 in 2004, 2005), separate counts of lens and non-lens forms of eyeflukes were not available. Consequently and for comparability reasons, the analyses were performed on total counts of *Diplostomum* spp. in perch. When data were available, the infection levels by other digenetic trematodes sharing the same first-intermediate host (gastropods) as *Diplostomum* spp. were analysed as described above. All statistical analyses were conducted with SAS release 9.4 (SAS Institute Inc., Cary, NC, USA).

3. Results

The abundance of *Diplostomum* spp. in one-year old spottail shiners at IVT and IPA varied significantly with year ($P < 0.0001$). At both sites, a sharp decrease occurred two years after round gobies were first observed in collections, that is in 2007 at IVT and in 2009 at IPA, and these low levels of infection were maintained up to

2016 (Fig. 1). Before the establishment of the round goby locally, eyeflukes were, by far, the most common helminths in juveniles of this native fish species. In some samples virtually all specimens examined were infected, the lowest prevalence being 97% at IVT and 80% at IPA during the pre-invasion period. During the post-invasion period, prevalence decreased to as low as 17% at IVT and 3% at IPA. From 2009 to 2016, the mean abundances of *Diplostomum* spp. were found significantly lower than in previous years at both localities as revealed by the post-hoc multiple comparisons (Fig. 1).

Diplostomum spp. were also the most frequent helminths found in one-year old round goby two years after that species' first sighting. The parasite was however less abundant than in the native spottail shiner (Fig. 1), the difference between the two hosts being significant at IVT in 2007 ($P < 0.0001$). Parasite examinations, which were mostly performed on thawed fish, did not allow parasite viability to be determined, but only very rarely did we notice a metacercaria of *Diplostomum* spp. showing signs of degradation. However, a few gobies were examined shortly after being euthanized, and in all cases their eyeflukes were alive. From highs of 50% at IVT in 2007 and 30% at IPA in 2009, the prevalence of infection in gobies drastically dropped to less than 5% at both sites from 2011 to 2016.

As in spottail shiners, levels of infections reached record lows in one-year old perch and golden shiners in 2011 at LSF-1 (Fig. 2). Although considerable variations occurred prior to that year, *Diplostomum* spp. abundance in 2011 was significantly lower than in previous samples of both perch and golden shiners ($P < 0.0001$). The 2011 sampling coincided with the first record of gobies at that site (which has not been visited since 2006). A similar collapse in the parasite levels was observed across the three fluvial lakes in two-year old perch from 2011 to 2016 (Fig. 3), with the exception of one site in northern Lake St. Louis (LSL-1) where the round goby did not establish detectable populations (St. Lawrence Global Observatory-SLGO, 2016 portal, www.ogsl.ca). Mean abundance at LSL-1 in 2013 was elevated and not different from that in 2000 ($P = 0.5800$). The among-year change in infection levels was significant but less marked at LSP-1, whereas the abundance of *Diplostomum* spp. after the goby's detection (2013) was not statistically different ($P = 0.1546$) from the abundance at one previous year (2004). On the north shore of Lake St. Pierre, gobies, although present, remained in very low numbers compare to the south shore of the same fluvial lake (St. Lawrence Global Observatory-SLGO, 2016 portal, www.ogsl.ca).

Other than *Diplostomum* spp., metacercariae of ten trematode species transmitted by snails and using fish as second intermediate hosts were found in the tissues/organs of spottail shiners collected at IVT and IPA during the study period. When pooled, the abundance of these metacercariae was lowest in 1998 and 1999 and highest in 2013 at both sites ($P < 0.0001$) with considerable fluctuations between these two years. Fig. 4 illustrates the variation of abundance for the two most prevalent of these trematodes, *Ornithodiplostomum* spp. and *Posthodiplostomum* spp. Neither these species, nor the other metacercariae infecting spottail shiners, were found in any round gobies examined herein.

Metacercariae of *Apophallus brevis* commonly infect the flesh of perch in the St. Lawrence River. As shown in Table 1, the mean abundance of *A. brevis* in one-year old perch remained elevated at IPA across years ($P = 0.1865$) and significantly increased at IVT ($P = 0.001$) following the goby's establishment, while perch infection by *Diplostomum* spp. decreased dramatically.

From 1997 to 2016, populations of ring-billed gulls downstream of Cornwall in the St. Lawrence River declined by approximately 36% (Fig. 5A). More than half of this reduction occurred after 2006. A number of nesting sites were completely abandoned over time. The largest known colony, located on Île Deslauriers close to IVT

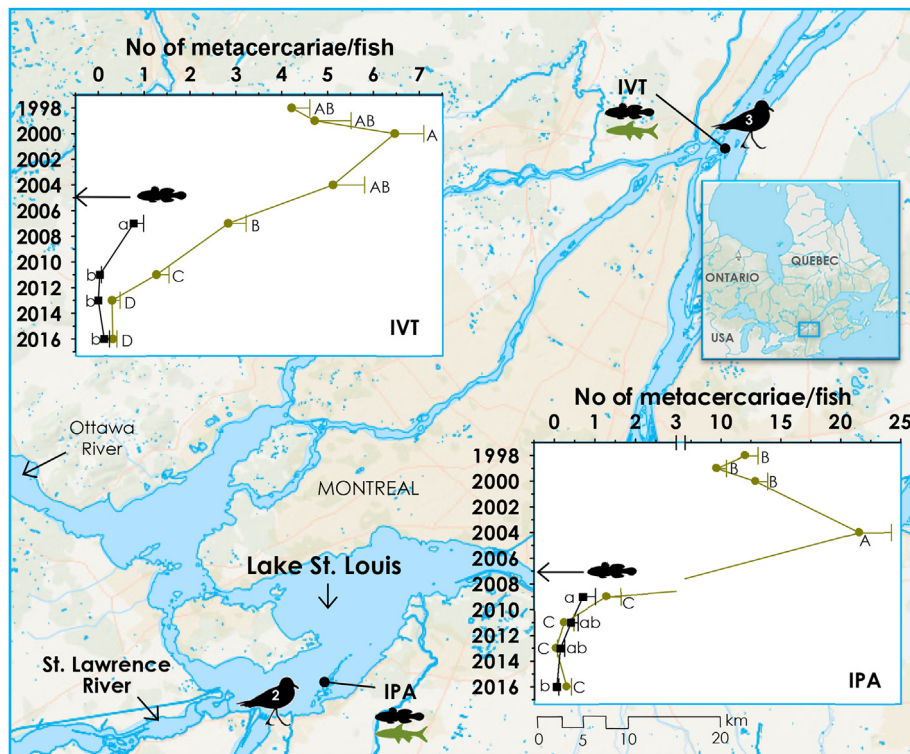


Fig. 1. Temporal changes in the mean abundance of *Diplostomum* spp. in spottail shiners (*Notropis hudsonius*) (green circle) and round gobies (*Neogobius melanostomus*) (black square) at two sites in the St. Lawrence River. Data are expressed as mean numbers of metacercariae of *Diplostomum* spp. per fish including uninfected ones \pm SEM. Significant differences among years within each locality are indicated by different lower-case letters (round gobies) and upper-case letters (spottail shiners). Arrows within graph panels point to year of first sighting of the invasive round goby at each site. On the background map, sampling sites (Îlet Vert = IVT, Îles de la Paix = IPA) are identified and the host species examined are represented by different fish silhouettes (green = spottail shiners, black = round gobies). Bird silhouettes indicate where main colonies of ring-billed gulls are localized: 2 = Beauharnois; 3 = Île Deslauriers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(colony 3) has lost as much as 20 thousand individuals between 2006 and 2016. In Cornwall colonies, upstream of Lake St. Francis (colony 1), gull counts have fallen by 20% between 1999 and 2008 (these populations were monitored on a decadal basis). Nevertheless, not all gull colonies of the St. Lawrence River declined. Two important populations, one on the south shore of Lake St. Louis (colony 2) and the other on Île Lefevre upstream of Lake St. Pierre (colony 4) have seen their numbers increased by respectively 30% and 20% from 2006 to 2016.

Fig. 5B illustrates the variation in water levels in early spring and late summer from 1998 to 2016 at two stations along the St. Lawrence River. Water levels in Lake St. Francis have been stable and did not show seasonal or yearly variations, whereas at the Montreal Jetty no. 1 station, spring highs and late summer lows fluctuated from year to year throughout the entire study period.

4. Discussion

Based on data collected over nearly two decades, this field study demonstrates that infection of native fish by eyefluke (*Diplostomum* spp.) declined sharply throughout the St. Lawrence River in the years following the introduction of the invasive round goby. Analyses of the most likely explanatory factors (Fig. 6) strongly suggests that these two events which coincide in time are also causally related, and that the round goby clearly contributed to the collapse of this once widespread and abundant pathogen.

The alternate hypotheses attributing the eyefluke decline to a reduction in definitive host numbers or changes in hydrological conditions were not well supported. Between 2006 and 2016, while *Diplostomum* spp. abundance in fish dropped precipitously to very

low levels, ring-billed gull numbers in the St. Lawrence River also experienced a marked decrease due in part to the control measures put in place to halt the expansion of this bird then considered a nuisance (Cotter et al., 2012). Given the implied potential reduction in the parasite's reproductive capacity, the decline of the eyefluke's main definitive host may seem a likely explanation for the reduction in fish infections. However, censuses show that the decrease in gull numbers had begun well before 2006 and that the species remained highly abundant across the St. Lawrence River up to 2016 (estimated as 73 000 individuals). Moreover, not all gull populations showed a declining trend; some sites where eyefluke abundance declined were located close to colonies which actually increased their numbers over the study period. Consequently, while the decrease in ring-billed gull populations has probably contributed to reducing the levels of fish parasitism by *Diplostomum* spp. in some areas, it cannot stand as the only and most satisfactory explanation for the observed phenomenon.

Hydrological conditions affect the ability of the free-living stages (cercariae) to reach and penetrate host fish (Moody and Gatlen, 1982; Stables and Chappell, 1986; Marcogliese, 2001). However, there is no indication that the reduced infection levels reported herein can be attributed to unfavorable high water levels during critical time windows for cercarial recruitment. In fact, water levels in early spring and late summer fluctuated considerably from one year to the next with no apparent shift in seasonal pattern after 2006 nor any correlation with the abundance of *Diplostomum* spp. in fish. Furthermore, huge reductions in eyefluke counts were observed after 2006 in Lake St. Francis, where water levels have been stabilized since early 1960s by water control infrastructures, with annual fluctuations being limited to less than

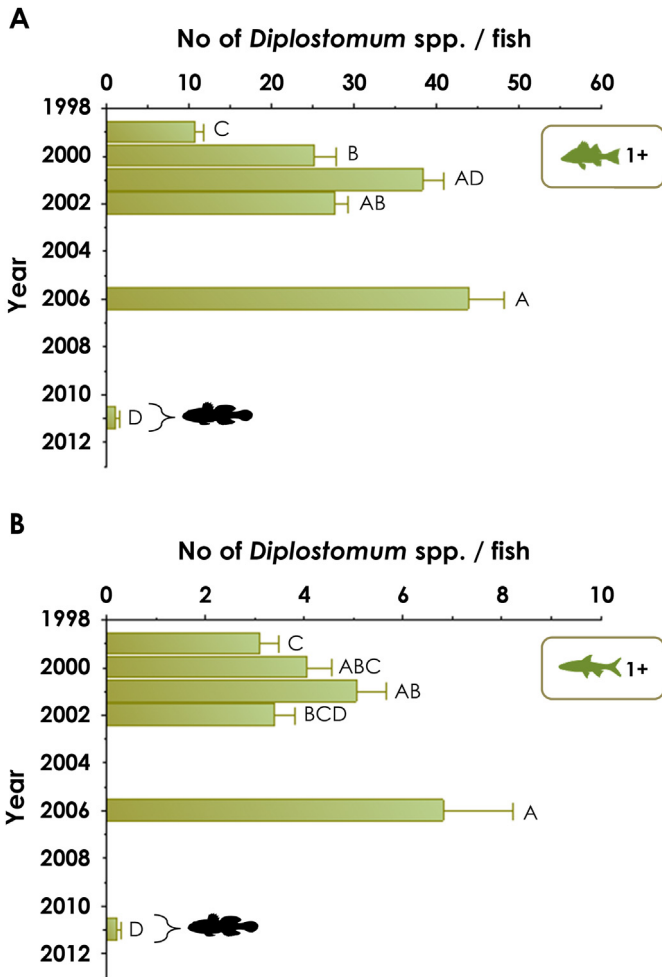


Fig. 2. Variation in *Diplostomum* spp. mean abundance over years in Lake St. Francis (LSF-1) in (A) one-year old yellow perch (*Perca flavescens*) and (B) one-year old golden shiner. Data are expressed as mean number of metacercariae of the genus *Diplostomum* per fish including uninfected ones \pm SEM. Significant differences among years within each locality are indicated by different letters above histograms. Black fish silhouettes within graph panels illustrate the occurrence of the invasive round goby among the fish captured at that site. See Fig. 3 for site location.

20 mm (Morin and Leclerc, 1998).

Although the influence of other unknown events or variables cannot be dismissed, the eyefluke decline in native fish appears to be closely associated with the establishment of successful populations of round goby. At sites where gobies were not detected or were scarce, eyefluke infection in native species did not change significantly over time, while declining everywhere where the exotic fish was prevalent. Gobies, which are suspected to be less tolerant to low levels of dissolved ions (Baldwin et al., 2011), were notably rare along the north shore of Lake St. Pierre and in north-western Lake St. Louis where the waters are poorly mineralized due to the inflow from the Ottawa River and other tributaries draining the Canadian Shield (Désilets and Langlois, 1989).

There are numerous mechanisms by which the round goby could have affected the transmission dynamics of *Diplostomum* spp. This invasive fish, a benthic feeder, is known to have altered the composition and density of macroinvertebrate assemblages both in its European and North American invaded ranges (Lederer et al., 2006; Mikl et al., 2016). In the St. Lawrence River, Kipp et al. (2012) reported significant reductions in the abundance of gastropods following the goby's introduction, including lymnaeid and

physid snails. Therefore, the decreased recruitment of *Diplostomum* spp. in fish could simply be symptomatic of the reduced abundance of the parasites' first intermediate host (lymnaeids). In line with this hypothesis, we found that infection by *Apophallus brevis* which develops in hydrobiids (Miller, 1946; Sinclair, 1971), a gastropod family not affected by goby's establishment (Kipp et al., 2012), remained stable in yellow perch or increased after the goby's invasion. On the other hand, two common digenans phylogenetically close to eyeflukes, *Ornithodiplostomum* spp. and *Posthodiplostomum* spp., did not decline in spottail shiners as would have been expected considering the goby-mediated depletion of physid snails (Kipp et al., 2012), their first intermediate hosts (Palmieri, 1975; Hendrickson, 1986). On the contrary, these two parasites have seen their abundance fluctuate over time, showing an increasing rather than a decreasing trend. Although temporal change is difficult to detect statistically in rare parasites, the same increasing trend was observed when all trematodes using snails and fish as intermediate hosts (except eyeflukes) were pooled together. Overall, *Diplostomum* spp. were both the only metacercariae declining after 2006 and the only ones acquired by the round goby.

To date, the round goby has been colonized by a limited number of generalist parasites in the St. Lawrence River, the most prevalent after *Diplostomum* spp. being *Neoechinorhynchus tenellus*, an acanthocephalan using gobies as paratenic hosts (Gendron et al., 2012). A large proportion of the cystacanths of *N. tenellus* died and degenerated rapidly in the tissues of the round goby suggesting that the exotic fish could act as a dead-end for that parasite (Gendron and Marcogliese, 2016). As of now, we have no evidence thereof for eyeflukes residing in the lens of gobies, all of which appeared intact. While it is true that eyeflukes are part of the parasite fauna of the round goby in Eurasia (Rolbiecki, 2006; Francová et al., 2011; Kvach and Winkler, 2011), the importance or the competence of the species as a host for *Diplostomum* spp. in its ancestral range is unknown. However, infection trials in which captive ring-billed gulls were fed each day for a 2-month-period with gobies collected in the St. Lawrence River resulted in only two adult worms established in the bird's intestine, a particularly low yield compared to the tens of worms recovered in routine gull infection experiments using cercarial-exposed fish hosts (rainbow trout), especially considering that in the latter trials, gulls were exposed only once (A.R. Lapierre and J. Forest, Concordia University, Montreal, Canada, pers. com.). Such poor infection success could be attributed to either the low prevalence of *Diplostomum* spp. in the gobies used for these experiments or a reduced infectivity of the metacercariae they carry, or both.

Following the above, the dilution of *Diplostomum* spp. observed in the St. Lawrence River could have resulted, at least in part, from the integration of the round goby into the diet of the main definitive host. Ring-billed gulls are opportunistic omnivorous birds that feed on prey according to their availability and abundance (Cotter et al., 2012). A recent analysis of stomach contents of ring-billed gulls in Lake Michigan revealed that the round goby was the most frequent prey item (76%), replacing other native forage fish, notably during the gull's post-breeding season (Essian et al., 2016). Assuming a comparable shift in the diet of gulls in the St. Lawrence River, it is reasonable to expect that they would have ingested fewer metacercariae of *Diplostomum* spp. than if they had fed exclusively on native fish, which were typically more heavily infected by eyeflukes than were gobies. This would lead in turn to a lowering of the abundance of adult *Diplostomum* spp., a decrease in the amount of eggs released in the aquatic environment, and therefore a general reduction in the recruitment of eyeflukes in all host fishes including the round goby itself. And the potential reduced infectivity of metacercariae from gobies could have enhanced this recruitment

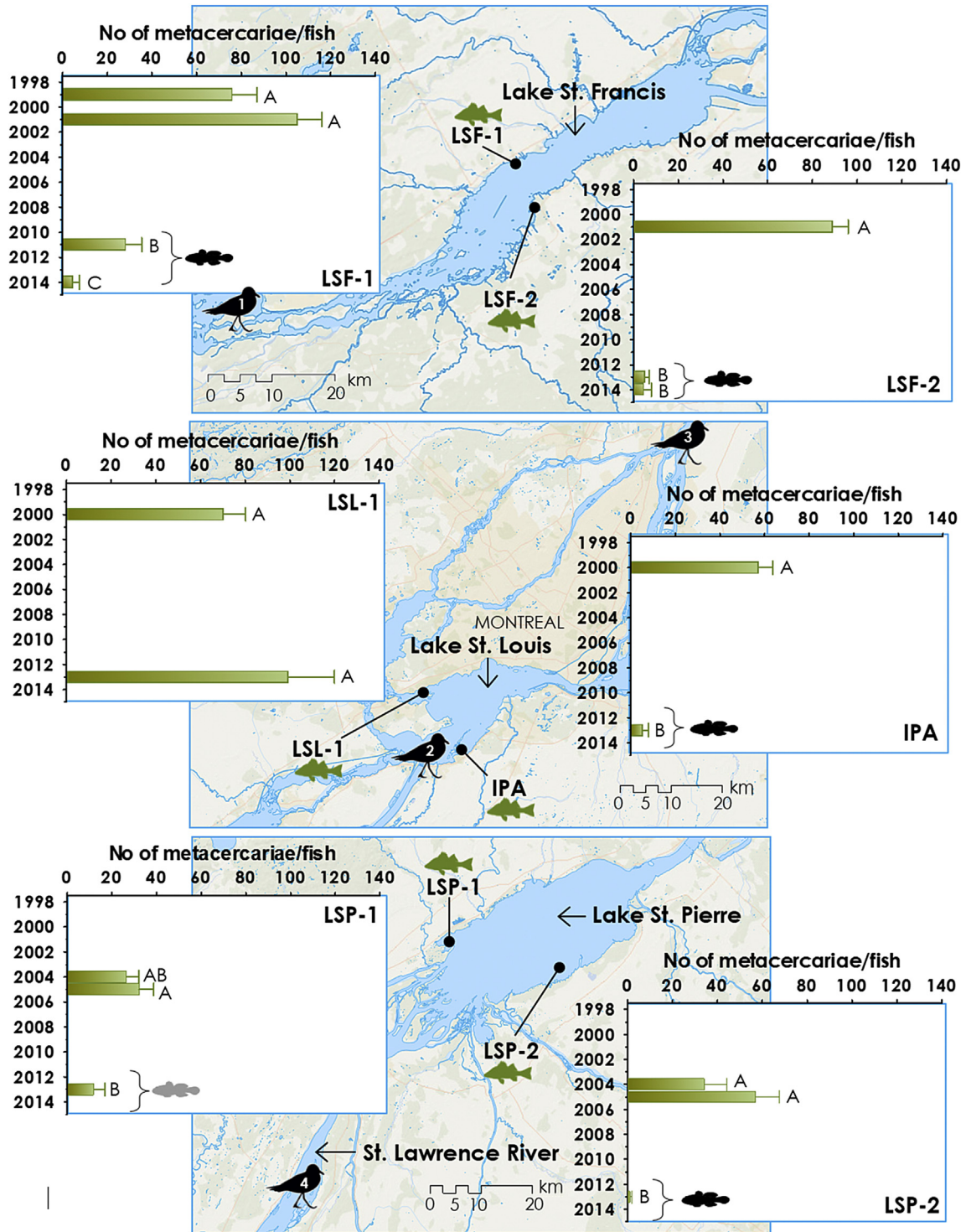


Fig. 3. Mean abundance of *Diplostomum* spp. in two-year old yellow perch (*Perca flavescens*) at sites from the three fluvial lakes of the St. Lawrence River between years before and after the establishment of the invasive round goby. Data are expressed as mean number of metacercariae of the genus *Diplostomum* per fish including uninfected ones \pm SEM. Significant differences among years within each locality are indicated by different letters beside histograms. Fish silhouettes within graph panels highlight the presence of the invasive round goby at that given site/year(s), the icon being gray if the species was only occasionally recorded. Main ring-billed gull colonies are illustrated on the map by bird silhouettes: 1 = Cornwall; 2 = Beauharnois; 3 = Île Deslauriers; 4 = Île Lefebvre.

failure. Interestingly, a survey of the gastrointestinal parasite fauna of 25 ring-billed gulls in the region of Montreal in 2011 (Aponte et al., 2014) reported intensity of infection by *Diplostomum* spp. lower than that found before goby's invasion in 1994 (Levy, 1997), although the prevalence of infection remained elevated (85%).

Nonetheless, considering that ring-billed gulls can travel distances of up to 25 km (Belant et al., 1998), a shift in the composition of their diet can hardly explain why high eyeflukes levels were maintained at the goby-free site in Lake St. Louis (LSL-1). Indeed, gulls foraging at that site would have visited surrounding areas as

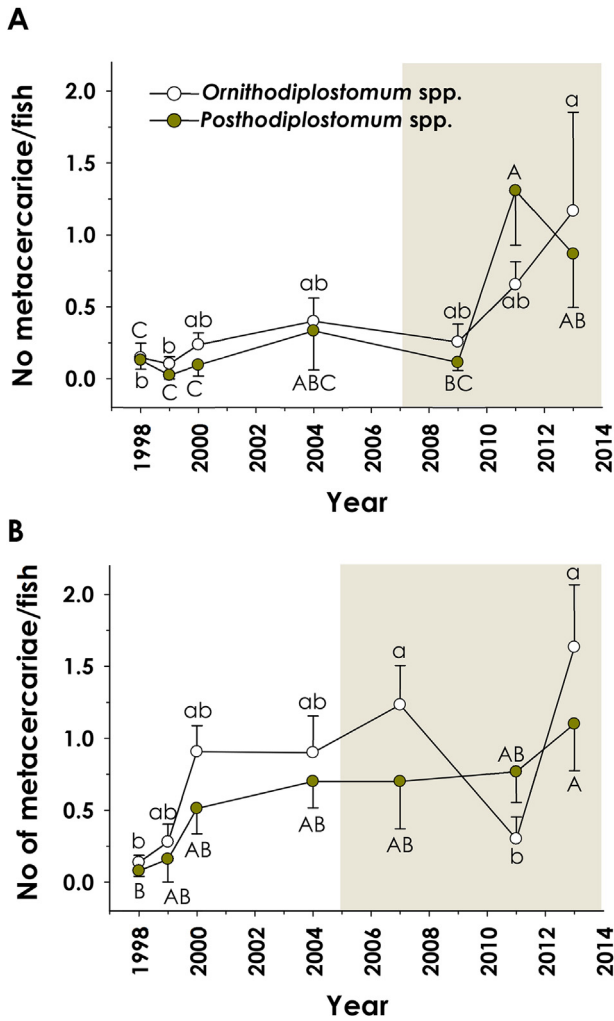


Fig. 4. Temporal variation in parasitism of spottail shiners (*Notropis hudsonius*) by two trematodes (Diplostomidae) using snails as first intermediate hosts at Îles de la Paix (IPA) (A) and Îlet Vert (IVT) (B). Data are expressed as mean numbers of metacercariae (\pm SEM) of *Ornithodiplostomum* spp. (white circles) or *Posthodiplostomum* spp. (green circles) in the tissues of the native fish host. Samples with different lower- and upper-case letters have significantly different infection levels for *Ornithodiplostomum* spp. and *Posthodiplostomum* spp. respectively. For each site, the shaded area denotes the post-invasion period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

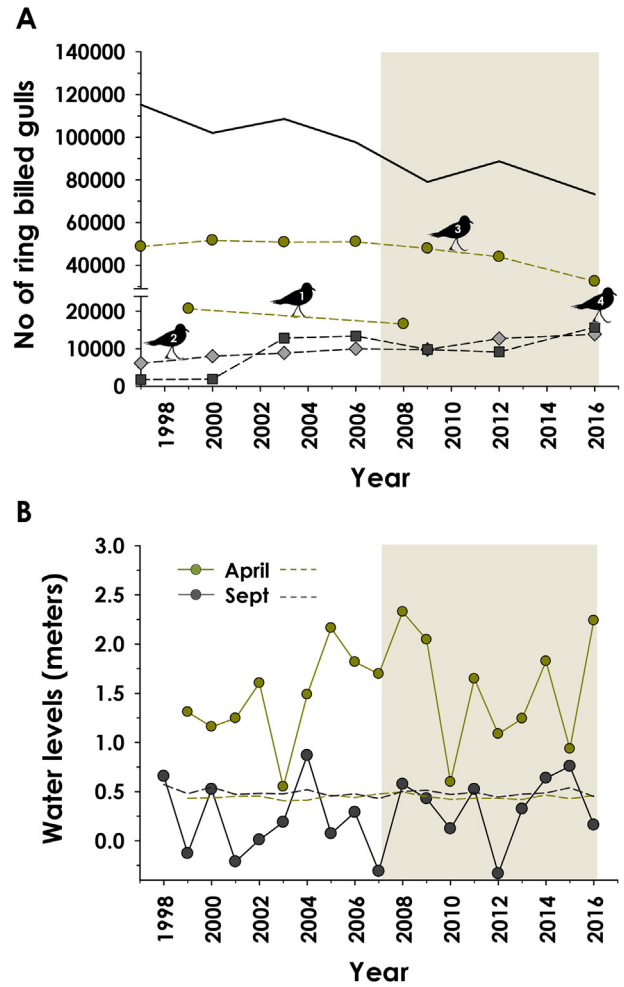


Fig. 5. Trends in ring-billed gull (*Larus delawarensis*) populations (A) and in water levels in the St. Lawrence River (B) during the study period (1998–2016). A: The solid black curve shows the variation over time of the total number of ring-billed gulls recorded along the St. Lawrence River from Cornwall to Trois-Rivières whereas dotted curves depict the change in gull counts in each of the main colonies within this area. The numbered bird icons match those shown in Figs. 1 and 3: Bird 1 = Cornwall; bird 2 = Beauharnois; bird 3 = Île Deslauriers; bird 4 = Île Lefebvre. B: Monthly mean water levels in April (green) and September (gray) at the Montreal Jetty no 1 station (solid lines) and at the Summerstown station (dashed lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Infection levels of one-year old yellow perch (*Perca flavescens*) by two native parasites, *Apophallus brevis* and *Diplostomum* spp., before and after the arrival of the round goby (*Neogobius melanostomus*) at two sites of the St. Lawrence River, Îlet Vert (IVT) and Îles de la Paix (IPA). For each parasite, between-year difference in mean abundance at a given site is considered statistically significant when $P < 0.05$. NA: Not available.

Parasite	Site	Year	Round goby	Abundance		Year effect
				Mean	SEM	P value
<i>Apophallus brevis</i>	IVT	2004	no	11.63	1.98	0.185
		2016	yes	14.67	3.01	
	IPA	2007	no	3.33	0.57	0.001
		2016	yes	7.78	0.92	
<i>Diplostomum</i> spp.	IVT	2004	no	6.52	1.58	0.0001
		2016	yes	0.38	0.31	
	IPA	2007	no	NA	NA	—
		2016	yes	0.53	0.28	

well, notably IPA, where gobies have become established and *Diplostomum* spp. have declined. Besides, the replacement of native fish by gobies in the diet of gulls should not only have induced a reduction in the abundance of *Diplostomum* spp. but also of *A. brevis*, which mature in the gastrointestinal tract of gulls (Levy, 1997; Aponte et al., 2014). However, *A. brevis* is known to have a much broader range of definitive hosts than *Diplostomum* spp. (Olsen, 1974; Hoffman, 1999; Kinsella and Forrester, 1999) and as such, would not have been expected to decrease to the same extent.

Alternatively, parasite dilution could have occurred if round gobies, which can reach high densities in shoreline habitats (Kipp et al., 2012), acted as physical sink and reduced encounters between competent native hosts and cercariae of *Diplostomum* spp. Free-living stages of eyefluks are short-lived (Lyholt and Buchmann, 1996) and frequent encounters with non-competent fish can deplete their availability to competent hosts or damage them, reducing their success when attempting to penetrate these hosts. Cercariae could also have been eliminated prematurely, due to host-parasite incompatibility, in the tissues of gobies as they migrated to the eye, before they reach the low-immunity environment of the lens (Locke et al., 2010) leading to a dilution effect. Similarly, native lungworms were suspected of succumbing to the immune response of invasive cane toads in Australia (Lettoof et al., 2013).

Encounter reduction by non-compatible or poor hosts has been

documented in several studies involving trematodes transmitted through free-living stages (Johnson and Thieltges, 2010). Studying the transmission of the trematode *Ribeiroia ondatrae*, Johnson and Hartson (2009) found that when competent larval toad hosts were raised together with treefrog tadpoles (less suitable hosts), the total success of transmission of cercariae was greatly reduced, leaving few metacercariae available for transmission to the definitive bird hosts. Similarly, Thieltges et al. (2009) experimentally demonstrated that two introduced molluscs (*Crassostrea gigas* and *Crepidula fornicata*) filtered cercariae from the water column, leading to encounter reduction between the trematode *Himasthla elongata* and its native mussel hosts (*Mytilus edulis*) which, again, acquired much fewer infections than in the absence of these invasive species.

The mechanisms discussed above are not mutually exclusive and could be acting in concert totally or in part. However, in light of the discussion above, the infection loss through encounter reduction appears to more thoroughly explain our findings and could be a core driver of the collapse of *Diplostomum* spp. in the St. Lawrence River. Laboratory infection experiments evaluating the relative competence of the invasive round goby as a host for *Diplostomum* spp. are needed to further explore this hypothesis.

The presence of invasive species has sometimes led to a reduction in parasite loads of native species, as with lungworms in native frogs sympatric with invasive cane toads in recently invaded

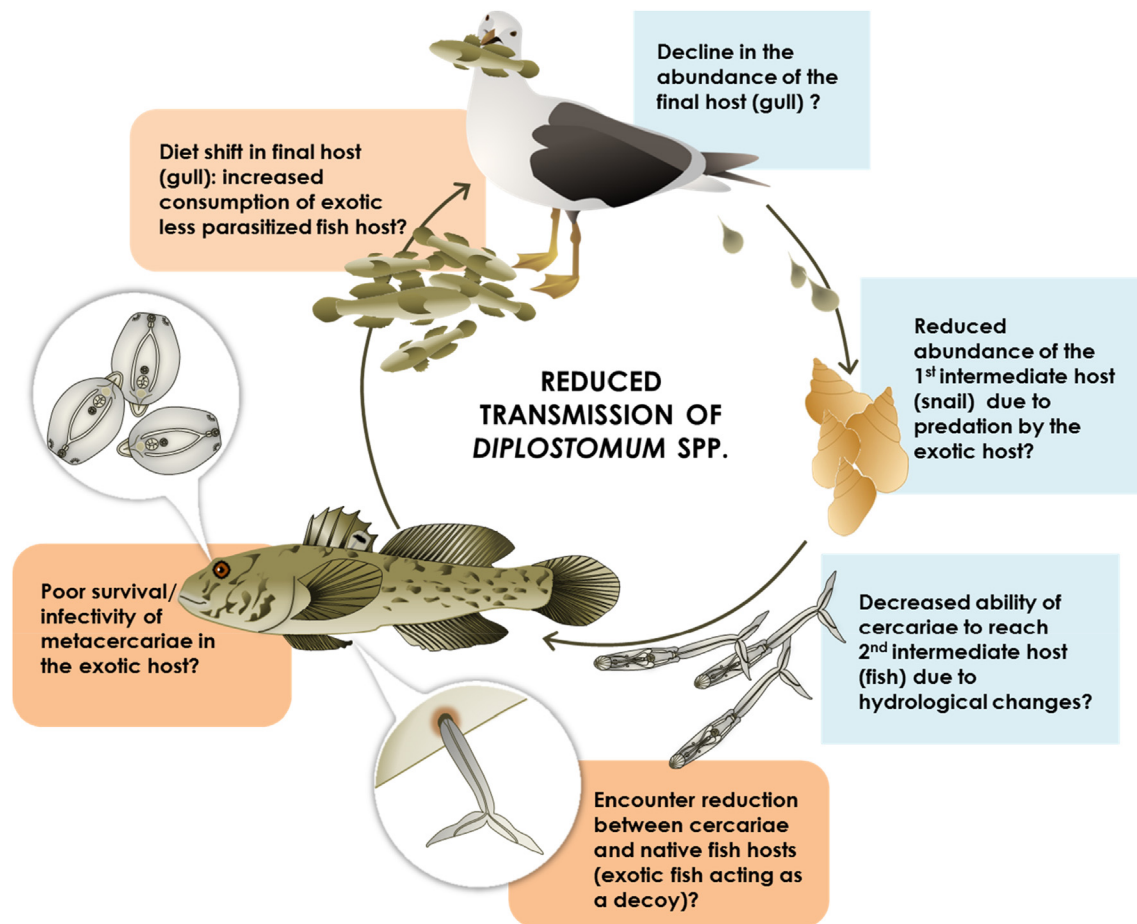


Fig. 6. Potential mechanisms to explain the observed sharp decline of *Diplostomum* spp. infection in fish in the St. Lawrence River. Those involving a dilution effect induced by the exotic round goby (*Neogobius melanostomus*) appears in pale red rectangles with rounded corners. Other biotic or abiotic factors are displayed in blue rectangles. Gastropod illustration, representing lymnaeid snails, is a graphic art by Tracey Saxby, provided by the Integration and Application Network (IAN), University of Maryland Center for Environmental Science (www.ian.umces.edu/imagelibrary). The bird image, used to illustrate a ring-billed gull (*Larus delawarensis*), is a public domain clipart downloaded from www.openclipart.org. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

areas (Lettoof et al., 2013). However, despite accumulating evidence of exotic fish being poor hosts for native parasites (Paterson et al., 2011, 2013a; Gendron and Marcogliese, 2016), demonstrated cases of parasite dilution induced by introduced fish are few (Kelly et al., 2009b) and, to our knowledge, our study is the first to document such an effect potentially induced by the round goby. Studying the impact of the invasive brown trout in New Zealand streams, Kelly et al. (2009b) notably showed that abundances of three trematode species in two native species of fish were negatively correlated with the abundance of brown trout.

The dilution concept was first introduced to describe the protective role that species richness may have on animal community health and in turn, how biodiversity loss can mediate an increase in disease risk (Keesing et al., 2006). Hence, many view parasite dilution as one of the rare beneficial effects that exotic species may have on the communities they invade (Kopp and Jokela, 2007; Kelly et al., 2009b). For instance, in New Zealand streams the upland bully (*Gobiomorphus breviceps*) demonstrated an inverse relationship between hepato-somatic index and abundance of one species of trematode, which experienced a decline in the presence of invasive brown trout. Based on these results, the authors suggested dilution could have improved the general condition of native fish (Kelly et al., 2009b). Eyeflukses (*Diplostomum* spp.) are considered important parasitic pathogens in wild and farmed fish (Chappell, 1995). As metacercariae accumulate in the lens, visual acuity is impaired resulting in reduced feeding efficiency, emaciation and poor host growth (Chappell, 1995). In the St. Lawrence River, eyefluke-induced cataracts and blindness especially in benthic fish (such as catostomids and ictalurids) frequently have been reported since the mid-1990s (Marcogliese and Compagna, 1999). If the low levels of eyefluke infection are maintained over the long term, we should see a reduction in these pathogenic effects.

Alternatively, given that parasites have direct effects on their hosts and indirect effects on species with which the host interacts (Prenter et al., 2004; Dunn et al., 2012), the collapse of a common pathogen may affect fish communities, their prey and predators in unpredictable ways. Furthermore, the reduction in *Diplostomum* spp. may impact the helminth communities of fish and other hosts in its life cycle through parasite-parasite direct competitive and indirect immune-mediated interactions (Dunn et al., 2012). Such interactions have been documented across parasite taxa (Lello et al., 2004; Telfer et al., 2010) and are not restricted to species inhabiting the same tissues or organ. In European perch (*Perca fluviatilis*), for example, infections with a larval cestode (*Triacanthophorus nodulus*) in liver have been associated with reductions in the gut-dwelling helminths *Acanthocephalus lucii* and *Camallanus lacustris*, presumably mediated via pathological or physiological processes (Morley and Lewis, 2017). In another study, two larval trematodes (*R. ondatrae*, *Echinostoma trivolvis*) infecting Pacific chorus frog (*Pseudacris regilla*) tadpoles were found to display apparent immune-mediated competition, each one reducing the intensity of the other (Johnson and Buller, 2011). Similarly here, the reduction in *Diplostomum* spp. infection in fish could have benefitted some other snail-transmitted trematodes for which abundance coincidentally increased. Further research is needed to assess the net effect of the goby-mediated *Diplostomum* spp. decline in terms of disease risk and its effect on the St. Lawrence River ecosystem (Young et al., 2017).

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References

- American Veterinary Medical Association, 2013. The AVMA Guidelines for the Euthanasia of Animals. Schaumburg, IL, 102 pp.
- Aponte, V., Locke, S.A., Gentes, M.L., Giroux, J.F., Marcogliese, D.J., McLaughlin, D., Verreault, J., 2014. Effect of habitat use and diet on the gastrointestinal parasite community of an avian omnivore from an urbanized environment. *Can. J. Zool.* 92, 629–636.
- Baldwin, B.S., Carpenter, M., Rury, K., Woodward, E., 2011. Low dissolved ions may limit secondary invasion of inland waters by exotic round gobies and dreissenid mussels in North America. *Biol. Invasions* 14, 1157–1175.
- Belant, J.L., Ickes, S.K., Seamans, T.W., 1998. Importance of landfills to urban-nesting herring and ring-billed gulls. *Landsc. Urban Plan.* 43, 11–19.
- Blasco-Costa, I., Faltynková, A., Georgieva, S., Skirnisson, K., Scholz, T., Kostadinova, A.S., 2014. Fish pathogens near the Arctic Circle: molecular, morphological and ecological evidence for unexpected diversity of *Diplostomum* (Digenea: Diplostomidae) in Iceland. *Int. J. Parasitol.* 44, 703–715.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83, 575–583.
- Chappell, L.H., 1995. The biology of diplostomatid eyeflukses of fishes. *J. Helminthol.* 69, 97–101.
- Cotter, R.C., Rail, J.-F., Boyne, A.W., Robertson, G.J., Weseloh, D.V.C., Chaulk, K.G., 2012. Population status, distribution, and trends of gulls and kittiwakes breeding in Eastern Canada, 1998–2007 Occasional Paper No. 120. Canadian Wildlife Service.
- Désilets, H.D., Locke, S.A., McLaughlin, J.D., Marcogliese, D.J., 2013. Community structure of *Diplostomum* spp. (Digenea: Diplostomidae) in eyes of fish: main determinants and potential interspecific interactions. *Int. J. Parasitol.* 43, 929–939.
- Désilets, L., Langlois, C., 1989. Variabilité spatiale et saisonnière de la qualité de l'eau du fleuve Saint-Laurent. Environment Canada, St. Lawrence Centre, Montreal, Quebec.
- Dunn, A.M., Torchin, M.E., Hatcher, M.J., Kotanen, P.M., Blumenthal, D.M., Byers, J.E., Coon, C.A.C., Frankel, V.M., Holt, R.D., Hufbauer, R.A., Kanarek, A.R., Schierenbeck, K.A., Wolfe, L.M., Perkins, S.E., 2012. Indirect effects of parasites in invasions. *Funct. Ecol.* 26, 1262–1274.
- Essian, D.A., Chipault, J.G., Lafrancois, B.M., Leonard, J.B.K., 2016. Gut content analysis of Lake Michigan waterbirds in years with avian botulism type E mortality, 2010–2012. *J. Gt. Lakes Res.* 42, 1118–1128.
- Flory, S.L., Clay, K., Thrall, P., 2013. Pathogen accumulation and long-term dynamics of plant invasions. *J. Ecol.* 101, 607–613.
- Francová, K., Ondračková, M., Poláčik, M., Jurajda, P., 2011. Parasite fauna of native and non-native populations of *Neogobius melanostomus* (Pallas, 1814) (Gobiidae) in the longitudinal profile of the Danube River. *J. Appl. Ichthyol.* 27, 879–886.
- Gendron, A., Marcogliese, D., 2016. Reduced survival of a native parasite in the invasive round goby: evidence for the dilution hypothesis? *Aquat. Invasions* 11, 189–198.
- Gendron, A., Marcogliese, D., Thomas, M., 2012. Invasive species are less parasitized than native competitors, but for how long? The case of the round goby in the Great Lakes-St. Lawrence Basin. *Biol. Invasions* 14, 367–384.
- Giraud, M., Bruneau, A., Gendron, A.D., Brodeur, P., Pilote, M., Marcogliese, D.J., Gagnon, C., Houde, M., 2016. Integrated spatial health assessment of yellow perch (*Perca flavescens*) populations from the St. Lawrence River, Quebec, Canada) part A: physiological parameters and pathogen assessment. *Environ. Sci. Pollut. Res.* 23, 18073–18084.
- Hendrickson, G., 1986. Observations on the life cycle of *Ornithodiplostomum ptychocheilus* (Trematoda: Diplostomatidae). *Proc. Helminthol. Soc. Wash.* 53, 166–172.
- Hershberger, P.K., van der Leeuw, B.K., Gregg, J.L., Grady, C.A., Lujan, K.M., Gutenberger, S.K., Purcell, M.K., Woodson, J.C., Winton, J.R., Parsley, M.J., 2010. Amplification and transport of an endemic fish disease by an introduced species. *Biol. Invasions* 12, 3665–3675.
- Hoffman, G.J., 1999. Parasites of North American Freshwater Fishes. Comstock Publishing Associates, Ithaca, NY, 539 pp.
- Johnson, P.T., Hartson, R.B., 2009. All hosts are not equal: explaining differential patterns of malformations in an amphibian community. *J. Anim. Ecol.* 78, 191–201.
- Johnson, P.T.J., Buller, I.D., 2011. Parasite competition hidden by correlated coinfection: using surveys and experiments to understand parasite interactions.

- Ecology 92, 535–541.
- Johnson, P.T.J., Thielgtes, D.W., 2010. Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *J. Exp. Biol.* 213, 961–970.
- Keesing, F., Holt, R.D., Ostfeld, R.S., 2006. Effects of species diversity on disease risk. *Ecol. Lett.* 9, 485–498.
- Kelly, D.W., Paterson, R.A., Townsend, C.R., Poulin, R., Tompkins, D.M., 2009a. Parasite spillback: a neglected concept in invasion ecology? *Ecology* 90, 2047–2056.
- Kelly, D.W., Paterson, R.A., Townsend, C.R., Poulin, R., Tompkins, D.M., 2009b. Has the introduction of brown trout altered disease patterns in native New Zealand fish? *Freshwat. Biol.* 54, 1805–1818.
- Kinsella, J.M., Forrester, D.J., 1999. Parasitic helminths of the common loon, *Gavia immer*, on its wintering grounds in Florida. *J. Helminthol. Soc. Wash.* 66, 1–6.
- Kipp, R., Hébert, I., Lacharité, M., Ricciardi, A., 2012. Impacts of predation by the Eurasian round goby (*Neogobius melanostomus*) on molluscs in the upper St. Lawrence River. *J. Gt. Lakes Res.* 38, 78–89.
- Kopp, K., Jokela, J., 2007. Resistant invaders can convey benefits to native species. *Oikos* 116, 295–301.
- Kvach, Y., Winkler, H.M., 2011. The colonization of the invasive round goby *Neogobius melanostomus* by parasites in new localities in the southwestern Baltic Sea. *Parasitol. Res.* 109, 769–780.
- Lederer, A., Massart, J., Janssen, J., 2006. Impact of round gobies (*Neogobius melanostomus*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. *J. Gt. Lakes Res.* 32, 1–10.
- Lello, J., Boag, B., Fenton, A., Stevenson, I.R., Hudson, P.J., 2004. Competition and mutualism among the gut helminths of a mammalian host. *Nature* 428, 840–844.
- Lettoof, D.C., Greenlees, M.J., Stockwell, M., Shine, R., 2013. Do invasive cane toads affect the parasite burdens of native Australian frogs? *Int. J. Parasitol. Parasites Wild.* 2, 155–164.
- Levy, M.S., 1997. Helminth communities of ring-billed gulls (*Larus Delawarensis*) collected along the St. Lawrence River and Estuary. Master thesis. Concordia University, Montreal, 123 pp.
- Litvintseva, A.P., Hartigan, A., Fiala, I., Dyková, I., Jirků, M., Okimoto, B., Rose, K., Phalen, D.N., Šlapeta, J., 2011. A suspected parasite spill-back of two novel *Myxidium* spp. (Myxosporidia) causing disease in Australian endemic frogs found in the invasive cane toad. *PLoS One* 6, e18871.
- Locke, S.A., Al-Nasiri, F.S., Caffara, M., Drago, F., Kalbe, M., Lapierre, A.R., McLaughlin, J.D., Nie, P., Overstreet, R.M., Souza, G.T.R., Ricardo, M., Takemot, K., Marcogliese, D.J., 2015. Diversity, specificity and speciation in larval Diplostomidae (Platyhelminthes: Digenea) in the eyes of freshwater fish, as revealed by DNA barcodes. *Int. J. Parasitol.* 45, 841–855.
- Locke, S.A., McLaughlin, J.D., Dayanandan, S., Marcogliese, D.J., 2010. Diversity and specificity in *Diplostomum* spp. metacercariae in freshwater fishes revealed by cytochrome c oxidase I and internal transcribed spacer sequences. *Int. J. Parasitol.* 40, 333–343.
- Locke, S.A., McLaughlin, J.D., Marcogliese, D.J., 2013. Predicting the similarity of parasite communities in freshwater fishes using the phylogeny, ecology and proximity of hosts. *Oikos* 122, 73–83.
- Lyholt, H.C.K., Buchmann, K., 1996. *Diplostomum spathaceum*: effects of temperature and light on cercarial shedding and infection of rainbow trout. *Dis. Aquat. Org.* 25, 169–173.
- Lymbery, A.J., Morine, M., Kanani, H.G., Beatty, S.J., Morgan, D.L., 2014. Co-invaders: the effects of alien parasites on native hosts. *Int. J. Parasitol. Parasites Wild.* 3, 171–177.
- Marcogliese, D.J., 2001. Implications of climate change for parasitism of animals in the aquatic environment. *Can. J. Zool.* 79, 1331–1352.
- Marcogliese, D.J., Compagna, S., 1999. Diplostomatid eye flukes in young-of-the-year and forage fishes in the St. Lawrence River, Quebec. *J. Aquat. Anim. Health* 11, 275–282.
- Marcogliese, D.J., Dautremepuits, C., Gendron, A.D., Fournier, M., 2010. Interactions between parasites and pollutants in yellow perch (*Perca flavescens*) in the St. Lawrence River, Canada: implications for resistance and tolerance to parasites. *Can. J. Zool.* 88, 247–258.
- Marcogliese, D.J., Dumont, P., Gendron, A.D., Mailhot, Y., Bergeron, E., McLaughlin, J.D., 2001. Spatial and temporal variation in abundance of *Diplostomum* spp. in walleye (*Stizostedion vitreum*) and white suckers (*Catostomus commersoni*) from the St. Lawrence River. *Can. J. Zool.* 79, 355–369.
- Marcogliese, D.J., Gagnon Brambilla, L., Gagné, F., Gendron, A.D., 2005. Joint effects of parasitism and pollution on oxidative stress biomarkers in yellow perch *Perca flavescens*. *Dis. Aquat. Org.* 63, 77–84.
- Marcogliese, D.J., Gendron, A.D., Plante, C., Fournier, M., Cyr, D., 2006. Parasites of spottail shiners (*Notropis hudsonius*) in the St. Lawrence River: effects of municipal effluents and habitat. *Can. J. Zool.* 84, 1461–1481.
- Mastitsky, S.E., Veres, J.K., 2010. Field evidence for a parasite spillback caused by exotic mollusc *Dreissena polymorpha* in an invaded lake. *Parasitol. Res.* 106, 667–675.
- Mikl, L., Adámek, Z., Všeticková, L., Janáč, M., Roche, K., Šlapanský, L., Jurajda, P., 2016. Response of benthic macroinvertebrate assemblages to round (*Neogobius melanostomus*, Pallas 1814) and tubenose (*Proterorhinus semilunaris*, Heckel 1837) goby predation pressure. *Hydrobiologia* 785, 219–232.
- Miller, M.J., 1946. The cercaria of *Apophallus brevis*. *Can. J. Res. D Zool. Sci.* 24, 27–29.
- Moody, J., Gaten, E., 1982. The population dynamics of eye-flukes *Diplostomum spathaceum* and *Tyloodelphys clavata* (Digenea: Diplostomatidae) in rainbow and brown trout in Rutland Water: 1974–1978. *Hydrobiologia* 88, 207–209.
- Morin, J., Leclerc, M., 1998. From pristine to present state: hydrology evolution of Lake Saint-François, St. Lawrence River. *Can. J. Civ. Eng.* 25, 864–879.
- Morley, N.J., Lewis, J.W., 2017. Influence of *Triaenophorus nodulosus* plerocercoids (Cestoda: Pseudophyllidea) on the occurrence of intestinal helminths in the perch (*Perca fluviatilis*). *J. Helminthol.* 1–7.
- Nelson, F.B.L., Brown, G.P., Shilton, C., Shine, R., 2015. Helpful invaders: can cane toads reduce the parasite burdens of native frogs? *Int. J. Parasitol. Parasites Wild.* 4, 295–300.
- Olsen, O.W., 1974. Animal parasites. Their life cycles and ecology. Dover Publications, New York, 662 pp.
- Ondračková, M., Hudcová, I., Dávidová, M., Adámek, Z., Kašný, M., Jurajda, P., 2015. Non-native gobies facilitate the transmission of *Bucephalus polymorphus* (Trematoda). *Parasites Vectors* 8, 1–11.
- Palmieri, J.R., 1975. Host parasite relationships and intraspecific variation in the strigeoid trematode *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). Ph D thesis. Iowa State University, Ames, 166 pp.
- Paterson, R.A., Lal, A., Dale, M., Townsend, C.R., Poulin, R., Tompkins, D.M., 2013a. Relative competence of native and exotic fish hosts for two generalist native trematodes. *Int. J. Parasitol. Parasites Wild.* 2, 136–143.
- Paterson, R.A., Rauque, C.A., Fernandez, M.V., Townsend, C.R., Poulin, R., Tompkins, D.M., 2013b. Native fish avoid parasite spillback from multiple exotic hosts: consequences of host density and parasite competency. *Biol. Invasions* 15, 2205–2218.
- Paterson, R.A., Townsend, C.R., Poulin, R., Tompkins, D.M., 2011. Introduced brown trout alter native acanthocephalan infections in native fish. *J. Anim. Ecol.* 80, 990–998.
- Paterson, R.A., Townsend, C.R., Tompkins, D.M., Poulin, R., 2012. Ecological determinants of parasite acquisition by exotic fish species. *Oikos* 121, 1889–1895.
- Poulin, R., Paterson, R.A., Townsend, C.R., Tompkins, D.M., Kelly, D.W., 2011. Biological invasions and the dynamics of endemic diseases in freshwater ecosystems. *Freshwat. Biol.* 56, 676–688.
- Prenter, J., MacNeil, C., Dick, J.T.A., Dunn, A.M., 2004. Roles of parasites in animal invasions. *Trends Ecol. Evol.* 19, 385–390.
- Rolbiecki, L., 2006. Parasites of the round goby, *Neogobius melanostomus* (Pallas, 1811), an invasive species in the Polish fauna of the Vistula Lagoon ecosystem. *Oceanologia* 48, 545–561.
- Searle, C.L., Cortez, M.H., Hunsberger, K.K., Grippi, D.C., Oleksy, I.A., Shaw, C.L., de la Serna, S.B., Lash, C.L., Dhir, K.L.A.D.M., 2016. Population density, not host competence, drives patterns of disease in an invaded community. *Am. Natur.* 188, 554–566.
- Sheath, D.J., Williams, C.F., Reading, A.J., Britton, J.R., 2015. Parasites of non-native freshwater fishes introduced into England and Wales suggest enemy release and parasite acquisition. *Biol. Invasions* 17, 2235–2246.
- Sinclair, N.R., 1971. Studies on the heterophyid trematode *Apophallus brevis*, the “sand-grain grub” of yellow perch (*Perca flavescens*). II. The metacercaria: position, structure, and composition of the cyst; hosts; geographical distribution and variation. *Can. J. Zool.* 50, 577–584.
- Stables, J.N., Chappell, L.H., 1986. *Diplostomum spathaceum* (Rud. 1819): effect of physical factors on the infection of rainbow trout (*Salmo gairdneri*) by cercariae. *Parasitology* 93, 71–79.
- Taraschewski, H., 2006. Hosts and parasites as aliens. *J. Helminthol.* 80, 99–128.
- Telfer, S., Bown, K.J., Sekules, R., Begon, M., Hayden, T., Birtles, R., 2005. Disruption of a host-parasite system following the introduction of an exotic host species. *Parasitology* 130, 661–668.
- Telfer, S., Lambin, X., Birtles, R., Beldomenico, P., Burthe, S., Paterson, S., Begon, M., 2010. Species interactions in a parasite community drive infection risk in a wildlife population. *Science* 330, 243–246.
- Thielgtes, D.W., Reise, K., Prinz, K., Jensen, K.T., 2009. Invaders interfere with native parasite–host interactions. *Biol. Invasions* 11, 1421–1429.
- Thilakarathne, I.D.S.I.P., McLaughlin, J.D., Marcogliese, D.J., 2007. Effects of pollution and parasites on biomarkers of fish health in spottail shiners *Notropis hudsonius* (Clinton). *J. Fish Biol.* 71, 519–538.
- Torchin, M.E., Mitchell, C.E., 2004. Parasites, pathogens, and invasions by plants and animals. *Front. Ecol. Environ.* 2, 183–190.
- Young, H.S., Parker, I.M., Gilbert, G.S., Sofia Guerra, A., Nunn, C.L., 2017. Introduced species, disease ecology, and biodiversity–disease relationships. *Trends Ecol. Evol.* 32, 41–54.