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Quantifying migratory capacity and dispersal of the invasive tench (*Tinca tinca*) in the St. Lawrence River using otolith chemistry

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Abstract: The study of distribution and dispersal of invasive fishes is challenging during the early stages of invasion. Quantification of trace elements incorporated into fish hard parts represents an innovative technique for this task. Otolith chemistry has been used to describe fish stock structure, migratory behaviour and to support the management of several species. We used otolith chemistry to study the dispersal and population structure of tench (*Tinca tinca*), an invader in the St. Lawrence River. Tench movements throughout the invaded portion of the system were reconstructed using a Random Forests algorithm. The results showed that, despite the presumed limited dispersal capacity of the species, tench are capable of extensive migratory movements (up to 250 km). The variability in migratory patterns among individuals, including both short- and long-distance movements, supports a stratified diffusion. Such a strategy may explain the successful invasion of tench in the St. Lawrence River ecosystem. Our study represents a flexible framework for the study of tench ecology in its invaded and native range, as well as for other freshwater invasive fishes.

Résumé : L'étude de la répartition et de la dispersion de poissons envahissants durant les premières étapes de l'envahissement n'est pas chose facile et, pour ce faire, la quantification d'éléments en traces incorporés dans les parties dures de poissons constitue une approche novatrice. La chimie des otolites a été utilisée pour décrire la structure de stocks et le comportement migratoire des poissons, ainsi que pour appuyer la gestion de plusieurs espèces. Nous avons utilisé la chimie des otolites pour étudier la dispersion et la structure de la population de tanche (*Tinca tinca*), une espèce envahissante dans le fleuve Saint-Laurent. Les déplacements des tanches dans toute la portion envahie du système ont été reconstitués à l'aide d'un algorithme de forêts aléatoires. Les résultats montrent que, malgré une capacité de dispersion limitée présumée pour cette espèce, les tanches sont capables d'effectuer de grands déplacements migratoires (jusqu'à 250 km). La variabilité des habitudes migratoires d'un individu à l'autre, qui comprend des déplacements tant sur de longues que sur de courtes distances appuie une stratégie de diffusion stratifiée. Une telle stratégie pourrait expliquer l'envahissement de l'écosystème du fleuve Saint-Laurent par la tanche. Notre étude offre un exemple d'approche polyvalente pour l'étude de l'écologie de la tanche dans ses aires de répartition indigène et envahis, mais aussi chez d'autres poissons d'eau douce envahissants. [Traduit par la Rédaction]

Introduction

The secondary spread of an invasive species following its initial introduction is of great importance to anticipate future distribution and potential impacts (Parker et al. 1999). Identifying the factors driving dispersal following the initial introduction allow managers to predict where and when new colonization might occur and may help to plan the most efficient response strategies to be implemented (Vander Zanden and Olden 2008). However, secondary dispersal can be difficult to study as the initial introductions could occur unnoticed, and subsequent spread may act rapidly thereafter. Dispersal potential for a given species can vary widely among individuals and work synergistically with other factors, such as environmental conditions and biotic characteristics of the newly invaded community (Catford et al. 2009), making prediction even more complex, especially for cryptic species. As observed migratory patterns in the invader native range could differ with what is observed in the invaded system (Broennimann and Guisan 2008; Hejda et al. 2009), caution is required when risk analysis are based on such information. The study of secondary dispersal is especially challenging for aquatic invasive species (AIS), which are rarely directly observed without capture. Technical advances in numerous fields have opened the way to more efficient detection and monitoring strategies of invasive species, notably through environmental DNA detection (Darling and Mahon 2011), genetic population structure (Bronnenhuber et al. 2011; Stepien et al. 2018), acoustic telemetry (Harris et al. 2021) and fish otolith chemistry (Carlson et al. 2017). From this perspective, otolith chemistry could be used for assessing dispersal mechanisms and identifying other relevant aspects of their biology like the origin of the fish, movement history during the early stages of colonization and the lifetime movement patterns (Campana 1999; Walther 2019).

Otoliths (ear stone) are calcium carbonate structures located in the fish inner ear. Analyses of otolith chemical composition had shown that some trace element (e.g., strontium and barium) are

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accreted in concentration influenced by ambient water composition at the time of deposition (Campana 1999), with minimal influence of diet (Walther and Thorrold 2006), temperature or physiological processes (Hüssy et al. 2020). Point- or transect-based (i.e., from core to margin) analyses of otolith composition have proven successful for reconstructing migration patterns (Morissette et al. 2016; Secor and Piccoli 2007) and for stock structure assessment (Lazartigues et al. 2016; Wright et al. 2018). Whereas otolith chemistry literature demonstrates an exponential growth since 1991 (Walther 2019), application in the realm of invasion biology remains marginal (Munro et al. 2005; Thibault et al. 2010), especially in freshwater systems where elemental gradients are often assumed to be too weak (Pracheil et al. 2014) or elusive. However, otolith chemical composition classification in freshwater habitat has been successfully used for discriminating between different drainage or large scale geographical gradients (Radigan et al. 2018; Whitledge 2009) and habitat types (Zeigler and Whitledge 2011) and show sufficient structure to enable for local or regional assignment (Morissette and Sirois 2021). Assessment of common carp (*Cyprinus carpio*) recruitment hotspots in Australia's Lachlan River (Crook et al. 2013), analysis of population structure and recruitment of the invasive bighead carp (*Hypopthalmichthys nobilis*) and silver carp (*Hypopthalmichthys molitrix*) in the Mississippi River (Norman and Whitledge 2015; Whitledge et al. 2019) and Lake Erie grass carp (*Ctenopharyngodon idella*; Chapman et al. 2013) are all demonstrating the relevance of otolith chemistry utility for AIS management.

The common dispersal pattern for invaders is "simple diffusion" where extension from the site of introduction is correlated with population demographic growth (Shigesada et al. 1995). Such diffusion may act slowly, especially for species displaying long life cycles, and represent a lower risk of extinction, as conspecifics remain close to each other, thus increasing density and facilitating reproduction and recruitment (Shigesada et al. 1995; Skalski and Gilliam 2000). Dispersal can also result from long-distance movements between suitable habitat patches (e.g., stepping-stone dispersal). In this case, dispersal has a higher risk of failure by increasing the probability of reaching ecological dead ends (e.g., Allee effect) or failure to find suitable habitats or reproduction partners, but could also produce faster and further dispersal to suitable habitats (Renault et al. 2018; Taylor and Hastings 2005). Hengeveld (1989) identified several cases where both short and long-distance dispersal were acting side-by-side; termed stratified diffusion. Such dispersal has been commonly seen in invasive species that are easily transported over long distance by humans, such as insects (Muirhead et al. 2006) and plants (Huebner 2010) but this phenomenon has also been observed in fishes (Bronnenhuber et al. 2011) where long-distance dispersal could be passive or active. Stratified diffusion results in faster dispersal, as speed of invasion appears to be governed by long distance movements, even when this behaviour is rare in the population (Neubert and Caswell 2000). In its early stages, stratified diffusion could be perceived as a stepping-stone strategy, but fundamental difference lies in the fact that the invaders could thrive and establish either in corridors or patches, named refuge in stepping-stone theory (Simberloff et al. 1992), and not just using them as transitional habitats. Stratified diffusion is also recognized to be a mechanism maintaining genetic diversity at the invasion front by the constant immigration from the genetically diverse long-invaded sites (Bronnenhuber et al. 2011).

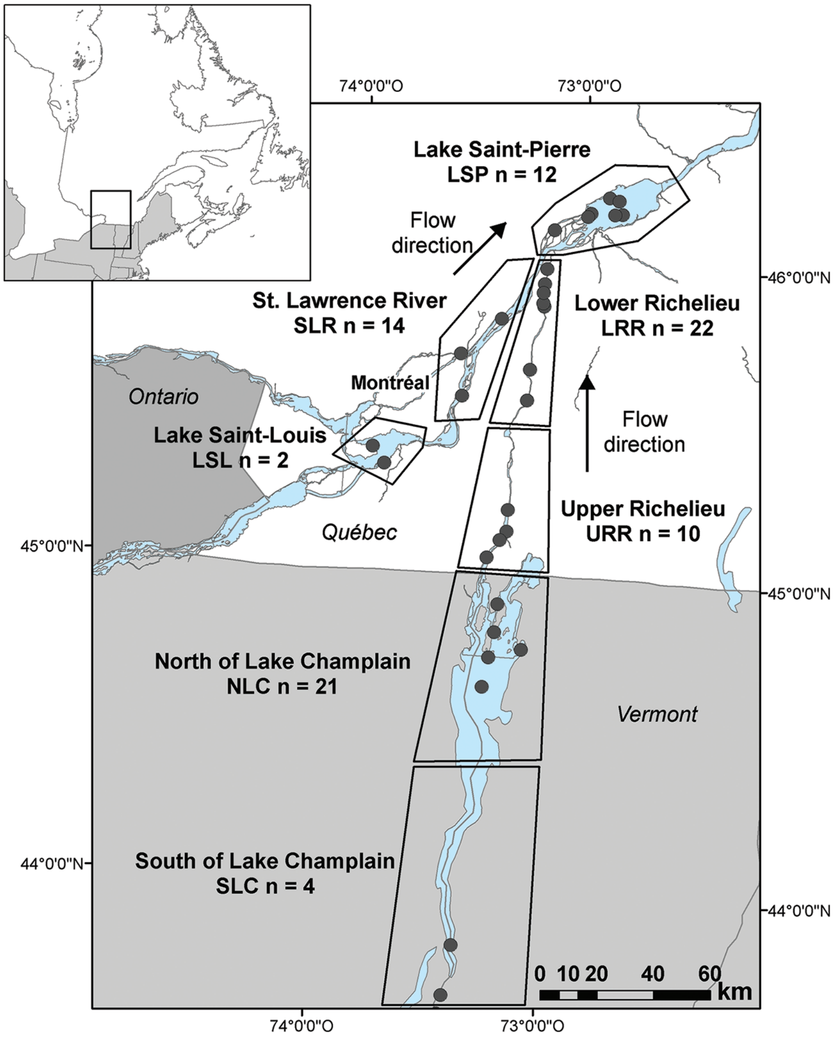
Knowledge of the dispersal capacity of numerous freshwater invaders is limited, such as is the case for the tench (*Tinca tinca*). Tench is an omnivorous freshwater cyprinid, typically found in shallow and vegetated waters and displaying high warm water tolerance (Cudmore and Mandrak 2011). Tench has been present in Quebec (Canada) since 1991, resulting from a deliberate illegal introduction in the Richelieu River (Avlijaš et al. 2018; Dumont et al. 2001). There is a lack of knowledge on tench migratory behaviour either in native or invaded ranges (Calles and Greenberg 2007; Donnelly et al. 1998; Kolar and Lodge 2002). Some authors suggest that the species is strictly non-migratory (Moyle 1976), probably presumed by an apparent sedentary life cycle in shallow water habitats, while others report foraging (Perrow et al. 1996) and spawning migrations (Pollux et al. 2006). A telemetry study on a single individual of the Grand Canal (Ireland) suggested that movements of several kilometers were possible (Donnelly et al. 1998) and were likely related to foraging and searching for prey. In Quebec, thirty years after the initial introduction in the Richelieu River, tench has spread to Lake Champlain (Carlson and Daniels 2004) and is progressing toward the Laurentian Great Lakes; in 2020 the species is occupying more than 500 km of riverine habitat. Owing to its peculiar introduction history (e.g., a single introduction event), tench in the St. Lawrence River system are assumed to still exhibit low genetic diversity and population structure. Hence, assessment of recruitment dynamics and the delineation of potential population genetic structure represent a challenge for wildlife managers.

The aim of this study was to investigate tench dispersal dynamics and population structure (including the identity of hatching sites) in the St. Lawrence and Richelieu rivers. Specifically, we used transect-based otolith chemistry by Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) to identify the individual's origin and migratory behaviour throughout the ecosystem. We tested the hypothesis that tench is behaving as a migratory fish in the St. Lawrence River, exhibiting a stratified dispersal strategy, which is driving its present rapid expansion. We consider that this study is providing a flexible framework of application of otolith chemistry for the assessment of invasive freshwater fishes ecology and subsequent management, as well as bringing relevant information on tench ecology and migratory capacity, both in its invaded and native range.

Method

Tench were collected during the summer of 2016 in the St. Lawrence River, Richelieu River and Lake Champlain (Fig. 1). All captures were provided by the Quebec Ministère des Forêts, de la Faune et des Parcs (MFFP) and McGill University fish surveys (Avlijaš et al. 2018). Fish were captured using arrays of two gillnets (60 m long × 1.8 m deep; eight panels of 25, 38, 51, 64, 76, 102, 127 and 152 mm stretched mesh), beach seine net (12.5 m long × 4.0 m deep and 3.2 mm stretched mesh) or electrofishing backpack units, which represent a combination of engine sufficient to capture most tench length classes present in sampled sites except young-of-the-year (<100 mm TL), which are consistently absent from annual governmental fish surveys, probably related to their divergent habitat utilization compared to other age classes. Maximum total length (TL, mm) was measured at the time of capture, before freezing. For each site sampled, specimens were selected to be representative of the local size distribution and abundance, explaining the low number of specimen captured at the invasion fronts (Lake St. Louis and South of Lake Champlain; Fig. 1). Ages were estimated using an age–length key (O. Morissette, unpublished data). Both asterisci and lapilli otolith pairs were extracted for each individual fish. Ostariophysian fishes, such as tench, possess an otolith morphology that greatly differs from non-ostariophysian fishes (i.e., Salmonidae or Percidae). Ostariophysian sagittal otoliths are reduced to needle-shaped structures, for which few experimental uses have been found (Vilizzi 2018). Low extraction success for lapilli, linked to the peculiar internal ear morphology, forced the use of the vateritic asterisci for LA-ICP-MS analyses. Chemistry data from both asterisci and lapilli were shown to provide similar discriminatory power, although absolute elemental concentrations (Mg, Mn, Sr, and Ba) are divergent between structures, likely associated with the different calcium composition of the otoliths; whereas asterisci is mostly

Fig. 1. Location of capture (grey circles) and the classification sites (black boxes) for the study, numbers of captured tench are shown for every site. Spatial extent of sites is only used for illustration purpose and is not representing strict boundaries. Map was realized with ArcMap 10.4.1 (Esri), with CanVec (Ressources naturelles Canada 2016) and BDTA 250k database (Ministère de l'Énergie et des Ressources Naturelles 2016).



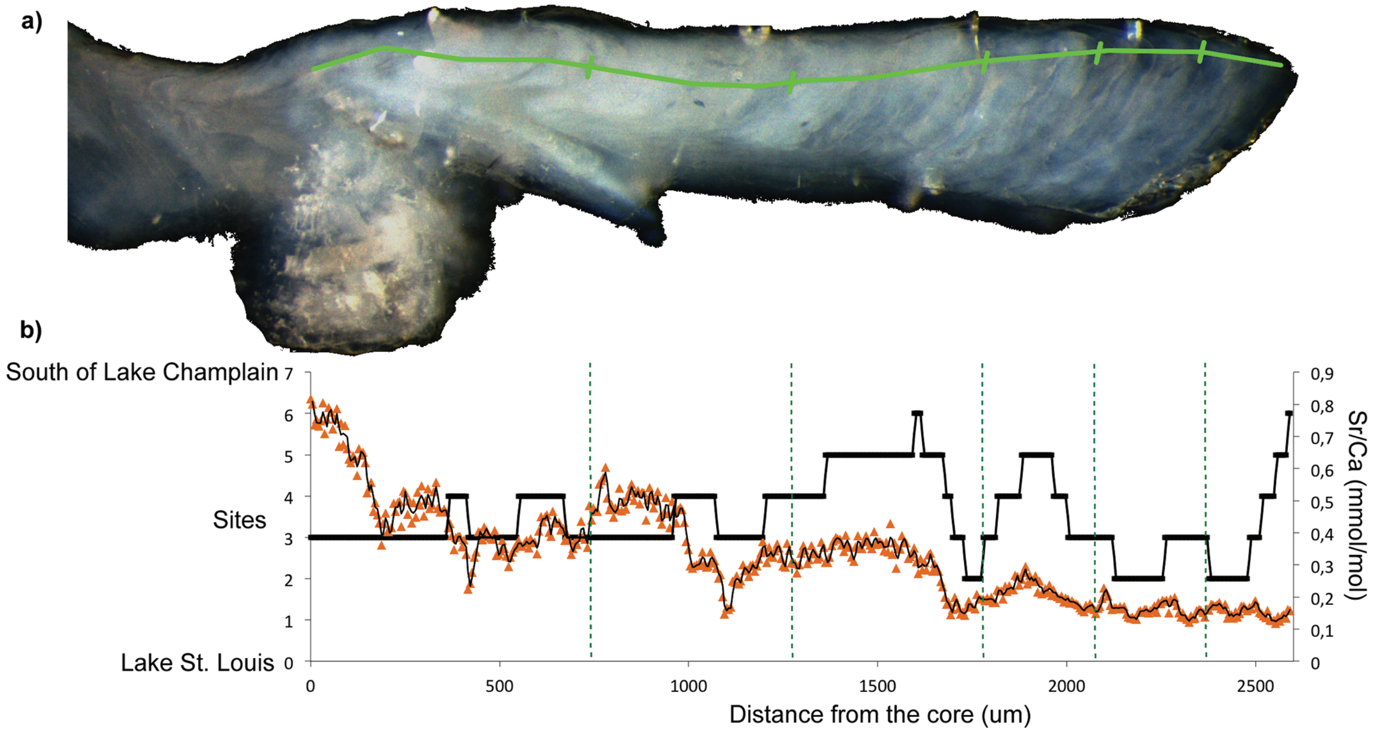
composed of vaterite, lapilli is mostly composed of aragonite (Macdonald et al. 2012).

After extraction, the right asterisci (otolith hereinafter) were rinsed three times in ultrapure water to remove any remaining organic material before drying under a class 100 laminar-flow fume hood for 24 hours. Otoliths were then embedded in two-part epoxy resin (Miapoxy 100, Miapoxy, Ohio, United States) before being sectioned (1 mm thick section) on the transversal plane with a low speed diamond bladed saw (Isomet saw, Buehler, Illinois, United States). After sectioning, core and macrostructure were exposed by successive use of polishing paper (Wetordry 2000 grains) and aluminium-oxide lapping film (1 and 5 μm; 3 M). Sections were mounted on a petrographic microscope slide using a thermoplastic glue (Crystalbond509; Aremco Products, New York, United States) and then sonicated in ultrapure water for 5 min followed by a 24 h drying under a laminar flow fume hood before ablation.

The LA-ICP-MS analyses were undertaken using a Resonetic Excimer 193 nm ArF laser coupled to an Agilent model 7900 ICP-MS (Agilent, Mississauga, Ontario, Canada) located in LabMaTer facilities (Université du Québec à Chicoutimi, Chicoutimi, Quebec, Canada). Laser ablation was realized in transect mode along the entire otolith axis from the dorsal margin to the ventral margin passing through the otolith core. The laser beam diameter was set to 19 μm, moving at a speed of 5 μm·s^{-1}, at a frequency of 20 Hz and a laser fluence of 5 J·cm^{-2}. A panel of 35 elements isotopes, representing routine otolith analyses in LabMaTer, were targeted (^{7}Li, ^{11}B, ^{23}Na, ^{24}Mg, ^{25}Mg, ^{27}Al, ^{29}Si, ^{31}P, ^{34}S, ^{39}K, ^{43}Ca, ^{44}Ca, ^{55}Mn, ^{56}Fe, ^{57}Fe, ^{59}Co, ^{60}Ni, ^{61}Ni, ^{63}Cu, ^{64}Zn, ^{65}Cu, ^{66}Zn, ^{69}Ga, ^{85}Rb, ^{86}Sr, ^{87}Sr, ^{88}Sr, ^{118}Sn, ^{119}Sn, ^{120}Sn, ^{136}Ba, ^{137}Ba, ^{138}Ba, ^{202}Hg and ^{206}Pb) for quantification. Each analysis was normalized to an expected calcium content (^{44}Ca) in otolith matrix (40% weight; Campana 1999). A NIST-610 glass reference material was measured regularly during 60 seconds after every 3–4 samples (~2 hours of LA-ICP-MS operation) to estimate element concentrations and correct for any analytical drift. Additional reference materials USGS MACS-3 and GP-4 were also measured for quality control. Carrier gas background without ablation were measured for 30 s before analysis and 15 s after, and subtracted from observed values.

Element concentrations from ICP-MS signal were estimated using Iolite (Paton et al. 2011), a free add-on in Igor Pro software (Wavemetrics Inc., Portland, Oregon, United States). Data integration was performed using the "trace elements IS" procedure in

Fig. 2. Example of (*a*) a single tench otolith (ID 57) with highlighted LA-ICP-MS transect (green solid line from otolith core to ventral margin) and annuli (green vertical ticks) and (*b*) classification results with relative annuli position (vertical dotted lines). Black line is the migratory history from the smoothed classification and orange triangles are Sr:Ca value and corresponding running mean. Sites are presented in increasing order linked to the westward–southward geographical gradient. Otolith image was cropped and exposure optimized for clarity. [Colour online.]



Iolite. To assess the validity of observed concentrations, elements limit of detection (LOD) was calculated as three times the standard deviation of the gas blank (SD_{blank}) divided by the sensitivity of the signal (Lazartigues et al. 2014). Element concentrations were normalised to ^{43}Ca as suggested by Campana (1999) and data were presented as concentration ratios in units of mmol·mol^{-1} for every element (e.g., Sr:Ca). Elements concentrations below LOD were excluded from statistical analyses (^{7}Li, ^{56}Fe, ^{59}Co, ^{60}Ni, ^{63}Cu, ^{64}Zn, ^{65}Cu, ^{66}Zn, ^{69}Ga, ^{85}Rb, ^{118}Sn, ^{119}Sn, ^{120}Sn, ^{202}Hg and ^{206}Pb). Along the transect, data consistent with CrystalBond thermoplastic glue contamination (i.e., ^{29}Si, ^{31}P and ^{34}S) were removed as well as data points with low calcium (^{43}Ca) concentration, indicative of cracks or irregularities in the otolith matrix. Similar to previous studies focusing on fishes otolith chemistry in the St. Lawrence River system (Benchetrit et al. 2017; Lazartigues et al. 2018; Morissette et al. 2016), four trace elements (^{25}Mg, ^{55}Mn, ^{88}Sr and ^{138}Ba) were selected for subsequent analyses (i.e., elemental fingerprint).

To maximize the resolution, the longest path available for laser ablation was used to quantify fish movement between water masses, for tench this corresponds to the path from core toward the ventral margin of the otolith (Fig. 2). Data were separated in three distinct zones; core of the otolith (first 10 analysis points from the core), otolith margin (10 last analysis points) and complete transect. Based on Sr:Ca values, 10 points of analysis appeared to be the optimal number to represent margin signal as it minimizes the standard error and standard deviation (see online Supplementary Fig. S1[1]). For all specimens, we assumed that margin elemental fingerprints were deposited at the sampling site.

All statistical analyses were realized using the R statistical software version 3.6.0 (R Development Core Team 2008). Difference of trace element concentration of otolith margin datasets for each site of capture were analyzed using a repeated-measure analysis of variance (ANOVA) (RM-ANOVA — function aov) using captures site (7 levels, Lake St. Louis, St. Lawrence River, Lake St. Pierre, lower Richelieu River, upper Richelieu River, North of Lake Champlain and South of Lake Champlain) as a single factor and specimen (ID) as a repeated factor, to account for non-independence of chemical signal within specimens. Post hoc differences were assessed with a Tukey honestly significant difference (HSD) test using the HSD.test function (agricolae R package version 1.3-1; de Mendiburu 2019). Sites were determined based on elemental fingerprint classification performance to optimize percentage of reclassification and geographic resolution (Fig. 1).

Classification of elemental compositions was done using the Random Forests (RF) machine learning algorithm (Breiman 2001) from the randomForest R package version 4.6-14 (Breiman and Cutler 2018). RF algorithm is built using a combination of tree predictors while reclassification is based on a random selection of node-splitting features from the same dataset. The classification is based on a consensus verdict of those multiple trees (i.e., the random forest), as generalization error tend to converge with an increasing number of trees added to the model. Like other classification algorithms based on decision trees, RF is mostly insensitive to absolute values and distribution of predictors, allowing untransformed data to be used for model building. Classification by RF was shown to be outperforming parametric models (e.g., linear discriminant analysis) for otolith chemistry data when raw data are not respecting multi-normality assumptions (Jones et al. 2017; Mercier et al. 2011), which is the case in the

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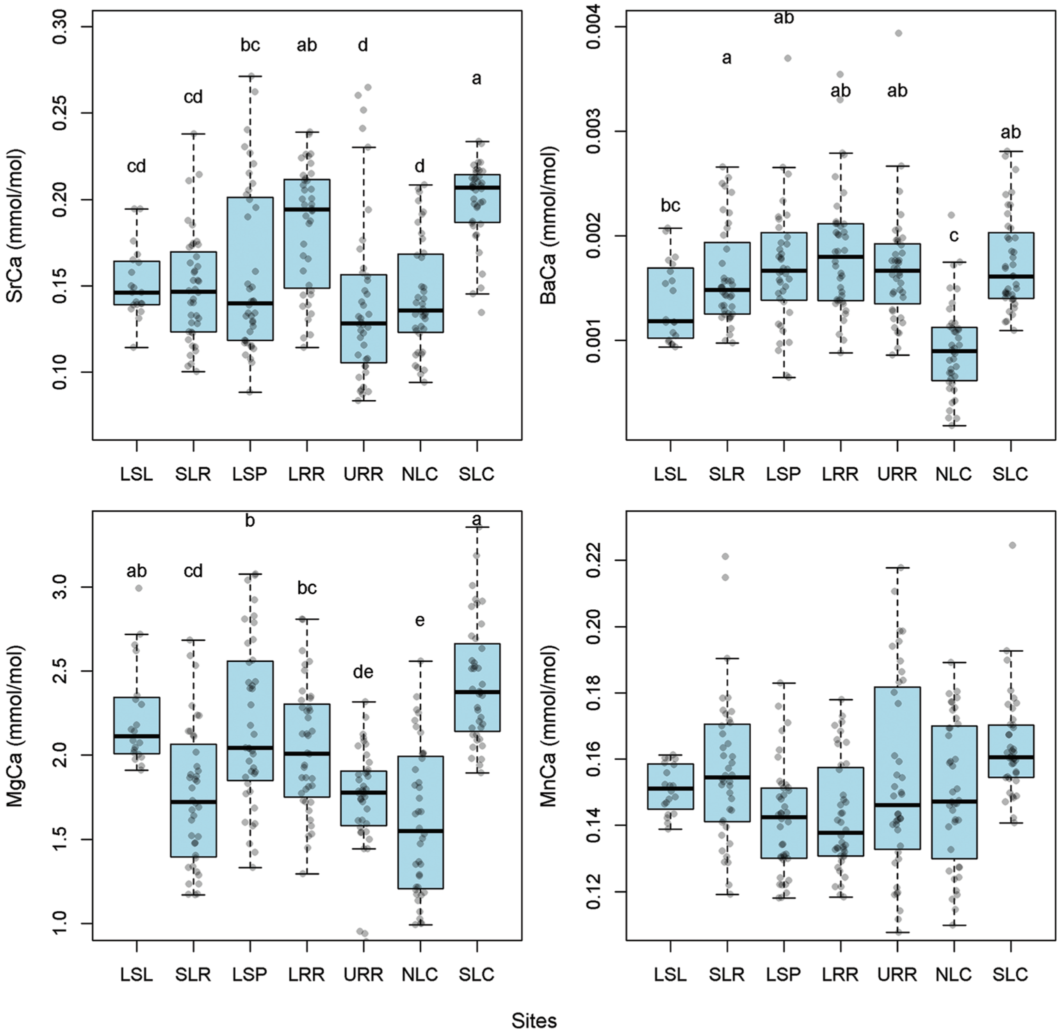
[1] Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0460.

Fig. 3. Concentrations of strontium, barium, magnesium, and manganese from otolith margins in sampled sites (see Table 1 or Fig. 1 for acronyms). Sites are presented in geographical relative position, from westward sites (LSL, Lake St. Louis) to southward sites (SLC, South of Lake Champlain). Different letters indicate statistically significant differences among sites.



present study. RF classification model was fitted using balanced elemental fingerprints from otolith margin datasets. We used 40 randomly selected points of analyses from every site (except LSL; 20 points, due to the smaller number of samples available) to avoid over-representing a specific site. Accuracy of the reclassification by the model was assessed using the function confusionMatrix (randomForest R package) which represents the average of 100 classifications procedures from 75 randomly selected otolith margin elemental fingerprints. Reconstruction of migratory history was made by RF classification of trace element values along otolith chemistry transect (from core to margin) obtained for each specimen.

Successive classifications of elemental fingerprint were denoised by a smoothing procedure. The smoothing procedure was designed to be coherent with the geographical succession of regions occupied by tench. Sites were transformed to numerical values from the "western" extremity of the distribution (Lake St. Louis = 1) to the "southern" (South of Lake Champlain = 7) extremity (see Fig. 1). Successions of numerical classifications along each otolith transect (representing migration history) were smoothed with a Loess procedure (stats R package) using α = 0.10, to remove occasional incorrect classifications by autocorrelations within the classification transect (smoothing of a given classification is correlated with the preceding values). As fish should move between sites sequentially, visiting a first region before reaching a second, use of transects autocorrelations has been assumed to represent this fish movements constrained in the system. Smoothed values were rounded to the nearer integer within the limits of the used numerical domain (e.g., from 1 to 7), providing a smoothed numerical assignment. The same RF classification model was also used for estimation of hatching sites, using the mode values of classification for the core elemental fingerprints (10 data points). Smoothed migration trajectories were visually compared with raw assignments to detect any false results that could have been induced by the method; none were detected in the present study.

Individual migratory behaviours were summarized by the calculation of two indices; the migratory direction (i.e., the resulting lifetime migration of the captured fish) and migratory variability (i.e., a quantification of the frequency and amplitude of movement, which is not directional). Along every individual transect, numerical value of a given classification (site) was subtracted by the preceding value. This calculation provided a movement value (m) for every data point. The obtained m values were considered as residency ($m = 0$), western migration toward Great Lakes ($m < 0$, referred as westward migration hereinafter) and southern migration toward southern Lake

Table 1. Random Forest classification model confusion matrix for otolith's margins chemistry, sites are shown along the downstream–upstream geographical gradient.

Site	LSL	SLR	LSP	LRR	URR	NLC	SLC	Error
Lake St. Louis (LSL)	**8**	0	5	0	2	1	4	0.60
St. Lawrence River (SLR)	2	**21**	4	4	4	3	2	0.48
Lake St. Pierre (LSP)	3	2	**21**	7	0	3	4	0.48
Lower Richelieu (LRR)	2	4	7	**17**	0	2	8	0.58
Upper Richelieu (URR)	1	5	1	3	**25**	3	2	0.38
North Lake Champlain (NLC)	3	7	1	2	2	**24**	1	0.40
South Lake Champlain (SLC)	2	1	4	4	0	1	**28**	0.30

Note: Table presents captures sites (rows), model classification (columns), and site classification errors.

Table 2. Number of fish classified with Random Forests to hatching sites (columns) inferred from otolith core composition by capture sites (rows), local capture (n = 15) are on the diagonal, upper-right corner are westward migrants (n = 41), and lower-left corner are southward migrants (n = 29).

	Hatching site (core elemental fingerprints)						
Capture site	LSL	SLR	LSP	LRR	URR	NLC	SLC
Lake St. Louis (LSL)	**0**	0	0	0	1	1	0
St. Lawrence River (SLR)	0	**2**	2	3	4	3	0
Lake St. Pierre (LSP)	0	0	**0**	3	4	5	0
Lower Richelieu (LRR)	0	0	0	**7**	4	11	0
Upper Richelieu (URR)	0	0	2	4	**4**	0	0
North Lake Champlain (NLC)	0	0	2	10	8	**1**	0
South Lake Champlain (SLC)	0	0	0	0	1	2	**1**
Percentage	0%	2.3%	7.1%	31.7%	30.6%	27.1%	1.2%

Champlain ($m > 0$, referred as southward migration hereinafter). Migratory direction was calculated as the mean of all m values for every specimen. Migratory variability was calculated as the standard deviations of m, representing the summarized extend of lifetime migratory movement experienced. Migratory tendencies were analyzed by a one-way ANOVA of migratory direction in function by capture sites. Migratory variability by hatching sites (e.g., data from the core) was analyzed with the same model. Similar one-way ANOVA models were also used to assess the effects of total length and age on migratory direction and variability.

Results

A total of 85 tench right asterisci were retrieved and selected for analyses, these fish were captured from the seven sites identified (Fig. 1). Tench were 375 mm total length on average (range 183–482 mm) and were aged between 2 and 11 years old, with 95% of fish being under age 5. There was no difference in age among sites (ANOVA, $F_{[6,77]} = 0.82$, $p = 0.56$), however there is a significant difference in length among sites (ANOVA, $F_{[6,77]} = 3.26$, $p = 0.006$). The latter difference is associated with the smaller average length for tench captured in the lower Richelieu River (mean: 339.8 mm, SD = 59.5 mm) compared to the other sites (mean: 398.6 mm, SD = 52.2 mm).

Average observed concentrations and limits of detection for retained elements were the following: ^{25}Mn (518.90 ppm, LOD = 0.56 ppm), ^{55}Mn (7.83 ppm, LOD = 2.34 ppm), ^{88}Sr (257.17 ppm, LOD = 0.01 ppm) and ^{138}Ba (2.56 ppm, LOD = 0.003 ppm). Significant differences of elements were observed among otolith margin values in relationship to sampling site (Fig. 3). Specifically, differences were observed for Sr:Ca (RM-ANOVA $F_{[6,62]} = 4.12$, $p = 0.002$), Ba:Ca (RM-ANOVA $F_{[6,62]} = 5.32$, $p = 0.0001$), Mg:Ca (RM-ANOVA $F_{[6,62]} = 7.52$, $p < 0.0001$) but not Mn:Ca (RM-ANOVA $F_{[6,62]} = 1.90$, $p = 0.09$). Considering that the inclusion of Mn in the classification model increased its accuracy (5% increase), this element was kept for subsequent analyses even if not displaying a significant difference among sites.

Classification accuracy of the RF model was estimated as 68.8% ± 0.05%; most classification errors were observed among adjacent sites (Table 1). Some classification errors between sites far apart were also observed but were less of a concern as they were later removed by the denoising and smoothing procedure. Classification of otolith core material revealed that tench analyzed in the present study were originating from all sampling sites except Lake St. Louis (Table 2). Lower Richelieu River was the site from which the most important proportion of specimens were originating (31.7%). Together, lower Richelieu River, upper Richelieu River and North of Lake Champlain represented the presumed hatching sites of 89.4% of the captured specimens. Local captures, defined as tench captured at the site of their presumed origin, were uncommon (17.6% of captures) compared to fish captured in a site westward of their presumed origin (48.2% of captures) or captured in a site southward of their presumed origin (34.2% of captures).

Migratory direction values were significantly correlated with the site of capture (ANOVA, $F_{[6,78]} = 9.73$, $p < 0.001$) where fish from newly invaded sites were mostly long-distance migrants from older invaded sites (highest or lowest m values, Fig. 4). Conversely, in the oldest sites invaded by tench, individual captured were either resident (direction = 0) or migrants. Total length (mm) of specimens was not significantly correlated to migratory direction (ANOVA, $F_{[1,83]} = 0.16$, $p = 0.69$), providing no evidence that size or age within the adult size-class are good predictors of migratory behaviour. Migratory variability was significantly correlated to hatching sites (ANOVA, $F_{[5,79]} = 2.55$, $p = 0.03$), but was not correlated to total length (ANOVA, $F_{[1,80]} = 7.27$, $p = 0.22$). Specimens hatched in sites newly invaded showed a higher migratory variability than individuals from sites invaded for a longer period of time (Fig. 5). When considering the average distance of 50 km between sites (Fig. 1) and comparing for each individual the site of capture and the presumed hatching site, the average lifetime distance migrated by individual tench was 81.8 km (SD = 56.2 km), with one specimen (372 mm, ~3 years old) that migrated at least 250 km.

Discussion

Using otolith chemistry, we found that the invasive tench is capable of extensive secondary dispersal. The estimated individual distance traveled (average of 81.8 km, maximum of 250 km) suggests that dispersal is best explained by a stratified diffusion model (Shigesada et al. 1995) where short- and long-distance dispersals are coexisting. The present study suggests that the migratory capacity of tench greatly exceeds what was previously assumed for this seemingly sedentary benthic species (Kolar and Lodge 2002). Studied specimens exhibited considerable variability in migratory behaviour, partly associated with their site of hatching. This dispersal strategy, along with observed migratory capacity, likely contributed to the success and relatively rapid dispersal of tench in southern Quebec.

Tench migration capacity and population structure

Individual migration distances inferred from otolith chemistry suggests that tench, at least in the St. Lawrence, is capable of long-distance movements. Such observations contradict the previous evaluations suggesting sedentary, yet nearly inactive behaviour, of other tench populations (Cudmore and Mandrak 2011; Moyle 1976). However, our observations are in accordance with tench migratory capacity proposed in studies conducted in its native range and other invaded sites in Europe (Donnelly et al. 1998; Perrow et al. 1996). Migration, along with deliberate introductions, are thought to be the primary mechanisms explaining the

Fig. 4. Average migratory direction of southward migratory ($m > 0$), westward migratory ($m < 0$) and resident ($m = 0$) tench by capture sites. Letters indicate the results of the post hoc Tukey HSD test among sites. [Colour online.]

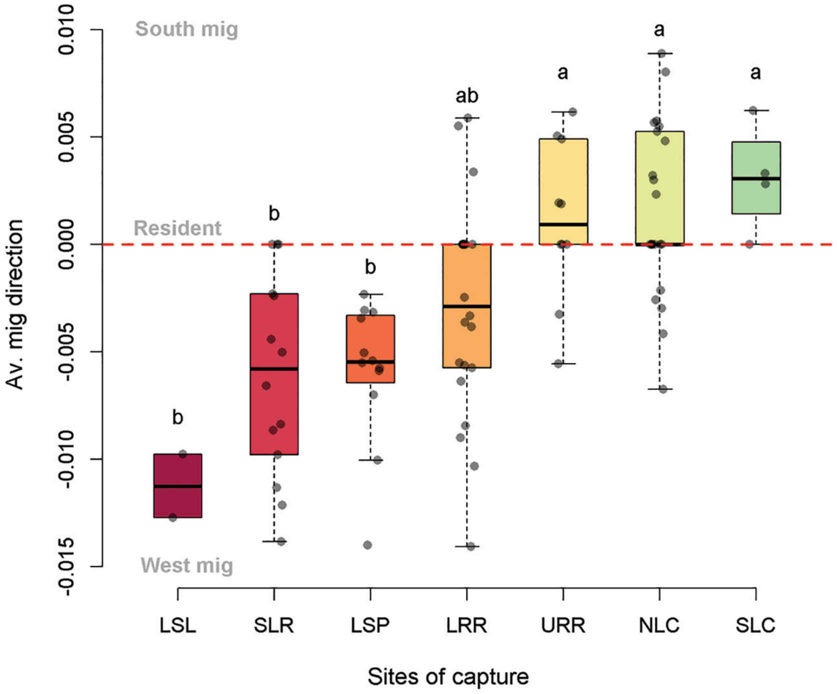
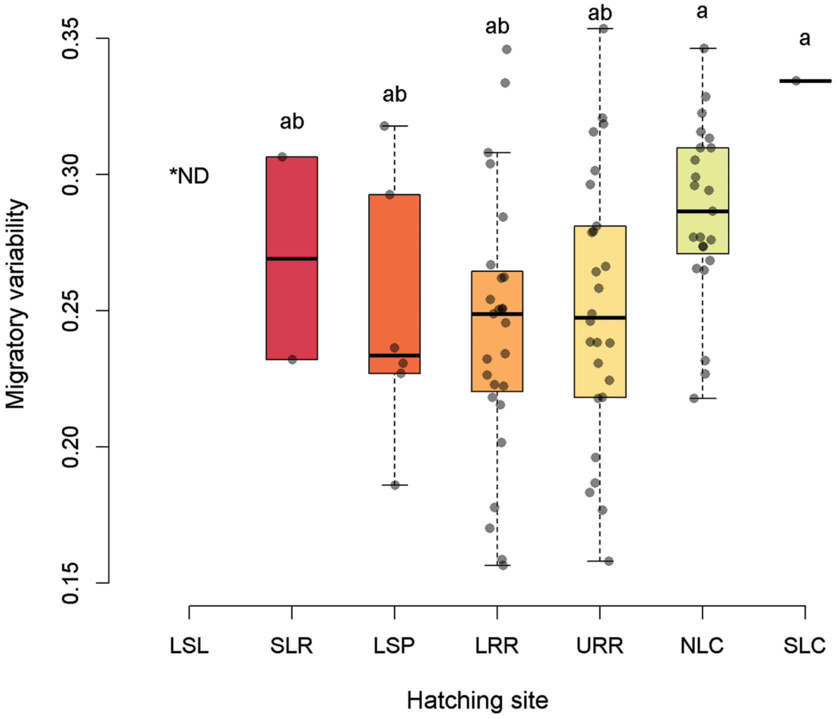


Fig. 5. Migratory variability (proxy of magnitude and frequency of migration) of captured tench by inferred hatching sites. Letters indicate the results of the post hoc Tukey HSD test among sites. *ND: no captured tench were identified as originating from Lake St. Louis (LSL). [Colour online.]



extensive distribution of tench within the Iberian Peninsula, challenging the presumption that the species is native to the region (Clavero 2019). Based on the present results, we suggest that future risk assessment should consider tench dispersal risk higher than previously assumed (Kolar and Lodge 2002). Migratory behaviours inferred from otolith chemistry are consistent with movements observed using acoustic telemetry study conducted on the same population in the St. Lawrence (J. Hill, unpublished data).

The identification of hatching sites of tench captured throughout the St. Lawrence revealed that a large proportion of individuals (31.7%) were born in the region of initial introduction (upper Richelieu River) or sites immediately adjacent (52.3%, lower Richelieu and North of Lake Champlain). Our results suggest a relatively low hatching origin from Lake St. Pierre for the 2011–2014 period, as only 7% of all specimens captured in the present study are presumed to originate from Lake St. Pierre, although 14% of our sample was actually captured in Lake St. Pierre. Interestingly, all tench captured in Lake St. Pierre have Richelieu River or Lake Champlain as their presumed hatching site. Such a result could be explained by sporadic hydrologic events, like the major flooding that occurred in the Richelieu River in 2011, that may have accelerated the dispersal of tench in the St. Lawrence River system (Masson et al. 2013) by favoring downstream movement of specimens hatched in the Richelieu River. Additionally, a 3-year-old specimen captured in the South of Lake Champlain was classified as hatched locally, suggesting that recruitment is happening in the South of Lake Champlain at least since 2013. Hence, 30 years after the original introduction, tench is still showing signs of steady dispersal throughout the system while the region where the species was first introduced remains an important spawning ground. Those results suggest that once established in a favorable habitat, tench possess a high potential of dispersal from this habitat. Hence, the core of the distribution remains important, even for highly distant populations that could appear independent. In invaded range, connectivity from site of introduction should be carefully assessed to produce appropriate risk analysis and importance of those population in maintenance of dispersal should not be eluded. On the other hand, in its native range tench may also exhibit extensive migratory behaviour from favorable habitats and its conservation, especially for threatened stocks, should then consider maintenance of connectivity from regions of high abundance as an important part of restoration plans.

The observed regional stock structure suggests that regional tench is behaving as a single entity. With the exception of recently colonized regions, such as Lake St. Louis and South of Lake Champlain, there was no dominant trend in emigration direction (westward or southward), showing that active migration is shaping the actual distribution. Taken together, our results reinforce the perspective that the downstream and upstream connectivity between and within the St. Lawrence and the Richelieu rivers are uninterrupted for tench. Despite the presence of a major dam in the lower Richelieu (St. Ours dam), the existence of a multispecific fishway at this dam (Vianney–Legendre fishway; Thiem et al. 2013) and the canals and locks system in the Richelieu River provide ample possibilities for tench to disperse without hindrance. Accordingly, a growing number of tench are observed migrating upstream at the Vianney–Legendre fishway in June since 2018 (N. Vachon, unpublished data). Tench were also removed from a stretch of the Chambly Canal near Saint-Jean-sur-Richelieu in 2019 winter and a few specimens were caught in the St. Ours lock and in the Vianney–Legendre fishway in autumn of the same year at the moment when the infrastructures were drained to perform maintenance (N. Vachon, personal communication). This observation is in accordance with the documented capacity of tench to use fishways for ascending passages (Calles and Greenberg 2007). Hence, the presence of locks along the St. Lawrence Seaway will probably not prevent future expansion of tench toward the Great Lakes region. The capture of two tench upstream of the Carillon lock and dam system (Ottawa River) in 2018 supports this assertion (MFFP, unpublished data). On a broader perspective, our results highlights that enhanced connectivity provided by navigation infrastructures (e.g., channels or navigation locks) or fish passage must be considered to realistically evaluate risks of secondary dispersion by introduced tench populations and strategically manage its expansion as an invasive species. On the other hand, our results also gives cues on how conservation efforts toward this species in its native range may take advantage of such infrastructures for providing or maintaining connectivity.

Tench dispersal: a stratified diffusion

Tench dispersal showed that groups observed in most sites were composed of a variable proportion of migrant and resident individuals. Composition could be mainly attributed to the time since first introduction at a given site, and represent a valuable proxy of their invasion status. Sites first invaded after the original introduction (i.e., >20 years) showed a higher proportion of resident individuals (lower Richelieu = 31.8%, upper Richelieu = 30.0%) compared to sites recently (i.e., 10–20 years) invaded (i.e., South of Lake Champlain = 25.0% and St. Lawrence River = 21.4%) or sites more recently colonized (Lake St. Louis and Lake St. Pierre), where no resident fish were observed. Overall, even if residency emerges once invasion is consolidated, long-distance migrants seem to be the main contributors to the biomass of invasive tench in most sites.

We propose that the pattern of tench dispersal in the St. Lawrence River is the result of a stratified diffusion strategy. This situation contrasts with a simple diffusion pattern, assumed based on previous risk assessment and presumed sedentary behaviour, where colonization of new sites occurs from adjacent habitats following stochastic density-dependent processes. Hence, stratified diffusion pattern is expected to result in a faster dispersal, higher frequency of vagrant specimens and higher retention of genetic diversity at the invasions fronts (Renault et al. 2018; Shigesada et al. 1995). This information is essential to assess the possible extent of secondary dispersal of tench in the St. Lawrence and its adjacent watersheds. As shown by previous studies, even at low frequency of an invader population, long-distance dispersal events are critical in shaping the speed of the invasion and overall dispersal capacity of the invader (Neubert and Caswell 2000; Shigesada et al. 1995).

Migratory magnitude also suggests that tench recruiting in newly invaded sites tended to make more frequent and extensive movements between sites, suggesting site-dependant intraspecific variation. Ecological and behavioural intraspecific variability has been identified in different invaders (Cerwenka et al. 2017; Chapple et al. 2012). Such phenomenon could be linked to exogenous signals (e.g., density, food availability and pheromones) favouring exploratory behaviour. It is proposed that individual traits (e.g., growth, condition, dispersal tendency or exploratory behaviour) are linked to invasion success, notably by increasing the probability of finding optimal reproductive or foraging habitat or maximizing survival (Cote et al. 2010; Russell et al. 2010). Hence, individual predisposed to dispersal behavior (Renault et al. 2018) could transmit their genetic background by spatial sorting and assortative mating (Shine et al. 2011), promoting both phenotypic and genetic variations among the invasion front and the core of the distribution (Laparie et al. 2013; Messager and Olden 2019) ultimately favouring preservation or further dispersal behaviour in some individuals. Although this test is well outside the scope of this study, it represents an interesting avenue to further develop the field of invasion biology.

Contributions to tench management

From a management standpoint, the species' migratory capacity and potential to colonize new habitat suggests that expansion toward the Great Lakes (Avlijaš et al. 2018) is plausible in the short term as new propagules do not require the presence of a high-density population in close vicinity. Such an assertion is in agreement with the recent capture of one tench in the Bay of Quinte (Lake Ontario, 2018). Whereas recruitment in Lake St. Pierre was probably not important prior to 2013–2014, recent commercial fishing creel surveys show that abundance in this region is likely increasing (P. Brodeur, personal communication, 2020), risking exacerbating its ecological and socio-economic impacts. However, tench impacts on freshwater ecosystems and fish communities are still not well assessed or understood. In its native range, tench presence seems to result in niche partitioning with common carp (Britton et al. 2018), generating a reorganisation of the littoral–benthic trophic network. This apparent competition and its cascading effects are likely to occur in the St. Lawrence River where common carp is locally abundant (Monette et al. 2006) and littoral fish community structure is already impacted by the presence of the invasive round goby (*Neogobius melanostomus*) (Morissette et al. 2018). In addition to the overall impact on the ecosystem, questions remain on the impacts tench will have on the endangered endemic copper redhorse (*Moxostoma hubbsi*) that shares the same habitats (Équipe de rétablissement du chevalier cuivré du Québec 2012; McAllister 2001; Mongeau et al. 1992).

The findings of our study have direct application in tench population mitigation and control in an attempt to preserve the local biodiversity and maintain the associated fishing industry, both recreational and commercial. The identification of a stratified diffusion strategy for tench implies that long-distance migrants can originate from any site with local recruitment and could be from any adult-sized fish class. Thus, removal of individuals from any size class from any known aggregation site could be useful for mitigating long-distance dispersal. In the present case, efforts directed toward high-density areas where removal efforts are optimized (i.e., highest CPUE) may be favoured compared to concentrating effort at sites located at the colonization front.

The unique contributions of otolith chemistry for AIS management

This study demonstrates that otolith chemistry can provide valuable and accurate data for understanding the dispersal and population dynamics of AIS even at early stages of invasion when other approaches commonly used (i.e., genetics, telemetry or fisheries surveys) are not suitable or require onerous logistics (e.g., telemetry receivers, mark-recapture, marker development). Complementary use could also provide a new layer of information when those approaches are combined, by example delineating observed migration (with otolith chemistry) and genetic population structure in the invaded range. Our experience shows that otolith chemistry has been successfully used to foresee ecology phenomenon before being validated through field-based observations. For example, otolith chemistry have been instrumental, among others, in the identification of the invasive common carp recruitment hotspots in Australia, guiding subsequent control efforts (Crook et al. 2013; MacDonald et al. 2010) or documenting colonisation route of the introduced Chinook salmon (*Oncorhynchus tshawytscha*) in Patagonia (Araya et al. 2014). Finally, the inert chemical nature of otolith (Patterson 1998; Vanhove et al. 2011) and the widespread availability of historic samples through institutional collections are all advantages that could be exploited to document the dynamics of invasive species during their initial stages of invasion.

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