UNIVERSITÉ DU QUÉBEC

# DES LARVES AUX ADULTES : EFFETS DE LA VÉGÉTATION AQUATIQUE ET DE LA QUALITÉ DE L'EAU SUR L'ABONDANCE DE LA PERCHAUDE DANS LE LAC SAINT-PIERRE (FLEUVE SAINT-LAURENT)

# FROM LARVAE TO ADULTS: THE EFFECT OF AQUATIC VEGETATION AND WATER QUALITY ON THE YELLOW PERCH ABUNDANCE IN THE LAKE SAINT-PIERRE (ST. LAWRENCE RIVER)

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*Ai miei cari, in particolare a mamma Milva, papá Angelo, a Marco e alla nonna Norma. Vi ringrazio dal profondo del cuore per la fiducia, il sostegno ed il conforto nei momenti piú bui. Vi devo tutto, anzi di piú. Questa tesi é per voi, perché é stato un percorso mio quanto vostro.*

*Grazie*

*No aphorism is more frequently repeated in connection with field trials, than that we must ask Nature few questions, or, ideally, one question, at a time. The writer is convinced that this view is wholly mistaken. Nature, he suggests, will best respond to a logical and carefully thought out questionnaire; indeed, if we ask her a single question, she will often refuse to answer until some other topic has been discussed.*

Sir Ronald Fisher (1926)

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# PREFACE

The main objective of this dissertation is to shed light on the decline of the yellow perch population of the Lake Saint-Pierre, and on the co-occurring degradation of aquatic vegetation beds. The chapters I, II and III of this thesis are presented as scientific articles. The analyses presented in these three chapters are based on data collected in the Lake Saint-Pierre, from its watershed, and from satellite imagery. Fish and environmental data collected in the Lake Saint-Pierre are the fruit of a jointed effort of many researchers from Ministère des Forêts, de la Faune et des Parcs (MFFP) and Université du Québec à Trois-Rivières (UQTR). I had the great opportunity to work with long-term time series, a mine of information as well as a true statistical challenge. Though, my scientific work has been greatly improved by integrating pre-collected data, and I am grateful to all the people actively working on sampling and sorting these data. Noteworthy, I had the very precious opportunity to participate to several standardized sampling surveys performed by the MFFP on the Lake Saint-Pierre. The work in the field is still fundamental for the modern ecologist: despite statistical computational skills are nowadays necessary, a strict contact with the environment is compulsory to a deep understanding of natural processes, biotic interactions, and geophysical forces.

All the material presented in this thesis, as well as the articles in preparation or already published, are the result of my personal work, with the support of my directors and the contribution of co-authors, who had a crucial role improving the quality of the manuscripts. I thus confirm my major implication in conceiving ideas, data analysis and writing of the original manuscripts, integrating suggestions, comments and revisions from my co-directors and co-authors following the process of manuscript revision. These three scientific articles are, or will be, submitted to scientific journals with peer review. The first chapter is published in *Science of the Total Environment*, the second is submitted to *Limnology and Oceanography*, and the third will be submitted to *Hydrobiologia*.

# RÉSUMÉ

Le déclin rapide et abrupt des populations de poissons exploitées à des fins commerciales est toujours à considérer comme un avertissement alarmant, présage d'un possible effondrement. Les populations assujetties aux fortes pressions anthropiques sont plus sensibles aux phénomènes naturels stochastiques, car elles se retrouvent déjà dans des conditions de stress chronique. Au lac Saint-Pierre, le plus grand lac fluvial du fleuve Saint Laurent, la population de perchaudes (*Perca flavescens*) a subi une très forte réduction de son abondance dans le milieu des années 1990, menant à des inquiétudes sur l'état de santé de cette population. À la suite de restrictions règlementaires pêche sur les prélèvements des pêches commerciales et récréative, et d'un moratoire complet sur toutes formes de pêche en 2012, la population n'a encore montré aucun signe de rétablissement, suggérant que le phénomène n'était pas seulement causé par la pêche.

L'objectif de la thèse est de comprendre les facteurs impliqués dans l'absence de rétablissement du stock de perchaudes après son effondrement, en dépit des mesures prises pour en limiter l'exploitation. Les hypothèses les plus probables sont la dégradation de l'habitat et le faible taux de recrutement, ce dernier étant probablement associé à une faible survie des jeunes perchaudes. Des études préliminaires avaient également constaté que l'abondance de la végétation aquatique submergée était en réduction dans certaines régions du lac. La détérioration de la qualité de l'eau, associée à l'augmentation des charges en nutriments, en pesticides et en matières en suspension, est un autre élément préoccupant au lac Saint-Pierre. Sur la base de ces observations, cette thèse vise spécifiquement à aborder la relation entre la qualité de l'eau, la végétation aquatique submergée, la population de perchaudes ainsi que la communauté de poissons du lac Saint-Pierre. L'objet de cette thèse demeure complexe en raison de l'interaction entre la dynamique de la population de perchaude et plusieurs facteurs environnementaux en constant changement, autant spatialement que temporellement. En effet, comme nous ne connaissons pas les classes d'âge qui pourraient être critiques pour la survie de l'espèce, le rôle qu'a pu jouer la disparition des herbiers dans l'effondrement de la population de

perchaudes et les variables environnementales qui pourraient interagir avec chaque stade de développement, cet objectif représente un défi important.

Le lac Saint-Pierre est un système complexe, où plusieurs pressions anthropiques interagissent entre elles. Son bassin versant draine une très grande région agricole (la plus grande et intensément cultivée du Québec), faisant en sorte que des quantités importantes de nutriments (principalement du phosphore et de l'azote) et de sédiments sont apportées dans le lac. Ce phénomène a contribué à l'enrichissement en nutriments dans l'eau ainsi qu'à une augmentation de la turbidité, surtout à cause de l'apport sédimentaire. De plus, ces apports ne sont pas constants pendant la saison (p. ex. érosion importante et fort apport de matière minérale pendant la fonte de neige), ce qui fait que la qualité de l'eau du lac Saint-Pierre se présente sous forme d'une mosaïque qui varie dans le temps et dans l'espace. Ce phénomène est exacerbé par une grande quantité de tributaires, chacun ayant ses propres propriétés physico-chimiques (transparence, contaminants, pesticides, nutriments, etc.).

Un premier chapitre s'est donc penché sur l'effet de la qualité de l'eau (propriétés optiques et concentration en nutriments) sur l'abondance de la végétation aquatique submergée. Les variations de plusieurs variables clés de l'écosystème du lac Saint-Pierre à partir des années 1980, notamment la charge en phosphore, en azote, en matières en suspension, la turbidité, les niveaux d'eau et la température, ont d'abord été évaluées en modélisant les apports des tributaires qui drainent le bassin versant. La reconstruction de l'abondance de la végétation aquatique à partir de 1960 à l'aide d'imagerie satellitaire a ensuite été réalisée dans le but d'analyser son évolution temporelle en relation avec les variables environnementales. Une forte augmentation de la végétation aquatique submergée a été constatée entre les années 1960 et 1980, probablement à cause de l'utilisation massive d'engrais par l'agriculture, suivie d'une période de stagnation. Une diminution a ensuite été observée à partir des années 1990, possiblement causée par une augmentation de la turbidité, due à l'apport sédimentaire provenant de l'érosion des terres agricoles labourées. À l'aide d'un système d'équations structurelles, les liens causals entre les apports provenant du bassin versant, l'abondance de la végétation aquatique et le stock de perchaudes (croissance des juvéniles et débarquements à la pêche commerciale) ont été déterminés. Les résultats suggèrent que la charge en phosphore s'avère être une variable importante favorisant le développement de la végétation aquatique, alors que la matière en suspension semble conduire à une réduction de l'abondance de la végétation sur le long terme. Une réduction de la végétation aquatique entraînerait à son tour une diminution du stock de perchaudes, tel qu'observée par une baisse dans les débarquements commerciaux. Les débarquements seraient également dépendant de la croissance de jeunes perchaudes, qui se trouve être plus faible à la suite de l'augmentation de la turbidité et des niveaux d'eau. Tous ces constats suggèrent que la dégradation de la qualité de l'eau est une cause commune de la diminution de la population de perchaudes et de la végétation aquatique. Le premier chapitre de cette thèse a donc permis de décrire la complexité des relations impliquées dans le déclin de la perchaude en lien avec la disparition des herbiers et la dégradation de la qualité de l'eau.

Le recrutement des jeunes perchaudes est par ailleurs une autre étape clef dans la compréhension de la dynamique du stock de perchaudes. Des études préliminaires ont en effet suggéré que des réductions dans le recrutement mènent à un vieillissement de la population et à des diminutions d'abondance du stock. Malgré l'absence de données visant à estimer explicitement la force des cohortes, l'étude du stade de vie larvaire de la perchaude, un des plus délicats en ce qui concerne la survie, le recrutement et l'abondance des adultes, a donc été réalisée. Au lac Saint-Pierre, les larves de perchaude sont soumises à une grande variété de stress, tels que les charges en pesticides, de fortes augmentations transitoires de turbidité et de matières en suspension, ainsi que le rayonnement UV. Étant donné que les larves de perchaude, transparentes et peu pigmentées, montrent un comportement de phototropisme positif pendant les premières semaines de vie que le lac est très peu profond et qu'il fournit peu d'abris contre la lumière incidente, il semblerait que les radiations UV puissent être impliquées dans la mortalité des larves. Même s'il est établi qu'il est de moindre importance par rapport aux processus écologiques comme la prédation et la compétition, l'effet du rayonnement UV pourrait constituer une pression supplémentaire sur la survie des larves d'une population déjà en péril. Notre objectif a donc été d'évaluer à la fois la capacité des larves à se déplacer dans la colonne d'eau afin

d'éviter le risque causé par les rayons UV, tout en tenant compte des propriétés optiques et structurelles de la colonne d'eau qui pourraient atténuer la pénétration de la lumière. Le risque du rayonnement UV a donc été évalué sur la base de la quantité et de la qualité de la lumière incidente, pondérée par la couleur de l'eau (fonction, entre autres de la matière en suspension, du carbone dissous), en incluant 'l'effet abris' fourni par la végétation aquatique au printemps. Les résultats ont montré que la distribution de larves de perchaude n'est pas aléatoire, avec des abondances plus élevées dans les filets profonds au sein d'une même station d'échantillonnage et dans l'isobathe la plus profonde. Bien qu'il n'y ait pas d'effet significatif du rayonnement UV sur l'abondance des larves, les résultats ont indiqué que ces dernières sont capables de se déplacer et semblent sélectionner les zones végétalisées. Un effet positif de la lumière visible sur l'abondance des larves a pu être constaté, indiquant une tendance à choisir des couches d'eau bien illuminées, ce qui pourrait faciliter la prédation du plancton. Ce résultat a par ailleurs été supporté par la relation négative entre la turbidité et l'abondance des larves dans les filets profonds, ce qui suggère une fois de plus que les larves de perchaude recherchent des couches d'eau bien éclairées. Enfin, un effet positif de la turbidité sur l'abondance des larves dans l'isobathe moins profonde a été remarqué, soutenant l'hypothèse que la mortalité causée par le rayonnement UV pourrait être atténuée quand celui-ci est réduit à cause de la turbidité.

Au niveau de la communauté, les changements d'abondance de végétation aquatique submergée et de turbidité devraient avoir un effet sur la composition et l'abondance des espèces de poissons. L'augmentation de végétation aquatique submergée devrait entrainer une augmentation de l'abondance, de la diversité et de la richesse en espèces de poissons qui ont besoin de sites végétalisés pour leur cycle vital. En revanche, la turbidité devrait avoir un effet inverse sur l'abondance et la diversité des espèces phytophiles et visuelles, et pourrait induire un décalage vers une plus grande abondance d'espèces adaptées à des milieux plus troubles. Les résultats ont révélé un effet significatif de l'abondance de la végétation aquatique sur l'abondance des poissons et sur la richesse en espèces. La végétation aquatique offrirait une source d'invertébrés et un abri contre la prédation, ce qui est fondamental pour la croissance et la survie des individus, surtout pour les jeunes de l'année. La végétation aquatique submergée a une fois de plus été confirmée comme variable importante de l'habitat pour la plupart des espèces de poissons du lac Saint-Pierre. Un effet négatif de la turbidité sur l'abondance de poissons ainsi qu'un effet positif sur la diversité et la richesse en espèces ont également été constatés. L'effet négatif de la turbidité est possiblement le résultat d'un phénomène de prédation plus intense dans les eaux turbides. Ce phénomène pourrait par la suite diminuer la compétition interspécifique, permettant la cohabitation de plusieurs espèces, même des compétiteurs plus faibles qui seraient normalement délogés, supportant ainsi la relation positive entre turbidité et, respectivement, richesse et diversité.

En conclusion, la population de perchaudes du lac Saint-Pierre est soumise à plusieurs menaces qui la rendent vulnérable. Cette thèse a d'abord examiné les effets de la dégradation de la qualité de l'eau, causée par des apports de nutriments et de sédiments du bassin versant, et de la disparition de la végétation aquatique submergée sur différents stades de développement de la perchaude. Elle a également montré que les larves et juvéniles de perchaudes, primordiales pour le maintien et l'équilibre de la population, sont soumises à plusieurs facteurs de stress comme la perte d'herbiers aquatiques, la turbidité, et les radiations solaires, qui pourraient menacer fortement le recrutement. Par ailleurs, les mêmes variables délétères pour la population de la perchaude affectent négativement plusieurs autres espèces de la communauté de poissons du lac Saint-Pierre.

Le travail réalisé dans le cadre de cette thèse a permis d'apporter une meilleure compréhension des phénomènes écologiques impliqués dans l'absence de reprise du stock de perchaudes, en dépit des mesures prises pour en favoriser le rétablissement. Ces résultats fourniront des informations cruciales pour la réhabilitation de cet écosystème, constitué non seulement du lac Saint-Pierre lui-même, mais de son bassin versant, qui représentent un continuum fonctionnel intégré.

**Mots-clés :** végétation aquatique submergée, perchaude, interactions bassin versant – écosystèmes aquatiques, dégradation de l'habitat, qualité de l'eau, turbidité.

# ABSTRACT

The marked and rapid decline of a commercially exploited fish population is always an alarming warning, presage of a possible collapse. The causes behind fish stocks depletion are often ascribable to habitat degradation and to overexploitation. Here, we address the case study of the yellow perch in the Lake Saint-Pierre, the largest fluvial lake of the St. Lawrence River (Québec, Canada). Lake Saint-Pierre drains one of the most impacted watersheds in Eastern Canada and had sustained a yellow perch fishery (worth up to 10 M$ CAN/year) until the population collapsed in the mid-1990s. In 2012, a complete moratorium on both the commercial and recreational fishing has been applied, but nevertheless the yellow perch population has not recovered yet. In this dissertation, we explicitly analyzed factors that might have been involved in the decline and lack of recovery of this yellow perch stock, assessing the potential links between anthropogenic stressors, environmental variables, and the fish community.

In Chapter I, we reconstructed the long-term change in key variables (nitrogen, phosphorous, suspended solids concentrations, and turbidity) structuring the Lake Saint-Pierre ecosystem. Submerged aquatic vegetation abundance showed an increase in abundance from 1960 to mid-1980s, probably due to the corresponding intensification of agricultural practices in the watershed of the Lake Saint-Pierre, leading to an increased nutrient discharge into the lake. The increase in submerged aquatic vegetation abundance was followed by a plateau, to finally decrease around the mid-1990s, partially overlapping with the yellow perch collapse. Using a structural equation modelling framework, we tested the links between submerged aquatic vegetation abundance, the yellow perch fishery (yield and age 1+ growth) and abiotic variables related to water quality. Our results spanning 18 years showed that submerged aquatic vegetation abundance and the yellow perch declines are causally dependent from anthropogenic nutrients and sediment loadings from the watershed. The sharp decrease in water transparency over the last decades is the main cause of submerged aquatic vegetation loss, which in turn explained the decline of yellow perch landings and to a

lesser extent, juveniles' growth. These results suggest a causal association between environmental degradation due to nutrients and sediments loading, aquatic vegetation loss and the yellow perch fishery.

In Chapter II, we evaluated the factors involved in the yellow perch larvae distribution across the lake. The larval stage is particularly critical for population dynamics, often being a bottleneck due to the high mortality risk, determining the strength of recruitment. Here, we focused on the effects of UV radiation and visible light penetration in the water column, mitigated by the water optical properties and by the presence of aquatic vegetation. Yellow perch larvae are among the smallest freshwater larvae, they are pelagic and poorly pigmented. UV radiation is known to induce lethal and sublethal effects for aquatic biota and might represent an additional source of mortality for the yellow perch population, which is already endangered. Despite visible light is not dangerous for aquatic life, these radiations have the potential to shape larvae distribution by modulating their position in the water column (phototropic behaviour), and possibly affecting their survival. Surprisingly, we found that larvae were always aggregated in the lower part of the water column especially in presence of both emerged and submerged aquatic vegetation. Although no effect of UV radiation on larvae distribution was detected, we found a positive relationship between larvae abundance and visible light radiation. Turbidity was found to modulate larvae abundance depending on the isobath, allowing a higher proportion of larvae to occur in shallow turbid (low UV risk) waters. These results confirmed the yellow perch preference for vegetated habitats and suggested a role of light penetration in driving yellow perch larvae taxis behaviour.

Facing a scenario of submerged aquatic vegetation loss and increased levels of turbidity during the last 30 years, an effect on fish species composition and abundance is expected. In Chapter III, we quantified the association among dominant fish species in the community, along a gradient of submerged aquatic vegetation and turbidity. We found that phytophile species were more likely associated to submerged aquatic vegetation and negatively associated to turbidity in summer habitats, compared to non-phytophile species. At the community level, submerged aquatic vegetation was positively associated

with species abundance, richness, and diversity. Turbidity was negatively related to abundance (likely because higher predation in turbid waters) and positively related to species richness and diversity, possibly because of a reduced interspecific competition due to predation. These results confirmed the importance of the submerged aquatic vegetation and turbidity as counteracting variables, structuring fish distribution in the Lake Saint-Pierre. Given the global trend of increase in turbidity and loss of aquatic vegetation, quantifying the association between fish species and habitat features might help to understand mechanisms structuring fish communities and to forecast changes in the fish community structure.

Throughout this thesis, we identified the causes of habitat degradation in the Lake Saint-Pierre and their effects on the yellow perch and on the fish community. The most concerning trends are the loss of submerged aquatic vegetation and the increase in turbidity, which have been found to affect all the ontogenetic stages of yellow perch as well as the fish community. Therefore, to allow the recovery of the yellow perch and to sustain many other fish species, it will be imperative to reduce sediments and nutrients discharges to the Lake Saint-Pierre, to favour a reduction in turbidity and the recovery of submerged aquatic vegetation.

**Keywords:** submerged aquatic vegetation, yellow perch, watershed aquatic ecosystem, habitat degradation, turbidity

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INTRODUCTION

GENERAL DISCUSSION

# INTRODUCTION

## Anthropogenic stressors, water quality degradation, and the danger of regime shifts

Human civilization has always been linked to the water, using rivers and watersheds for resources, energy, and transportation (Gleick 2003). Therefore, exploitation and pollution of waterways are old as humanity. Nevertheless, after the Industrial Revolution, the development of technology and the increase in human population have exacerbated the magnitude of the anthropic impact (Gleick 2003). Freshwater ecosystems face major anthropogenic stressors threatening their integrity. For instance, sewage treatment plants discharge their waste waters into freshwater ecosystems, pesticides and fertilizers used in agriculture leach into the soil, ditches and rivers, and many freshwater bodies are exposed to fishing/overfishing (Brinson and Malvárez, 2002; Barbier et al., 2011). In watersheds dominated by agriculture, land-water interactions are particularly deleterious for aquatic ecosystems. High concentrations of sediments and nutrients are brought to rivers and lakes mainly by runoff from intensively cultivated areas (Foley et al., 2005). Sediment runoff is primarily caused by soil labour (García-Ruiz et al. 2015), and to the scarce soil retention capacity of poorly rooted annual crops. These contributions to freshwaters have a high-polluting potential, affecting water optical properties (i.e., the light environment) and altering the trophic status, eventually leading to eutrophication. Such changes in water quality might trigger regime shifts when critical thresholds are exceeded (Scheffer et al., 1993; Scheffer and van Nes, 2007; Capon et al., 2015; Hilt et al., 2018). One of the most undesirable scenarios in shallow waters is the switch from a clear-water state dominated by submerged aquatic vegetation (hereafter SAV) in favour of a turbid state in which SAV is outcompeted by phytoplankton/periphyton because of light limitations (Sand-Jensen and Borum, 1991; Scheffer et al., 1993; Hidding et al., 2016; Hilt et al., 2018). Such a trophic switch (which might be gradual, but most often abrupt, Hilt et al., 2011; Phillips et al., 2016) is not desirable, because it is associated with a loss of fundamental ecosystem services like water depuration, fish habitat and nurseries, as well as physical protection for the shore (Lefcheck et al., 2018). For instance, in the clear-water regime of shallow lakes, extensive beds of macrophytes act stabilizing sediments, reducing phosphorus availability to phytoplankton (Jeppesen et al. 1999). When phosphorus concentrations increase (e.g., because of agricultural fertilizers use), phytoplankton can be competitively advantaged, growing at the point of shading SAV beds, leading them to important biomass loss due to light limitations for photosynthesis (Scheffer et al., 1993). In such a situation, benthivorous fish species might increase their abundance boosted by nutrient enrichment, damaging rooted macrophytes and resuspending sediments (Folke et al., 2004). In cases of extensive aquatic vegetation loss, sediments are less consolidated and more easily resuspended, increasing phosphorous recycling. Phosphorous availability favours phytoplankton growth and consequently a more turbid regime (Folke et al., 2004). This positive feedback might lead to a stable turbid state. Reverting to the clear-water regime is a hard task, requiring the reduction in nutrient inputs and eventually the removal of benthivorous fish, but still the turbid regime might be resilient (Folke et al., 2004). Compelling examples of ecosystem bimodality that have been seminal for the development of the regime shift theory are represented by the Swedish lakes Takern and Krankesjön, in which periods of clear water and abundant aquatic vegetation have alternated with periods of rare vegetation and turbid waters (Blindow et al., 1992, Scheffer et al., 1993). Many examples of important aquatic vegetation loss exist in the literature, as it is the case for many lakes in Denmark (Sand-Jensen et al., 2000), Sweden (Blindow, 1992), Germany (Körner et al., 2002), Alberta (Jackson et al., 2003) and the USA (Lefcheck et al., 2017). However, a loss of SAV itself is not necessarily a sign of an incoming regime shift, despite the fact that it should be perceived as a prodrome of a future potential ecosystem change. Evaluating the trophic level of the ecosystem in relation with SAV loss and water quality is fundamental to forecast eventual regime shifts.

## Habitat degradation and trophic webs

In an ecosystem, biotic and abiotic compartments are in strict connection. It is not surprising that a change in water physicochemical properties could affect SAV abundance, inducing changes in invertebrate and fish species community composition. For instance, in Cootes Paradise March (Ontario, Canada), a decrease in water clarity and augmentations in nutrients concentrations due to sewage effluent pollution, induced a marked decline in macrophyte species diversity and coverage, which resulted in long-term changes in planktonic, benthic and fish community composition, leading to a successional change (Chow-Fraser et al., 1998). Noteworthy, once a treatment plant was put in place, phosphorous concentration dropped tenfold, but no increase in water clarity was detected, suggesting the presence of a stable, resilient state. Other studies showed that a reduction in SAV abundance induced a decline in benthic invertebrate species (e.g., Caires et al., 2013; Whatley et al., 2014) and changes in fish species relative abundance (Sheppard et al., 2011). In New Zealand lakes that undergone regime shifts towards turbid states and macrophytes loss, the trophic network has been found to be affected, both at the level of the food chain length and food web complexity (Kelly and Schallenberg, 2019).

The aim of this section was to report few examples showing the huge cascade potential induced by physicochemical water parameter changes, which can have repercussions at different trophic levels, if not at the extent of the whole trophic web, potentially triggering a stable change in community assemblages.

## Context and thesis objectives

The scientific work reported in this dissertation origins from the observation that the Lake Saint-Pierre (LSP) underwent major environmental changes during the last decades. The yellow perch (YP, *Perca flavescens*) population abruptly declined in the mid-1990s (Magnan et al., 2004), water quality decreased (especially due to increased turbidity levels), and SAV beds seemed to have decreased in abundance, apparently in favour of cyanobacteria mats (Vis et al., 2008; Hudon et al., 2012; Hudon et al., 2018). These observations raised concern about the stability of the ecosystem and on the potential for a regime shift.

The LSP is the largest fluvial lake ($\approx 400$ km$^2$) of the St. Lawrence River (Fig. 1). It is shallow (mean depth = 3.5 m, except for an artificial navigation channel with depth > 11 m), it lacks a true pelagic area, and has a relatively slow current ($< 0.5$ m $\times$ s$^{-1}$)

(Hudon and Carignan, 2008). Its floodplain covers approximately 14 000 ha during 5-9 weeks of the spring freshet, representing an important spawning ground for YP (Bertolo et al., 2012). The LSP is characterized by distinct water masses flowing parallel to the main channel through the entire length of the system (Frenette et al., 2012). The LSP receives water from several tributaries, each one being characterized by different physical and biogeochemical features (Frenette et al., 2003). For instance, tributaries from the south shore drains a highly cultivated area and carry high inputs of nutrients, sediments, and contaminants, while tributaries from the north shore are less polluted (Simoneau, 2017). The LSP shorelines are gently sloping, forming large, sheltered bays, supporting large emergent marshes and extensive SAV beds (Hudon 1997). In summer, SAV is very abundant (although very patchy), covering about the 85% of the lake area (260 km$^2$) (Vis et al., 2008), often occupying the whole water column and forming a canopy at the surface (Hudon et al., 2012). The most abundant submerged species are American eel-grass (*Vallisneria americana*) and pondweeds (*Potamogeton richardsonii* and *Stuckenia pectinata*), whereas emergent vegetation is mainly represented by bulrushes (*Schoenoplectus fluviatilis*, *S. lacustris*, and *S. pungens*), broadfruited bur-reed (*Sparganium eurycarpum*), and broad-leaved arrow-leaf (*Sagittaria latifolia*) (Massicotte et al., 2015). The fish community counts about 80 species (Laviolette et al., 2003).

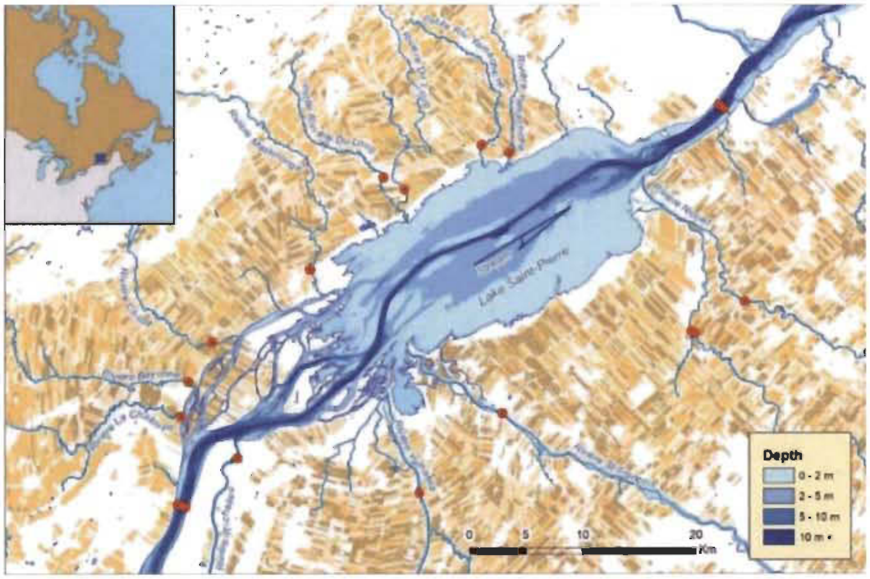

**Fig. 1.** Lake Saint-Pierre (LSP), its watershed and major tributaries, and the surrounding agricultural regions. Orange dots represent water quality survey stations.

Between the 1960s and mid-1990s, the LSP had supported an important commercial fishery (Magnin, 1966). The most important fish species was the YP (Mailhot et al., 2015), worth up to 10M$ CAN/year (estimate for the mid-1980s). However, the population started to decline in the mid-1990s, shedding concern on the stability of the population, and presaging an imminent collapse (Fig. 2). Despite major reductions in the commercial fishing effort between 1997 and 2008, mainly through fisher license buybacks, followed by an increase of the minimum legal length for collection, and the application of a complete moratorium on both the commercial and recreational fisheries in 2012, the YP population has not yet recovered (Mailhot et al., 2015).

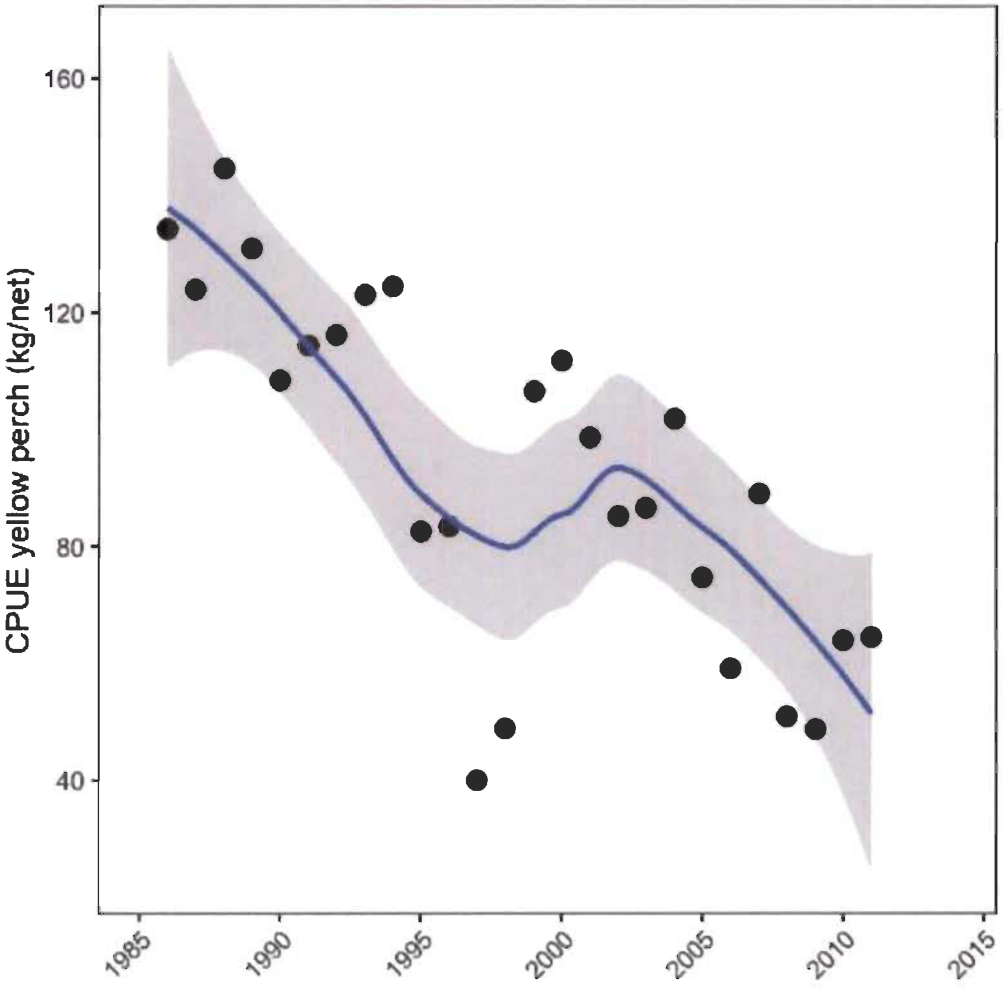

**Fig. 2.** Yellow perch commercial landings expressed as catch per unit effort (CPUE).

The scientific work reported in this thesis aims to shed light on the factors involved in the decline and lack of recovery of the YP population in the LSP, after the application of several measures to reduce the fishing effort culminating with the moratorium. The principal axis of this thesis is based on the relationships between water quality, SAV, the YP, and the fish community. Whereas the LSP is clearly undergoing changes in water and habitat quality, a quantitative assessment of these trends is lacking. Therefore, our first aim is to evaluate the long-term temporal changes of several key environmental variables such as water optical properties (e.g., turbidity), nutrient concentrations, and SAV biomass. Given that measures for these variables are fragmentary or absent for the LSP, we integrated data from the watershed tributaries to calculate the discharge of sediments and nutrients into the lake and we reconstructed the SAV abundance by using remote sensing and back calculation.

In Chapter I, our objective is to evaluate the effect of nutrients and sediments inputs from the watersheds on SAV biomass and on the YP population. To model these complex relationships, we will implement a network model based on a priori knowledge of the system to estimate the links of causality between variables and the strength of these relationships. The idea is to depict the cascade effects within the network, disentangling the direct and indirect relative contribution of each variable on another. We hypothesize a direct negative effect of sediments and excessive nutrient concentrations on the SAV abundance. In turn, a reduction in SAV abundance is expected to negatively affect YP commercial landings, both directly by providing a lower quality habitat for adults, and indirectly by affecting the juvenile's growth, delaying the attainment of the legal length for collection.

In Chapter II, we will specifically focus on YP larvae as a critical mortality ontogenetic stage. YP larvae are among the smallest freshwater fish larvae, highly exposed to predation and therefore might represent a vulnerable stage for population dynamics, determining the strength of recruited cohorts. UV radiation risk might simply represent an additional term of stochasticity, affecting the recruitment for a healthy population, but might be a rather severe stressor for a population already declining. In this chapter, we aim to address the link between larvae distribution, underwater light environment, and aquatic vegetation. YP larvae are positively phototactic but unpigmented, and therefore ultraviolet radiation might be particularly detrimental, inducing lethal and sub-lethal effects. The interplay between UV irradiance, water properties, and habitat features mitigating light penetration, will be used to determine the overall UV risk for larvae. We will evaluate how spatial variation in the water optical properties and in the vegetation abundance (this latter providing a shelter from UV radiation) affect YP larvae distribution.

In Chapter III, we will evaluate how turbidity and SAV abundance influence fish species distribution across the LSP. Given the different habitat optimum of each species, differences in habitat quality and availability (e.g., turbidity and SAV abundance) should mirror a change in species relative abundance. We expect visual and phytophile species (e.g., YP and pike) to be less abundant in degraded sites, leading to an increase in chemo-sensorial and/or non-visual species (e.g., sturgeon and channel catfish). We also expect turbidity and SAV abundance to structure the fish community, affecting species richness, diversity, and their abundance. Our objective is to quantify the association between species and environmental variables, to predict fish species relative abundance change in a scenario of further turbidity augmentation and SAV loss.

Throughout this dissertation, we describe key phenomena the LSP underwent during the last 30 years, by using an integrative approach considering cultivated lands and the LSP aquatic ecosystem as a continuum rather than separate compartments. We provide information on mechanisms behind water quality degradation, and SAV and YP decline, and on the way they interplay. We investigate the relationship between habitat attributes and the YP at different ontogenetic stages (larvae, juveniles, and adults), as well at the level of the fish community. The content of this thesis provides relevant information to practitioners in their attempt to rehabilitate SAV beds and the YP population.

# CHAPTER I

# LINKING FISHERIES TO LAND USE: HOW ANTHROPOGENIC INPUTS FROM THE WATERSHED SHAPE FISH HABITAT QUALITY

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## Author contributions

Giacomazzo M., Bertolo A., Magnan P., Brodeur P. conceived the idea. Brodeur P. provided data. Massicotte P. pre-treated satellite pictures. Giacomazzo M. performed statistical analyses. All authors contributed critically to the manuscript and gave final approval for publication.

## Abstract

Aquatic ecosystems are increasingly threatened by anthropogenic stressors, both at local and larger scales. For instance, runoff from intensively cultivated areas leads to higher nutrient and sediment concentrations deteriorating water quality, which potentially trigger trophic state changes. Unfortunately, we have a poor understanding of the complex relationships linking water quality degradation and different ecosystem components. Here we analyze the long-term cascading effects of several anthropogenic stressors on both submerged aquatic vegetation (SAV) and the key traits of an exploited yellow perch (*Perca flavescens*, YP) population from the watershed of Lake Saint-Pierre – the largest fluvial lake of the St. Lawrence River (Québec, Canada). Lake Saint-Pierre drains one of the most impacted watersheds in Eastern Canada and had sustained a YP fishery (worth up to 10 M$ CAN/year) until the population collapsed in the mid-1990s. SAV abundance has declined since the 1980s, partially overlapping with the YP collapse. Within a structural equation modeling framework, we tested the links between changes in both SAV abundance and the YP fishery with abiotic stressors acting at both local and larger scales. Our results show that both SAV and YP declines are causally associated with anthropogenic nutrient and sediment loadings from the watershed. The decline of YP landings is also explained by a reduction in SAV abundance and YP juvenile growth, mainly caused by a sharp decrease in water transparency over the last decades. These results suggest a causal association between environmental degradation due to nutrients and sediments and different components of the trophic aquatic network. Such an integrative approach is crucial for the development of management strategies that consider cultivated lands and aquatic systems as a continuum rather than separate compartments. SAV restoration is thus a critical feature contributing to water depuration and promoting the recovery of fish populations threatened by habitat degradation.

**Keywords:** watershed-aquatic ecosystem interactions, yellow perch, piecewise SEM, anthropogenic stress, fisheries management, submerged aquatic vegetation

## Introduction

Freshwater ecosystems face major anthropogenic stressors threatening their integrity, such as water level drawdowns, pollution, habitat degradation, and fish stock depletion (Brinson and Malvárez, 2002; Barbier et al., 2011; Lefcheck et al., 2017). Land-water interactions greatly affect the health of shallow aquatic systems, especially those located in watersheds dominated by agriculture. In such systems, runoff from intensively cultivated areas leads to high nutrient and sediment loads to aquatic systems, which alter their trophic status and potentially trigger regime shifts when critical thresholds are exceeded (Scheffer et al., 1993; Scheffer and van Nes, 2007; Capon et al., 2015; Hilt et al., 2018). Two alternative stable states are possible in this case (Scheffer et al., 1993; Hilt et al., 2018): (i) a clear-water state dominated by submerged aquatic vegetation (SAV) or, conversely, (ii) a turbid state in which SAV is outcompeted by phytoplankton/periphyton because of light limitation (Sand-Jensen and Borum, 1991; Hidding et al., 2016). Switching from one equilibrium to another is often an abrupt phenomenon (Hilt et al., 2011), although gradual transitions have also been reported for many systems (Phillips et al., 2016). The SAV-dominated state is more desirable because it provides fundamental ecosystem services like water depuration, fish habitat, and nurseries as well as physical protection for the shore (Lefcheck et al., 2018). Whereas the factors driving SAV abundance can operate at different scales (e.g., localized anthropogenic impacts vs. large-scale climate change), their joint effects are rarely considered (but see Russel et al., 2009).

In the last decades, much effort has been devoted to promoting SAV recovery by reducing nutrient inputs (e.g., Jeppesen et al., 2005; Hilt et al., 2018; Lefcheck et al., 2018). However, the response of SAV to nutrient reduction can be ecosystem specific, depending on nutrient limitation levels. For instance, while SAV may decline in eutrophic systems when exposed to further loads (Hudon et al., 2012; Lefcheck et al., 2018), it may respond positively to nutrient enrichment in oligo-mesotrophic systems (Hudon et al., 2012). While several restoration programs have aimed to re-establish SAV beds in both freshwater and marine eutrophic systems (e.g., Hilt et al., 2018; Lefcheck et al., 2018), there are few mechanistic studies linking the potential consequences of SAV changes on fish populations (but see Hargeby et al., 2005).

In this study, we investigate the relationships between SAV and fisheries dynamics in Lake Saint-Pierre (Québec, Canada; hereafter LSP; Fig. 1), the largest fluvial lake of the St. Lawrence River. This shallow lake (mean depth approx. 3 m) receives water from several tributaries draining some of the most heavily impacted agricultural watersheds in Eastern Canada (Goyette et al., 2016). Riverine inputs, macrophyte beds, and heterogeneous morphology and hydrology cause high variability in LSP water quality (Hudon and Carignan, 2008), with some water masses close to oligo-mesotrophy and others almost eutrophic (Hudon et al., 2012).

Over the last decades, temperature, turbidity, and nutrient concentrations have shown a marked increase in LSP (Goyette et al., 2016; Hudon et al., 2018) (see Fig. 2 for trends); this has been observed in many aquatic systems worldwide (Schindler, 2001; Jackson et al., 2016). In LSP tributaries, nitrogen (N) loads are mainly of agricultural origin (85%) (Hébert and Blais, 2017), whereas phosphorus (P) loads are due to both diffuse agricultural inputs (68%) and municipal waste waters (22%) (Patoine, 2017; Simoneau, 2017). In an attempt to reduce water pollution, the Québec law on environmental quality was adopted in 1972 and was followed by a vast series of programs and interventions to regulate urban and industrial wastewater discharges, manure and slurry, fertilizer use, and fish farming waste (refs in MELCC, 2013). Whereas these efforts allowed a slight reduction in P concentrations, N continued to increase (Simoneau, 2017).

There is some evidence that SAV biomass declined during the same period (Hudon et al., 2012; Hudon et al., 2018), even though the magnitude of this change was not assessed quantitatively over the whole lake. Furthermore, the observed SAV decline was often associated with a shift towards an increase in benthic cyanobacteria communities (Vis et al., 2008; Hudon et al., 2012). Cyanobacteria mats are likely poor habitats for fish since they provide low structural complexity, scarce invertebrate biomass, and might produce toxic chemicals (Vis et al., 2008; Hudon et al., 2012). These changes raised concerns about ecosystem stability and potential effects on commercially exploited species. LSP had supported an important yellow perch (*Perca flavescens* (Mitchill, 1814); hereafter YP) fishery (Magnin, 1966), worth up to 10 M $ CAN/year (estimate for the mid-1980s) between the 1960s and its collapse in the mid-1990s (Mailhot et al., 2015). Despite major reductions in the commercial fishing effort between 1997 and 2008, mainly through fisher licence buybacks and a complete moratorium on both the commercial and recreational fishing in 2012, the YP population has not yet recovered (Mailhot et al., 2015).

Here we explicitly analyze the potential links between anthropogenic stressors and the decline of both SAV and YP (adult landings and juvenile growth) in LSP with structural equation modelling. Based on Lefcheck et al. (2018), who recently highlighted a potential mechanistic link between land use change and SAV, we hypothesize that i) local stressors related to water quality (i.e., N, P, turbidity, and total suspended solids [TSS]) will negatively affect SAV abundance. More precisely, we expect that increases in both TSS and turbidity as well as excessive nutrient loads will be associated with lower SAV biomass. We also hypothesize that ii) larger-scale stressors such as temperature and water levels will be associated with changes in SAV. For example, sub-optimal temperatures will negatively affect SAV growth and metabolism, and thus SAV biomass (Barko and Smart, 1981), and excessively low or high water levels will negatively affect SAV through dry-out and light limitation, respectively (Blindow, 1992). Moreover, we hypothesize iii) SAV to be a positive driver of YP growth and thus iv) YP commercial landings are hypothesized to be positively related to both SAV abundance and juvenile YP growth. Lastly, we hypothesize v) TSS and turbidity to negatively affect YP growth, mainly by impairing visual foraging, and vi) higher temperatures and water levels to positively affect YP growth by modulating metabolism and prey/habitat availability. In addition to testing these direct links between stressors and both SAV and YP growth, our aim here is to analyze their potential indirect effects on fishery landings. Our work allowed us to test for the first time the cascading effects of long-term changes in abiotic variables at both the local and regional scale (i.e., related to agricultural and climate change) on both SAV and a commercially exploited fish population.

## Material and Methods

### *Study area*

Lake Saint-Pierre (Québec, Canada; hereafter LSP; Fig. 1) is the largest fluvial lake of the St. Lawrence River (approx. 400 $km^2$). LSP has a slow water velocity ($< 0.5$ m $s^{-1}$) and is shallow (mean depth approx. 3 m), except for the artificial navigation channel that is approximately 11 m deep (Hudon and Carignan, 2008). LSP receives water from several tributaries, the most important of which are the Richelieu, Yamaska, Saint-François, and Nicolet rivers on the south shore and l'Assomption and du Loup rivers on the north shore. Each tributary is characterized by different physical and biogeochemical features (Frenette et al., 2003). For instance, the Yamaska and Saint-François rivers drain watersheds from the south shore that are mainly characterized by agricultural areas, carrying high inputs of nutrients and sediments as well as a wide spectrum of contaminants, while north shore tributaries have lower nutrient concentrations and are generally less polluted (Simoneau, 2017). The lake's floodplain covers approximately 140 $km^2$ during spring flood (lasting five to nine weeks) and represents an important spawning ground for YP. The aquatic vegetation provides feeding and growth habitat for YP. It is very abundant during the summer (although very patchy), often occupying the whole water column and forming a canopy at the surface (Hudon et al., 2012). The most abundant submerged species are American eel-grass (*Vallisneria americana*) and pondweeds (*Potamogeton richardsonii* and *Stuckenia pectinata*), whereas emergent vegetation is mainly represented by bulrushes (*Schoenoplectus fluviatilis*, *S. lacustris,* and *S. pungens*), broad-fruited bur-reed (*Sparganium eurycarpum*), and broad-leaved arrow-leaf (*Sagittaria latifolia*) (Massicotte et al., 2015).

### *Environmental data*

Spring water level was calculated as the average of daily measurements (m) for May and June (i.e., SAV regrowth period) (Fig. 2), representing an index of water availability for both SAV and YP during two months that are critical for their development. During this period, yellow perch perform an ontogenetic shift from pelagic larvae to littoral juveniles

(Théberge, 2008); this important step affects both growth and survival (Roswell et al., 2014, and references therein).

Total annual loads of P, N, and TSS (kg/year) to LSP were calculated by multiplying water concentrations of total P, total N, and TSS by river flow, and then summed to obtain a measure of the annual charge of P ($10^5$ kg/year), N ($10^6$ kg/year), and TSS ($10^9$ kg/year) entering LSP (Simoneau, 2017; Fig. 2). The N/P ratio was calculated by dividing total annual N loads by total annual P loads (Fig. S1). Seven major LSP tributaries were included (eight stations; Bayonne, Maskinongé, du Loup, Richelieu, Yamaska, Saint-François, Nicolet southwest, and Nicolet rivers). Technical details on laboratory methods used to measure total P and total N concentrations are reported in Simoneau (2017). Turbidity (NTU) was calculated as the average of May, June, and July (critical months for SAV and YP growth) (Fig. 2) and $\log_{10}$ transformed before modelling to improve normality. To provide a global water transparency proxy, we averaged values from 20 stations in tributaries Bayonne, Chicot, Du Loup, La Chaloupe, Maskinongé, Nicolet (north and south), Petite du Loup, Petite Yamachiche, Richelieu, Saint François, Yamaska (two stations), Yamachiche; three stations in the St. Lawrence River at the LSP inlet (Tracy north, center, and south); and three at the outlet (Trois-Rivières north, center, and south).

Water temperature was estimated by averaging May, June, and July air temperature (°C) and was intended as an index of regional climate change. Air temperature is a good proxy of water temperature in rivers, especially on a monthly time scale, because data averaging reduces the variation due to the lag of air-to-water temperature (Erickson and Stefan, 2000). For modelling purposes, data were averaged to get one value per variable per year.

Water levels were obtained from Fisheries and Oceans Canada (DFO, 2018). Annual loads of total N, P, and TSS were obtained from Simoneau (2017). Turbidity values were obtained from the "Banque de données sur la qualité du milieu aquatique" (BQMA; Ministry of Environment Canada; MELCC, 2019). Temperature data were obtained from the Environment Canada website
(http://climate.weather.gc.ca/historical_data/search_historic_data_e.html).

### *SAV estimation*

Lake-wide SAV abundance was back-calculated between 1960 and 2012 based on the difference in water level between the inlet and the outlet of LSP (hereafter summer Δ water level) at SAV biomass peak (based on Morin, 2001; Fig. 1). The variable summer Δ water level was thus calculated as the daily difference in water levels (m) between the LSP's inlet and outlet averaged over the July–August period. The underlying assumption is that SAV abundance influences water retention time by exerting attrition (i.e., sediment and physical matter affecting bottom rugosity), such that the summer Δ water level increases as a function of water flow reduction (Morin, 2001). The most important variables affecting this measure are ice cover and SAV abundance (Morin, 2001). During summer, Δ water level increases because of higher bottom rugosity due to SAV growth. This measure integrates submerged vegetation as well as the submerged parts of emerged vegetation, giving a global measure of total SAV abundance. We verified the validity of the summer Δ water level index by comparing it to the enhanced vegetation index (EVI) obtained from satellite imagery (Landsat 5 and 7). The EVI index is very sensitive to dense vegetation, especially in cases of high biomass and surface canopy (Gao et al., 2000; Huete et al., 2002), and was shown in LSP to correlate with quantitative SAV biomass samples collected *in situ* (Massicotte et al., 2015). Given that both submerged and emergent vegetation provide similar ecosystem functions and are difficult to differentiate using remote sensing techniques, we hereafter refer to both as SAV. Because EVI sensitivity is depth-dependent, only areas shallower than 2 m were analyzed. Nevertheless, shallow areas represent a huge proportion of LSP (see Fig. 1) and justify the comparison between EVI and summer Δ water level data at the scale of the entire LSP. Mean EVI values on a 90 × 90 m (3 × 3 pixels) buffer were calculated for a minimum of 46 to a maximum of 335 stations, depending on the year, from 1985 to 2012 (no data available prior to 1985 or for 1986, 1996, and 2008). The calibration, correction, and treatment for atmospheric effects on satellite images were performed as in Massicotte et al. (2013). To explore the non-linear relationship between EVI and the explanatory variables, we fitted a generalized additive mixed model (GAMM) including day of the year and depth as smoothed fixed effects. Residuals were extracted and used to validate the summer Δ water level based on Pearson's correlation. Satellite data were obtained for the period of the summer peak in SAV abundance, corresponding to the summer Δ water level calculation (pictures taken between day of the year 190 and 270) in all but two outliers (day of the year 157 and 162). Therefore, the validation was performed on both the full data set and after removing these two potentially biased values. Pearson correlations between EVI values and summer Δ water level were 0.55 for the complete dataset and 0.56 once these two data points were removed (Fig. S2).

### ***Fish data***

A standardized fish sampling survey of the fluvial section of the St. Lawrence River has been conducted since 1995 in late summer/early fall by Québec governmental authorities. LSP was sampled in 1995, 1997-2000, 2002, 2007, 2009, 2011, and 2013. Sampling sites were systematically distributed in all habitat types except for the navigation channel. At each site, two experimental multi-mesh monofilament gillnets (60 m long by 1.8 m deep; eight panels of 25, 38, 51, 64, 76, 102, 127, and 152 mm stretched mesh) were anchored on the bottom, parallel to the shore, for approximately 24 hours (La Violette et al., 2003). Opercular bones collected from individual YP sampled during the surveys were used to back-calculate length at the end of the first year following the body-proportional hypothesis (Francis, 1990) and based on regression coefficients calculated for the LSP YP population (P. Brodeur, unpublished data). Length at age 1 was used as a proxy of juvenile YP growth, reflecting the size reached by young-of-the-year fish at the end of their first growth season (Fig. 3).

Annual catch per unit of effort (CPUE; Fig. 3) of YP from 1986 to 2012 was estimated from declared commercial landings (fyke netting) and were corrected for the annual fishing effort (number of nets) and the effect of fisheries regulations established between 1997 and 2012 (GLV Environnement Inc., 1999; GLV Environnement Inc., 2001; Magnan, 2002; Mailhot et al., 2015; Y. Mailhot, Ministère des Forêts, de la Faune et des Parcs, unpublished data). Commercial landings consist mostly of individuals four years old and older (minimum legal length of 165 mm from 1997 to 2000 and 190 mm until 2012).

### *Statistical analyses*

The first objective of our statistical analyses was to highlight the potential direct and indirect links between explanatory variables and the fishery for the period for which commercial landings data are available (i.e., from 1990 to 2007; see analyses for structural equation models below). Complete time series for all environmental variables were available for this period. In addition, it has also been possible to explore the relationship between some key environmental variables and the long-term change in SAV for a longer period. More specifically, we performed a linear model with a first-order autocorrelation term (AR1) using temperature and water levels as explanatory variables (scaled by their standard deviation) to explain variations in SAV between 1966 and 2012. To assess the relative importance of different potential pathways explaining variations in SAV abundance, YP landings, and juvenile growth, we developed structural equation models (SEMs) including the main hypotheses about the potential drivers of these variables (Figs. 4A and S3A). SEMs are probabilistic models aiming to assess statistical causality between variables in complex systems (Grace, 2006; Lefcheck, 2016). In an SEM, variables are connected in a network, so they may act at the same time as response (endogenous) or predictor variables. In this way, it is possible to assess the cascading effects of one on the other, evaluating both direct and indirect relationships (Grace, 2006). The pathways constituting the model represent specific hypotheses based on an *a priori* knowledge of the system (Lefcheck, 2016). Such theoretical structures constitute the conceptual model, which is then translated into a series of structured equations (Lefcheck, 2016). This means that SEM allows for testing multiple hypotheses within a single inclusive model, quantifying the direct and indirect cascade effects (Lefcheck, 2016) and allowing an evaluation of the strength of the statistical causality between variables.

In this study, we used a variant of SEM known as piecewise SEM (i.e., confirmatory path analysis, given the lack of latent variables in the model; hereafter pSEM), in which hypothesized pathways are specified as linear equations and evaluated individually (Lefcheck, 2016). pSEM allows for the fitting of several distributions and deals with data non-independence (e.g., spatial and temporal autocorrelation) (Lefcheck, 2016; Lefcheck et al., 2018). pSEM is based on Shipley's test of direct separation, which tests the conditional independence of variables; this implies that the provided structure of the model does not omit causal relationships between unconnected variables (Shipley, 2000). Therefore, if no claim of independence is significant at $p<0.05$, pathways are correctly specified (Lefcheck et al., 2018).

While dealing with time series, data non-independence (e.g., spatio-temporal autocorrelation) may be problematic because most of the statistics assume data independence. To solve the issue of autocorrelation among years, we included an AR1 in our pSEM. Once fitted, we verified the lack of an autocorrelation structure by means of the *acf*() R function. Model assumptions were visually evaluated for normality, linearity, homoscedasticity, and outliers. None of the independence claims specified in the model were significant, meaning that we did not miss any fundamental relationships among the selected variables (Laliberté et al., 2014). Goodness-of-fit was estimated for all the pSEMs built *a priori,* and none of them were rejected based on d-sep tests ($p>0.05$). Backward model selection was then applied by dropping the least significant variables one at a time (based on p-value) then choosing the most parsimonious model maximizing $R^2$ values for each endogenous variable. Once the best model was selected, we reported standard coefficients, standard errors, and $R^2$ for each pathway (the latter for endogenous variables only).

Our pSEM approach is based on a conceptual model founded on expert knowledge of the system, bridging the land–water gap, linking anthropogenic inputs from the watershed and climate change proxies with SAV abundance and YP commercial CPUE and growth. Within this framework, SAV abundance (i.e., summer $\Delta$ water level), YP CPUE, and YP growth represent the response variables, while we include nutrients (N and P or N/P), TSS, turbidity, spring water levels, and temperature as predictors. The fitted pSEM including all these variables is hereafter referred to as the full model. Given the broad difference in value magnitudes and units of measure, we scaled variables by their standard deviation to obtain dimensionless coefficients comparable for different models (Duffy et al., 2015; Lefcheck et al., 2018). We fixed covariation ($\sim\sim$) between terms sharing the same exogenous source of error (turbidity $\sim\sim$ TSS, P $\sim\sim$ N) as well as meaningless independent claims (P $\sim\sim$ YP length, N/P $\sim\sim$ YP length) to avoid spurious correlation. Here we considered two variants of the conceptual model presented above (based on N and P or N/P, respectively) and consequently built the corresponding sets of pSEMs. In the main set of pSEMs, P and N loads were used as predictors to model SAV abundance (Fig. 4), whereas we replaced P and N loads by their ratio in the alternative set (Fig. S3A) with all the other predictors being unchanged. The two sets of pSEMs (main and alternative) were then submitted to the backward selection procedure. Overall fitting parameters for all competing pSEMs and for both conceptual models are reported respectively in Table S1 and Table S2. Standard coefficients, standard errors, and P-values for each pathway and $R^2$ for endogenous variables are reported in Table S3 and Table S4 for the two best models. All statistical analyses were performed using the R language environment (version 3.1.1). pSEMs were fitted using the R package *piecewiseSEM* (version 2.0, https://github.com/jslefche/piecewiseSEM/tree/2.0; Lefcheck, 2016).

## Results

SAV has shown a dome-shape abundance curve over the last 50 years, with the decrease beginning in the late 1980s (Fig. 5). Although temperature has increased since the beginning of the century (data not shown), no effect of this variable was detected on SAV for the period under study (i.e., 1966-2012; linear model: effect size = 0.114, SE = 0.110, $p = 0.31$). Despite a tendency to decline since 1975, spring water levels showed high inter-annual variability (Fig. 2), potentially hindering the detection of its effects on SAV (effect size = 0.071, SE = 0.123, $p = 0.56$). Therefore, we have no support for the hypothesis that these proxies of climate change affected long-term SAV dynamics.

A more complete assessment of the effects of both local (e.g., turbidity) and large-scale (e.g., temperature) drivers on SAV as well as YP was conducted for the 1990-2007 period, for which we have a complete time series. Within the main set of pSEMs, the best model (Fisher's C = 6.8, df = 16, p-value = 0.98) revealed that P and TSS are the most important drivers of SAV abundance, the former promoting SAV biomass and the latter inhibiting it (Fig. 4B). In turn, SAV abundance positively influenced YP commercial catch per unit effort (CPUE) (Fig. 4B). Both turbidity and higher spring water levels exerted a negative impact on YP growth, which is a determinant of YP commercial CPUE (Fig. 4B; refer to the electronic supplementary material for further discussion on non-significant pathways). However, the fitted model does not completely support our hypotheses, given that YP growth is not directly a function of SAV abundance. This means that the strength of commercially recruited cohorts is a function of both SAV abundance and YP juvenile growth, but that SAV is nevertheless not a driver of YP growth. However, we could not completely dismiss this potential pathway since this link is retained by competing models that are less supported by the data but still not rejected (Table S1).

Within the alternative set of pSEMs, the best model (Fisher's C = 7.2, df = 12, p-value = 0.85; Fig. S3B) revealed that N/P and temperature are the most important drivers of SAV abundance, both being negatively related to SAV biomass. Besides these differences, all the other components of the pSEM remained unchanged.

## Discussion

Our study suggests that inputs from the watershed can impact freshwater fisheries via a reduction in fish habitat quality, leading to potential consequences at both environmental and socio-economic levels. Our results showed that YP landings were affected by changes in watershed inputs to the lake based on two different pathways: i) through the effects of P and TSS on SAV and ii) by the effects of turbidity and spring water levels on YP juvenile growth. These results thus show that changes at the watershed-level inputs can impact YP landings both directly, by affecting YP growth, and indirectly, by altering fish habitat quality. The relationship between SAV and YP growth suggests a less clear-cut pathway, since this link was retained in the competing models (less supported by the data but still not rejected; Table S1) but not in the best SEM. Accordingly, other studies have found that both growth and recruitment of the Eurasian perch (a species phylogenetically and ecologically very close to YP) were associated with SAV (Hargeby et al., 2005). In our case, the observed link between SAV and YP landings might thus be more a function of survival than growth. Unfortunately, data on cohort survival are difficult to acquire, and we cannot explicitly test the strength of the relationship between SAV, survival, and landings (but see below). To our knowledge, the present study is one of the few empirical examples at the ecosystem level that link secondary production and changes in SAV bed habitat quality caused by nutrient and sediment inputs from the watershed (but see Hargeby et al., 2005 and Lefcheck et al., 2017).

### *SAV abundance drivers: the role of P and TSS*

Our analysis highlights the role of TSS as a major driver of SAV abundance (Fig. 4B). TSS, whose main anthropogenic source in our system is sediment runoff from farmland and municipal waste waters (Hébert and Blais, 2017), was negatively related to SAV abundance, likely because of decreased light penetration into the water column. TSS both scatter and absorb solar radiation, thus reducing light availability for photosynthesis (Kirk, 1985; Blondeau-Patissier et al., 2009; Moore, 2009). A recent study showed that the maximum colonization depth of SAV in LSP decreased by about 50 cm over the last decades because of increased turbidity (Hudon et al., 2018). A similar result was found in Chesapeake Bay, where the mean depth of SAV beds has decreased dramatically since 1984, shifting 165 m closer to the shore as consequence of increased turbidity (Lefcheck et al., 2017). In the LSP watershed, agriculture progressively switched from a predominance of perennial culture in the 1960s to mostly intensive annual crops in the 1990s (Dauphin and Jobin, 2016), a tendency that has been observed worldwide (Tilman et al., 2002). Plowed soils are more vulnerable to erosion, leading to sediment runoff into aquatic systems (Foley et al., 2005); this has likely led to the observed increases in TSS and turbidity that affected SAV in LSP.

Although P is not limiting in LSP tributaries, we observed a positive correlation between P and SAV (Fig. 4B). In this context, the decreasing abundance of SAV in the second part of the dome-shape curve (Fig. 5) can be interpreted as a response to the reduction in P discharge that followed the implementation of programs to reduce water pollution (Simoneau, 2017). Given that many LSP water masses are oligo-mesotrophic, a reduction in P is more likely to have led SAV to decrease rather than to increase; this response is expected in more eutrophic systems, where a reduction in P load would re-establish conditions more favourable to SAV through a reduction of either phytoplankton or periphytic algae (Lefcheck et al., 2018). In contrast, no relationship was observed with N, whose concentrations were still increasing in 2015, corroborating the idea that P is the limiting factor for SAV in LSP. This is in accordance with the theoretical hump-shaped curve proposed by Hudon et al. (2012), where SAV biomass increases from an oligotrophic to a mesotrophic state, reaches a plateau, and finally decreases once a eutrophic state is reached. The mechanisms behind this model are nutrient limitation for the increasing part of the curve and periphyton overgrowth for the decreasing part (Olsen et al., 2015). This scenario is compatible with the loss of SAV beds observed in eutrophic ecosystems (Lefcheck et al., 2018).

Although absolute nutrient concentrations are probably key in determining SAV decline, it has also been suggested that variations in the N/P ratio are better predictors of this phenomenon (Lacoul and Freedman, 2006). However, the best alternative pSEM (Fig. S3), although well supported by the data, showed a weaker relationship between the N/P ratio and SAV than what was found with P alone (Fig. 4). With the data at hand, it is difficult to conclude whether the observed effect is due to P alone or to an imbalance between N and P.

Our study clearly illustrates the opposite effects of TSS and P on SAV. This is an interesting finding: nutrients often increase, and the degradation of the underwater optical environment tend to have synergic negative effects on SAV development, especially in eutrophic systems (e.g., Phillips et al., 2016; Hilt et al., 2018). Light limitation (e.g., due to TSS) *per se* is always negative for SAV, inducing stress, decreases in photosynthetic potential, and further decreasing SAV abundance. Conversely, the effect of nutrients on SAV is dependent on the trophic state. Many studies have focused on eutrophic ecosystems, mainly finding that an excess of nutrients was deleterious for SAV (Scheffer et al., 1993; Phillips et al., 2016; Hilt et al., 2018). In contrast, in oligo-mesotrophic lakes like LSP, the effect of nutrient increases on SAV is potentially beneficial (Rejmánková, 2001; Gaiser et al., 2005), and in turn increasing the carrying capacity for secondary producers (Chesney et al., 2000). In contrast, Bakker et al. (2010) found a negative effect on Charophytes in a mesocosm experiment in which SAV communities were exposed to a relatively high concentration of N and P.

Although LSP is still in an oligo-mesotrophic state, it has been dramatically enriched by both P and N over the last century (Goyette et al., 2016; Simoneau 2017), and the process –at least for N– is probably far from being reversed (Goyette et al., 2016). Agricultural lands surrounding LSP have been enriched to the point that the soil's buffer capacity to retain nutrients has been exceeded, with an estimate of centuries to millennia to return to below-threshold values (Goyette et al., 2018). This means that N and P stocked in agricultural soils are likely to be exported to LSP for centuries, interfering with efforts to reduce nutrient inputs from other sources (Goyette et al., 2018). Moreover, the establishment of feedback loops, such as the release of sediments that also keep nutrient concentrations elevated, might greatly delay SAV recovery (Hilt et al., 2006).

Given that most reported cases of SAV losses are caused by a degradation of the underwater optical environment (Chambers et al., 1999; Hilt et al., 2006; Lefcheck et al., 2017), improving light availability to SAV is essential for its recovery. This is clearly shown by one of the most compelling cases of SAV management, which occurred in Chesapeake Bay, the largest estuary in the USA and among the largest in the world (Shafer and Bergstrom, 2010). SAV reduction has been recognized to be caused by an increase in turbidity related to eutrophication (Shafer and Bergstrom, 2010; Lefcheck et al., 2017). To allow SAV recovery and improve water clarity, a restoration effort started in 1978 involved the large-scale planting of whole plants, cuttings, seeds, and tubers of several seagrass species (i.e., *Zostera marina*, *V. americana*, and *Ruppia maritima*), followed by an environmental program established in 1987 that aimed to reduce nutrient inputs by 40% by the year 2000 (Hennessey 1994; Boesch 2006; Shafer and Bergstrom, 2010). SAV is currently recovering in several areas of the estuary (mostly fresh and oligohaline waters), but not at the scale of the whole bay, mostly because turbidity is still strongly limiting SAV development (Orth et al., 2010; Shafer and Bergstrom, 2010).

### *Factors affecting yellow perch landings*

We found a negative relationship between turbidity and early ontogenetic stages of YP, probably because of impaired foraging (Radke and Gaupisch, 2005; Wellington et al., 2010) and therefore decreased survival. Energy allocation is an important step for young-of-the-year YP because they need to reach a minimum size to survive severe winter conditions (Post, 1990; Farmer et al., 2015) and reduce predation. We hypothesized that high spring water levels positively drive YP growth, especially because of increased plankton productivity when shallow areas are flooded, as predicted by the flood pulse concept (Junk et al., 1989). Young-of-the-year YP are known to depend almost entirely on zooplankton during their first few months and later switch to zoobenthos (Wu and Culver, 1992). Surprisingly, we found a negative relationship between spring water levels and YP growth. One possible explanation for this result might be that higher water levels are associated with increased turbidity in littoral YP nursery and feeding areas, interfering with visual foraging by YP. In our pSEM, turbidity was a key variable negatively affecting YP growth. Another possibility is that high spring water levels lead to an array of factors deleterious for YP, such as pesticide and contaminant runoff from littoral areas, which are heavily cultivated with corn and soya (Giroux, 2018). Another explanation might be the increased density-dependent competition among larvae because of better recruitment (Claessen et al., 2000). Indeed, higher spring water levels might increase intra-cohort competition through a positive effect on spawning area availability, egg survival, and larval hatching. However, this does not fit with our data on cohort strength, which show a relatively high correlation (Pearson correlation = 0.54) between the growth of one-year-old individuals and recruitment (1982-1984, 1991-1998; see Guénette et al., 1994; Mailhot and Dumont, 2003).

Our study identified that turbidity and spring water level variations are key drivers of YP growth, which affects commercial landings (thus providing a rough proxy of adult YP population abundance). However, YP population dynamics are also driven by other factors. For instance, there is evidence of low YP recruitment over the last decade, and this could have been due to net loss of the best YP spawning areas because of changes in land use in the floodplain (Mailhot et al., 2015). By the early 1990s, the extensive agriculture practiced in the floodplain increasingly included intensive annual crops (i.e., corn and soy; Richard et al., 2011). Agriculture development has resulted in a net loss of 5000 ha of key fish spawning and nursery habitats, rendering yellow perch more vulnerable to recruitment failure. This loss can represent more than 50% of the potential spawning habitat during years of high spring floods (Lecomte et al., 2012).

Another factor likely impeding the rehabilitation of perch stocks is the double-crested cormorant (*Phalacrocorax auritus*), a YP predator that recently appeared in Lake Saint-Pierre (Mailhot et al., 2015). Colonies have rapidly expanded since the end of the 1990s, from 66 nesting pairs in 1998 to 575 in 2001 and 948 in 2004. In addition, a few thousand migrating cormorants arrive in the lake in late summer (Mailhot et al., 2015). Predation on the perch stock was probably not responsible for initiating the collapse, but it represents another source of mortality likely reducing recruitment and hindering the effectiveness of management plans (Magnan et al., 2008; Mailhot et al., 2015). In recent years, the population has stabilized at about 100-200 nesting pairs following control efforts on adults, through culling (Strickland et al., 2011), and recruitment, through eggs-oiling (Shonk et al., 2004). YP is also potentially threatened by the arrival of new invasive fish species in LSP, especially the tench (*Tinca tinca*) (Mailhot et al., 2015). This species is thought to compete with YP for feeding and nursery grounds, although the effects of such competition are difficult to assess.

To our knowledge, the present study is the first to establish a link of statistical causality between SAV and a fishery rather than simple correlations. Jackson et al. (2001) provided a detailed review on the role of seagrasses in sustaining fisheries species, but they focused mostly on the function of seagrasses as habitat for animal species (e.g., foraging, nursery, shelter, settlement) rather than on fishery yield. Chesney et al. (2000) found that fishery landings correlated with the extension of estuarine vegetation. Gillanders (2006) reported some examples on the loss of SAV or changes in seagrass species composition and commercial fisheries. For instance, severe declines in soft shell and razor clams, lobster, and mud crab were reported at Cape Ann (Massachusetts, USA) following seagrass reduction in the 1930s. In Western Port Bay (Australia), a 70% decline of the seagrass cover was associated with a 40% decline in commercial fish catches (Jenkins et al., 1993). Wyda et al. (2002) also found that fish biomass, number, and species proportion decreased in seagrass-degraded areas. Finally, Lefcheck et al. (2017) estimated that the decline of eelgrass in Chesapeake Bay (21% loss since 1991) led to a reduction of 523-1403 million juvenile blue crabs (potential economic loss of $ US 28.6-76.7 million). While all these examples are in accordance with our findings, none of the studies explicitly analyzed the complex links between the multiple factors linking SAV and fisheries.

The aim of this study was to shed light on the complex interactions between environmental drivers (both at local and global scales), aquatic vegetation, and fisheries landings. Our results show how anthropogenic inputs from the watershed might negatively affect key components of the freshwater ecosystem within the LSP. It is worth noting that, since SAV responded to changes in P load, the system is probably able to slowly return to a more oligotrophic state. However, although this shows that P reduction policies have been at least partially effective, the negative impact of TSS on SAV suggests that the degradation process has not been reversed. This result points to a degradation of the water column's optical environment that is mainly caused by agricultural activities in the watershed. Despite the coarseness of the available data, our hypothesis-driven approach was robust enough to reveal the independent (and apparently contradictory) effects of these factors on SAV. By explicitly testing potential causal pathways linking changes in the watershed to SAV and fisheries, our study highlights the key role of fish habitat (e.g., decrease in SAV beds, impaired optical properties of the water column) as a link between anthropogenic activity in the watershed and the long-term viability of the fisheries. Our results showed how these changes at the watershed level can affect fish populations –either directly or indirectly– by driving SAV dynamics. Fisheries management practices should thus explicitly take into account land use in the watershed and not only the aquatic ecosystem.

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## References

Bakker ES, Van Donk E, Declerck SAJ, Helmsing NR, Hidding B, Nolet BA. 2010 Effect of macrophyte community composition and nutrient enrichment on plant biomass and algal blooms. *Basic. Appl. Ecol.* 11, 432-439. (doi: 10.1016/j.baae.2010.06.005).

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011 The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169-193.

Barko JW, Smart MR. 1981 Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecol. Monogr.* 51, 219-236.

Blindow I. 1992 Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. *Freshw. Biol.* 28, 15-27.

Blondeau-Patissier D, Brando VE, Oubelkheir K, Dekker AG, Clementson LA, Daniel P. 2009 Bio-optical variability of the absorption and scattering properties of the Queensland inshore and reef waters, Australia. *J. Geophys. Res.* 114, 1-24. (doi:10.1029/2008JC005039).

Boesch DF. 2006 Scientific requirements for ecosystem-based management in the restoration of Chesapeake Bay and coastal Louisiana. *Ecol. Eng.* 26, 6-26. (doi:10.1016/j.ecoleng.2005.09.004).

Brinson MM, Malvárez AI. 2002 Temperate freshwater wetlands: types, status, and threats. *Environ. Conserv.* 29, 115-133. (doi:10.1017/S0376892902000085).

Capon SJ, Lynch AJJ, Bond N, Chessman BC, Davis J, Davidson N, Finlayson M, Gell PA, Hohnberg D, Humphrey C, Kingsford RT, Nielsen D, Thomson JR, Ward K, Mac Nally R. 2015 Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Sci. Total. Environ.* 534, 122-130. (doi:10.1016/j.scitotenv.2015.02.045).

Chambers PA, DeWreede RE, Irlandi EA, Vandermeulen H. 1999 Management issues in aquatic macrophyte ecology: a Canadian perspective. *Can. J. Bot.* 77, 471-487.

Chesney EJ, Baltz DM, Thomas RG. 2000 Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecol. Appl.* 10, 350-366.

Claessen D, de Roos AM, Persson L. 2000 Dwarfs and giants: Cannibalism and competition in size-structured populations. *Am. Nat.* 155, 219-237.

Dauphin D, Jobin B. 2016 Changements de l'occupation du sol dans la plaine inondable du lac Saint-Pierre entre les années 1950 et 1997. *Le Naturaliste canadien* 140, 42-52. (URI: id.erudit.org/iderudit/1034097).

DFO (Fisheries and Oceans Canada). 2018 Répertoire des données historiques de niveau d'eau. (http://www.isdm.gc.ca/isdm-gdsi/twl-mne/inventory-inventaire/interval-intervalle-eng.asp?user=isdm-gdsi&region=LAU&tst=1&no=15930) (access date: April 7, 2019).

Duffy JE, Reynolds PL, Boström C, Coyer JA, Cusson M, Donadi S, ... & Fredriksen, S. 2015 Biodiversity mediates top–down control in eelgrass ecosystems: a global comparative-experimental approach. *Ecol. Lett.* 18, 696-705. (doi:10.1111/ele.12448).

Erickson TR, Stefan HG. 2000 Linear air / water temperature correlations for streams during open water periods. *J. Hydrol. Engineering* 5, 317-321. (doi:org/10.1061/(ASCE)1084-0699(2000)5:3(317)).

Farmer TM, Marschall EA, Dabrowski K, Ludsin SA. 2015 Short winters threaten temperate fish populations. *Nat. Commun.* 6, 1-10. (doi:10.1038/ncomms8724).

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, ... & Helkowski, JH. 2005 Global consequences of land use. *Science*, 309, 570-574.

Francis RICC. 1990 Back-calculation of fish length: a critical review. *J. Fish Biol.* 36, 883-902.

Frenette JJ, Arts MT, Morin J. 2003 Spectral gradients of downwelling light in a fluvial lake (Lake Saint-Pierre, St-Lawrence River). *Aquat. Ecol.* 37, 77-85.

GLV Environnement Inc. 1999 Suivi de la pêche à la perchaude au lac Saint-Pierre, printemps 1999. Étude réalisée pour le compte de l'Association des Pêcheurs Commerciaux du lac Saint-Pierre. Nicolet, Québec.

GLV Environnement Inc. 2001 Évaluation des impacts des mesures de gestion de la pêche commerciale à la perchaude au lac Saint-Pierre, saison 2000. Étude réalisée pour le compte de l'Association des Pêcheurs Commerciaux du lac Saint-Pierre. Nicolet, Québec.

Gaiser EE, Trexler JC, Richards JH, Childers DL, Lee D, Edwards AL, Scinto LJ, Jayachandran K, Noe GB, Jones RD. 2005 Cascading ecological effects of low-level phosphorus enrichment in the Florida Everglades. *J. Environ. Qual.* 34, 1-8.

Gao X, Huete AR, Ni W, Miura T. 2000 Optical-biophysical relationships of vegetation spectra without background contamination. *Remote Sens. Environ. 74, 609-620.* (doi:10.1016/S0034-4257(00)00150-4).

Gillanders BM. 2006 Seagrasses, fish, and fisheries. Seagrasses: Biology, ecology and conservation. A.W.D. Larkum AWD, Orth RJ, Duarte CM (eds.), Springer, pp. 503-536.

Giroux I. 2018 État de situation sur la présence de pesticides au lac Saint-Pierre, Québec. Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques, Direction de l'information sur les milieux aquatiques. www.mddelcc.gouv.qc.ca/eau/lac-st-pierre/etat-presence- pesticides.pdf

Goyette JO, Bennett EM, Maranger R. 2018 Low buffering capacity and slow recovery of anthropogenic phosphorus pollution in watersheds. *Nat. Geosci.* 11, 921-925. (doi:10.1038/s41561-018-0238-x).

Goyette JO, Bennett EM, Howarth RW, Maranger R. 2016 Changes in anthropogenic nitrogen and phosphorus inputs to the St. Lawrence sub-basin over 110 years and impacts on riverine export. *Global Biogeochem. Cycles* 30, 1000-1014.

Grace JB. 2006 Structural equation modeling and natural systems. Cambridge University Press.

Guénette S, Mailhot Y, McQuinn I, Lamoureux P, Fortin R. 1994 Paramètres biologiques, exploitation commerciale et modélisation de la population de perchaudes (*Perca flavescens*) du lac Saint-Pierre, Québec. Ministère de l'Environnement et de la Faune, Direction Régionale Mauricie–Bois-Francs, Univériste du Québec à Montréal, Département des Sciences Biologiques.

Hargeby A, Blom H, Blindow I, Andersson G. 2005 Increased growth and recruitment of piscivorous perch, *Perca fluviatilis*, during a transient phase of expanding submerged vegetation in a shallow lake. *Freshw. Biol.* 50, 2053-2062. (doi:10.1111/j.1365-2427.2005.01446.x).

Hébert S, Blais D. 2017 Territoire et qualité de l'eau : développement de modèles prédictifs. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques, Direction générale du suivi de l'état de l'environnement et Direction de l'expertise en biodiversité, ISBN 978-2-550-77770-0 (PDF), 30 pp.

Hennessey TM. 1994 Governance and adaptive management for estuarine ecosystems: the case of Chesapeake Bay. *Coastal Management* 22, 119-145.

Hidding B, Bakker ES, Hootsmans MJM, Hilt S. 2016 Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. *Oikos* 125, 1489-1495. (doi:10.1111/oik.03104).

Hilt S, Nuñez A, Marta M, Bakker ES, Blindow I, Davidson TA, ... & Jeppesen E. 2018 Response of submerged macrophyte communities to external and internal restoration measures in north temperate shallow lakes. *Front. Plant. Sci. 9*, 194. (doi:10.3389/fpls.2018.00194).

Hilt S, Gross EM, Hupfer M, Morscheid H, Mählmann J, Melzer A, Poltz J, Sandrock S, Scharf EV, Schneider S, van de Weyer K. 2006 Restoration of submerged vegetation in shallow eutrophic lakes – A guideline and state of the art in Germany. *Limnologica* 36, 155-171. (doi:10.1016/j.limno.2006.06.001).

Hilt S, Köhler J, Kozerski HP, van Nes EH, Scheffer M. 2011 Abrupt regime shifts in space and time along rivers and connected lake systems. *Oikos* 120, 766-775. (doi:10.1111/j.1600-0706.2010.18553.x).

Hudon C, Carignan R. 2008 Cumulative impacts of hydrology and human activities on water quality in the St. Lawrence River (Lake Saint-Pierre, Quebec, Canada). *Can. J. Fish. Aquat. Sci.* 65, 1165-1180. (doi:10.1139/F08-069).

Hudon C, Cattaneo A, Tourville Poirier AM, Brodeur P, Dumont P, Mailhot Y, Amyot JP, Despatie SP, de Lafontaine Y. 2012 Oligotrophication from wetland epuration alters the riverine trophic network and carrying capacity for fish. *Aquat. Sci.* 74, 495-511. (doi:10.1007/s00027-011-0243-2).

Hudon C, Jean M, Létourneau G. 2018 Temporal (1970–2016) changes in human pressures and wetland response in the St. Lawrence River (Québec, Canada). *Sci. Total Environ.* 643, 1137-1151. (doi:10.1016/j.scitotenv.2018.06.080).

Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG. 2002 Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* 83, 195-213.

Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB. 2001 The importance of seagrass beds as a habitat for fishery species. *Oceanogr. Mar. Biol.: An Annual Review* 39, 269-303.

Jackson MC, Loewen CJG, Vinebrooke RD, Chimimba CT. 2016 Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Glob. Chang. Biol.* 22, 180-189. (doi:10.1111/gcb.13028).

Jenkins GP, Edgar GJ, May HMA, Shaw C. 1993 Ecological basis for parallel declines in seagrass habitat and catches of commercial fish in Western Port Bay, Victoria. *Bureau of Resource Sciences Proceedings* pp. 124-136.

Jeppesen E, Søndergaard M, Jensen JP, Havens KE, Anneville O, Carvalho L, ... & Gerdeaux D. 2005 Lake responses to reduced nutrient loading– An analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* 50, 1747-1771. (doi:10.1111/j.1365-2427.2005.01415.x).

Junk WJ, Bayley PB, Sparks RE. 1989 The flood pulse concept in river-floodplain systems. Proceeding of the International Large River Symposium *Can. Spec. Publ. Fish. Aquat. Sci.*, pp. 110-127.

Kirk JTO. 1985 Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiologia* 125, 195-208.

Lacoul P, Freedman B. 2006 Environmental influences on aquatic plants in freshwater ecosystems. *Environ. Rev.* 14, 89-136. (doi:10.1139/A06-001).

Laliberté E, Zemimik G, Turner BL. 2014 Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345, 1602-1605.

La Violette N, Fournier D, Dumont P, Mailhot Y. 2003 Caractérisation des communautés de poissons et développement d'un indice d'intégrité biotique pour le fleuve Saint-Laurent, 1995-1997. Faune et Parcs Québec, Direction de la recherche sur la faune, Québec.

Lecomte F, Mingelbier M, Brodeur P, Dumont P, Mailhot Y, Vachon N, Richard G, Morin J. 2012 How human alterations and natural variations explain opposite responses in yellow perch stocks along the St. Lawrence River. Poster presented at the annual conference of the International Association for Great Lakes Research. Cornwall, Canada. 13-17 May 2012.

Lefcheck JS, Orth RJ, Dennison WC, Wilcox DJ, Murphy RR, Keisman J, ... & Patrick CJ. 2018 Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proc. Natl. Acad. Sci. USA*. (doi:10.1073/pnas.1715798115).

Lefcheck JS. 2016 piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573-579. (doi:10.1111/2041-210X.12512).

Lefcheck JS., Wilcox DJ, Murphy RR., Marion SR, Orth RJ. 2017 Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Global Change Biol.* 23, 3474-3483. (doi:10.1111/gcb.13623).

Magnan P. 2002. Avis scientifique sur l'état du stock de perchaudes au lac Saint-Pierre, les indicateurs biologiques utilisés pour effectuer son suivi et la pertinence de protéger la période de fraye de façon partielle ou totale.

Magnan P, Mailhot Y, Dumont P. 2008 État du stock de perchaude du lac Saint-Pierre en 2007 et efficacité du plan de gestion de 2005. Comité aviseur scientifique sur la gestion de la perchaude du lac Saint-Pierre, Université du Québec à Trois-Rivières et Ministère des Ressources naturelles et de la Faune du Québec, Québec.

Magnin E. 1966 La pêche commerciale sur le fleuve Saint-Laurent et sa place dans l'ensemble des pêches commerciales de la province de Québec. Université de Montréal, Département des Sciences biologiques, Québec.

Mailhot Y, Dumont P, Paradis Y, Brodeur P, Vachon N, Mingelbier M, Lecomte F, Magnan P. 2015 Yellow perch (*Perca flavescens*) in the St. Lawrence River (Québec, Canada): Population dynamics and management in a river with contrasting pressures. Biology of Perch, eds Couture P, Pyle G (CRC Press), pp. 101-147.

Mailhot Y, Dumont P. 2003 Another yellow perch population decline in the 1990s: The Lake St. Pierre case study, St. Lawrence River, Quebec, pp. 135-136. Barry TP, Malison JA (eds.). Proceedings of Percis III: The third International Percid Fish Symposium, University of Wisconsin Sea Grant Institute, Madison, Wisconsin.

Massicotte P, Bertolo A, Brodeur P, Hudon C, Mingelbier M, Magnan P. 2015 Influence of the aquatic vegetation landscape on larval fish abundance. *J. Great Lakes Res.* 41, 873-880. (doi:10.1016/j.jglr.2015.05.010).

Massicotte P, Gratton D, Frenette JJ, Assani AA. 2013 Spatial and temporal evolution of the St. Lawrence River spectral profile: A 25-year case study using Landsat 5 and 7 imagery. *Remote Sens. Environ.* 136, 433-441.

MELCC (Ministère de l'Environnement et de la Lutte contre les changements climatiques). 2013 Le Lac Saint-Pierre, un joyau à restaurer. (doi:978-2-550-69236-2).

MELCC (Ministère de l'Environnement et de la Lutte contre les changements climatiques). 2019 Banque de données sur la qualité du milieu aquatique (BQMA), Québec, Direction générale du suivi de l'état de l'environnement. (http://www.environnement.gouv.qc.ca/eau/Atlas_interactif/donnees_recentes/donnees_iqbp.asp) (access date: April 7, 2019)

Moore KA. 2009 Submerged aquatic vegetation of the York River. *J. Coastal Res.* 57, 50-58. (doi:10.2112/1551-5036-57.sp1.50).

Morin J. 2001 Modélisation des facteurs abiotiques de l'écosystème fluvial du lac Saint-François, fleuve Saint-Laurent. Université du Québec, Institut national de la recherche scientifique, INRS-Eau. PhD thesis.

Olsen S, Chan F, Li W, Zhao S, Søndergaard M, Jeppesen E. 2015 Strong impact of nitrogen loading on submerged macrophytes and algae: a long-term mesocosm experiment in a shallow Chinese lake. *Freshw. Biol.* 60, 1525-1536. (doi:10.1111/fwb.12585).

Orth RJ, Williams MR, Marion SR, Wilcox DJ, Carruthers TJB, Moore KA, Kemp WM, Dennison WC, Rybicki N, Bergstrom P, Batiuk RA. 2010 Long-term trends in submersed aquatic vegetation (SAV) in Chesapeake Bay, USA, related to water quality. *Estuaries Coast.* 33, 1144-1163. (doi:10.1007/s12237-010-9311-4).

Patoine M. 2017 Charges de phosphore, d'azote et de matières en suspension à l'embouchure des rivières du Québec – 2009 à 2012, Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques, Direction générale du suivi de l'état de l'environnement, ISBN 978-2-550-77490-7 (PDF), 25 pp. and 11 annexes. (http://www.mddelcc.gouv.qc.ca/eau/eco_aqua/phosphore/charge-phosphore-azote-mes2009-2012.pdf).

Phillips G, Willby N, Moss B. 2016 Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? *Aquat. Bot.* 135, 37-45. (doi:10.1016/j.aquabot.2016.04.004).

Post JR. 1990 Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): *in situ* estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* 47, 554-560.

Radke RJ, Gaupisch A. 2005 Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): Possible implications for fish community structure in lakes. *Naturwissenschaften* 92, 91-94. (doi:10.1007/s00114-004-0596-7).

Rejmánková E. 2001 Effects of experimental phosphorus enrichment on oligotrophic tropical marshes in Belize, Central America. *Plant Soil* 236, 33-53.

Richard G, Côté D, Mingelbier M, Jobin B, Morin J, Brodeur P. 2011 Utilisation du sol dans la plaine inondable du lac Saint-Pierre (fleuve Saint-Laurent) durant les périodes 1950, 1964 et 1997 : interprétation de photos aériennes, numérisation et préparation d'une base de données géoréférencées, Québec, Tech. Rep. Prepared for the Ministère des Ressources naturelles et de la Faune and Environnement Canada.

Roswell CR, Pothoven SA, Höök TO. 2014 Patterns of age-0 yellow perch growth, diets, and mortality in Saginaw Bay, Lake Huron. *J. Great Lakes Res.*, 40, 123-132. (doi:10.1016/j.jglr.2014.01.008).

Russell BD, Thompson J-AI, Falkenberg LJ, Connell SD. 2009 Synergistic effects of climate change and local stressors: $CO_2$ and nutrient-driven change in subtidal rocky habitats. *Glob. Chang. Biol.* 15, 2153-2162.

Sand-Jensen K, Borum J. 1991 Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquat. Bot.* 41, 137-175.

Scheffer M, Hosper SH, Meijer M-L, Moss B, Jeppesen E. 1993 Alternative equilibria in shallow lakes. *Ecol. Evol.* 8, 275-279.

Scheffer M, van Nes EH. 2007 Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia.* 584, 455-466. (doi:10.1007/s10750-007-0616-7).

Schindler DW. 2001 The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish Aquat. Sci.* 58, 18-29. (doi:10.1139/f00-179).

Shafer D, Bergstrom P. 2010 An introduction to a special issue on large-scale submerged aquatic vegetation restoration research in the Chesapeake Bay: 2003-2008. *Restor. Ecol.* 18, 481-489. (doi:10.1111/j.1526-100X.2010.00689.x).

Shipley B. 2000 A new inferential test for path models based on directed acyclic graphs. *Struct. Equ. Model.* 7, 206-218.

Shonk KA, Kevan SD, Weseloh DV. 2004 The effect of oil spraying on eggs of double-crested cormorants. *The Environmentalist.* 24, 119-124. (doi: 10.1007/s10669-004-4802-0).

Simoneau M. 2017 Qualité de l'eau des tributaires du lac Saint-Pierre : évolution temporelle 1979-2014 et portrait récent 2012-2014. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques. Direction générale du suivi de l'état de l'environnement, ISBN 978-2-550-76229-4 (PDF), 54 p. + 13 ann. (http://www.mddelcc.gouv.qc.ca/eau/lac-st-pierre/qualite-eau-tributaires.pdf). Bibliothèque et Archives nationales du Québec.

Strickland BK, Dorr BS, Pogmore F, Nohrenberg G, Barras SC, McConnell JE, Gobeille J. 2011 Effects of management on double-crested cormorant nesting colony fidelity. J. *Wildl.* Manage. 75, 1012-1021. (doi: 10.1002/jwmg.141).

Théberge M. 2008 Variation de la croissance, de l'alimentation et de la composition spécifique des jeunes perchaudes de l'année (*Perca flavscens*) dans un lac fluvial, fleuve Saint-Laurent (Québec, Canada). M. Sc. Thesis, Université du Québec à Trois-Rivières, Québec, Canada. 89 p.

Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S. 2002 Agricultural sustainability and intensive production practices. *Nature* 418, 671-677.

Vis C, Cattaneo A, Hudon C. 2008 Shift from chlorophytes to cyanobacteria in benthic macroalgae along a gradient of nitrate depletion. *J. Phycol.* 44, 38-44. (doi:10.1111/j.1529-8817.2007.00429.x).

Wellington CG, Mayer CM, Bossenbroek JM, Stroh NA. 2010 Effects of turbidity and prey density on the foraging success of age 0 year yellow perch *Perca flavescens*. *J. Fish. Biol.* 76, 1729-1741. (doi:10.1111/j.1095-8649.2010.02612.x).

Wu L, Culver DA. 1992 Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): A size-related response to zooplankton density. *Can. J. Fish. Aquat. Sci.* 49, 1932-1937. (doi:10.1139/f92-214).

Wyda JC, Deegan LA, Hughes JE, Weaver MJ. 2002 The response of fishes to submerged aquatic vegetation complexity in two ecoregions of the mid-Atlantic Bight: Buzzards Bay and Chesapeake Bay. *Estuaries* 25, 86-100.

## Supplementary material

### *The main set of models*

Here we report a short discussion about the non-significant pathways for the best (N and P) model within the main set of models (for significant results, see text). Whereas TSS was found to be significant for shaping SAV abundance, we found no effect of TSS on YP growth. Laboratory tests showed that YP larvae and juveniles consumed fewer zooplankton prey while exposed to phytoplanktonic turbidity, but no significant effect was detected for sedimentary turbidity (Wellington et al., 2010). Similar results were found for the Eurasian perch (*Perca fluviatilis*), for which the effect of sedimentary turbidity (bentonite) on age 1 and 2 specimens was almost nil, whereas phytoplanktonic turbidity was found to have a negative impact (Radke and Gaupisch, 2005). For these reasons, even though both sources of turbidity contribute to the reduction of light penetration in the water column and thereby affect visual cues, the way they disrupt predation seems different. Because both YP growth and recruitment depend on visual foraging, increased turbidity due to eutrophication (caused by intensive cultivation) could weaken year-class strength (Wellington et al., 2010).

Water level variation is another major driver influencing light reaching the bottom as well as the total amount of substrate available for SAV (e.g., summer dry-out at low water levels; Blindow, 1992). Changes in water levels and floods may influence SAV abundance, often depending on magnitude and duration, making it difficult to assess their net effects on SAV (Bornette and Puijalon, 2011). Water level variations were high during the last decades (Fig. 2). Such variability is caused by natural water regimes and also by artificially regulated water flow–there are several dams situated on the St. Lawrence River and tributaries upstream the LSP. However, according to our model, water levels do not seem to be involved in shaping SAV abundance.

The results concerning the main set of models give no support to a causal relationship between temperature and either SAV or YP growth (but see the alternative model below). Whereas temperature was expected to influence SAV abundance by its effects on phenology (and thus the timing of the SAV summer peak), physiology, and metabolic rate (Barko and Smart, 1981), we found no evidence supporting this hypothesis. We expected a spring–summer average temperature to affect YP growth as well, mostly via metabolic rate modulation (Kitchell et al., 1977; Post, 1990). Again, no effect of temperature on YP growth was detected. Many authors investigated this relationship, but previous attempts were often unsuccessful, leading to the conclusion that prey availability and type are the predominant factors (Henderson, 1985).

### *The alternative set of models*

In many aquatic ecosystems, SAV decline was attributed to an imbalance between N and P rather than their absolute concentrations (Lacoul and Freedman, 2006). Nitrogen-fixing cyanobacteria are known to outcompete SAV along an N depletion gradient when P is available; this phenomenon has also been reported in LSP (Vis et al., 2008; Hudon et al., 2012). To investigate the nutrient imbalance hypothesis, we performed a set of alternative pSEMs replacing N and P concentrations by their ratio (N/P). The best model was well supported by the data (Fisher's C = 7.2, df = 12, p-value = 0.85), even though the relationship between N/P and SAV was weaker than with P concentration alone. Many studies have assessed SAV growth as a function of N/P and found very different values for both the lower (from 7 to 14) and the upper (from 16 to 23) threshold, the former indicating N limitation and the latter usually associated with P limitation (Koerselman and Meuleman, 1996; Verhoeven et al., 1996; see references in Søndergaard et al., 2017). The N/P in LSP suggests an P limitation for the overall study period. However, N/P showed a marked linear increase over the last decades, reaching the present values of around 10-12 (Fig. S1). This trend could lead to a future P limitation, in accordance with the results of our pSEM. This seems to be the consequence of a reduction in P (but not N) fertilizers in use since the 1990s (Simoneau, 2017), after the implementation of several programs to reduce water pollution following application of the Quebec law on environmental quality. However, it has been pointed out that biological interpretations based only on N/P might be misleading because of the risk of not identifying the limiting nutrient (Nikolai and Dzialowski, 2014). A comparison between N/P and their absolute concentrations is thus recommended. In our sets of models, replacing N and P concentrations with their ratio did not greatly affect the overall fit. However, for the two best models, N/P explained less variance in SAV than P concentration alone (respectively $R^2 = 0.34$ and $R^2 = 0.44$). As result, the residual variance on SAV was better explained by temperature than TSS. Whereas we do not have a clear explanation for mechanisms behind the negative effect of temperature on SAV, this result is consistent with what previously found by Lefcheck et al. (2018) and deserves more attention in the future. Nevertheless, the two models were very consistent with *a priori* knowledge of the ecosystem, and all the other relationships in the model remain unchanged (compare Fig. 4B with Fig. S3B).

## Supplementary references

Barko JW, Smart MR. 1981 Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecol. Monogr.* 51, 219-236.

Blindow I. 1992 Long-and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. *Freshw. Biol.* 28, 15-27.

Bornette G, Puijalon S. 2011 Response of aquatic plants to abiotic factors: a review. *Aquat. Sci.* 73, 1-14. (doi: 10.1007/s00027-010-0162-7).

Henderson BA. 1985 Factors affecting growth and recruitment of yellow perch, *Perca flavescens* Mitchill, in South Bay, Lake Huron. *J. Fish. Biol.* 26, 449-458.

Hudon C, Cattaneo A, Tourville Poirier AM, Brodeur P, Dumont P, Mailhot Y, Amyot JP, Despatie SP, de Lafontaine Y. 2012 Oligotrophication from wetland epuration alters the riverine trophic network and carrying capacity for fish. *Aquat. Sci.* 74, 495-511. (doi:10.1007/s00027-011-0243-2).

Kitchell JF, Stewart DJ, Weininger D. 1977 Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish Res. Board. Can.* 34, 1922-1935.

Koerselman W, Meuleman AFM. 1996 The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* 33, 1441-1450.

Lacoul P, Freedman B. 2006 Environmental influences on aquatic plants in freshwater ecosystems. *Environ. Rev.* 14, 89-136. (doi:10.1139/A06-001).

Nikolai SJ, Dzialowski AR. 2014 Effects of internal phosphorus loading on nutrient limitation in a eutrophic reservoir. *Limnologica* 49, 33-41. (doi:10.1016/j.limno.2014.08.005).

Post JR. 1990 Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): *in situ* estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* 47, 554-560.

Radke RJ, Gaupisch A. 2005 Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): Possible implications for fish community structure in lakes. *Naturwissenschaften* 92, 91-94. (doi:10.1007/s00114-004-0596-7).

Simoneau M. 2017 Qualité de l'eau des tributaires du lac Saint-Pierre : évolution temporelle 1979-2014 et portrait récent 2012-2014. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques. Direction générale du suivi de l'état de l'environnement, ISBN 978-2-550-76229-4 (PDF), 54 p. + 13 ann. (http://www.mddelcc.gouv.qc.ca/eau/lac-st-pierre/qualite-eau-tributaires.pdf). Bibliothèque et Archives nationales du Québec.

Søndergaard M, Lauridsen TL, Johansson LS, Jeppesen E. 2017 Nitrogen or phosphorus limitation in lakes and its impact on phytoplankton biomass and submerged macrophyte cover. *Hydrobiologia* 795, 35-48. (doi:10.1007/s10750-017-3110-x).

Verhoeven JTA, Koerselman W, Meuleman AFM. 1996 Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: Relations with atmospheric inputs and management regimes. *Trends Ecol. Evol.* 11, 494-497. (doi:10.1016/S0169-5347(96)10055-0).

Vis C, Cattaneo A, Hudon C. 2008 Shift from chlorophytes to cyanobacteria in benthic macroalgae along a gradient of nitrate depletion. *J. Phycol.* 44, 38-44. (doi:10.1111/j.1529-8817.2007.00429.x).

Wellington CG, Mayer CM, Bossenbroek JM, Stroh NA. 2010 Effects of turbidity and prey density on the foraging success of age 0 year yellow perch *Perca flavescens*. *J. Fish. Biol.* 76, 1729-1741. (doi:10.1111/j.1095-8649.2010.02612.x).

## Tables

**Table S1.** Results of the model comparison for the main conceptual model (based on N and P as predictors of SAV abundance). The first model (full model) includes all the hypothesized relationships. The best fitting model choice was based on the backward selection criterion, dropping the less significant variables one at a time. All models fitted the data well ($p>0.05$), and the best model choice (in bold) was based on the parsimony criterion without penalizing the $R^2$ of endogenous variables.

| STRUCTURAL EQUATION MODEL FORMULA | Fisher's C | P-value | df | AIC | $R^2$ |
|---|---|---|---|---|---|
| - SAV ~ WATER LEVEL + log(TURBIDITY) + TSS + TEMPERATURE + P + N<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ SAV + TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 10.19 | 0.75 | 14 | 54.19 | 0.45<br>0.14<br>0.50 |
| - SAV ~ WATER LEVEL + log(TURBIDITY) + TSS + TEMPERATURE + P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ SAV + TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 6.86 | 0.74 | 10 | 48.86 | 0.45<br>0.14<br>0.50 |
| - SAV ~ WATER LEVEL + TSS + TEMPERATURE + P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ SAV + TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 7.15 | 0.85 | 12 | 47.15 | 0.45<br>0.14<br>0.50 |
| - SAV ~ TSS + TEMPERATURE + P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ SAV + TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 7.24 | 0.93 | 14 | 45.24 | 0.45<br>0.14<br>0.50 |
| - SAV ~ TSS + TEMPERATURE + P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 8.10 | 0.95 | 16 | 44.10 | 0.45<br>0.14<br>0.50 |

**Table S1** (Follows)

| **STRUCTURAL EQUATION MODEL FORMULA** | **Fisher's C** | **P-value** | **df** | **AIC** | **$R^2$** |
|---|---|---|---|---|---|
| - SAV ~ TSS + P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 9.21 | 0.96 | 18 | 43.21 | 0.44<br>0.14<br>0.50 |
| - SAV ~ TSS + P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ WATER LEVEL + log(TURBIDITY) + TSS | 5.68 | 0.97 | 14 | 37.68 | 0.44<br>0.14<br>0.52 |
| **- SAV ~ TSS + P**<br>**- CPUE ~ SAV + GROWTH**<br>**- GROWTH ~ WATER LEVEL + log(TURBIDITY)** | **6.82** | **0.98** | **16** | **36.82** | **0.44**<br>**0.14**<br>**0.50** |
| - SAV ~ P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ WATER LEVEL + log(TURBIDITY) | 5.72 | 0.93 | 12 | 33.72 | 0.28<br>0.14<br>0.50 |
| - SAV ~ P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ WATER LEVEL | 4.76 | 0.78 | 8 | 30.76 | 0.28<br>0.14<br>0.40 |

**Table S2.** Results of the model comparison for the alternative conceptual model (based on N/P ratio as predictor of SAV abundance). The first model (full model) includes all the hypothesized relationships. The best fitting model choice was based on the backward selection criterion, dropping the less significant variables one at a time. All models fitted the data well ($p>0.05$), and the best model choice (in bold) was based on the parsimony criterion without penalizing the $R^2$ of endogenous variables.

| STRUCTURAL EQUATION MODEL FORMULA | Fisher's C | P-value | df | AIC | $R^2$ |
|---|---|---|---|---|---|
| - SAV ~ WATER LEVEL + log(TURBIDITY) + TSS + TEMPERATURE + N/P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ SAV + TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 4.98 | 0.89 | 10 | 46.98 | 0.39<br>0.14<br>0.50 |
| - SAV ~ log(TURBIDITY) + TSS + TEMPERATURE + N/P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ SAV + TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 5.30 | 0.95 | 12 | 45.30 | 0.39<br>0.14<br>0.50 |
| - SAV ~ log(TURBIDITY) + TSS + TEMPERATURE + N/P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 6.02 | 0.97 | 14 | 44.02 | 0.39<br>0.14<br>0.50 |
| - SAV ~ TSS + TEMPERATURE + N/P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ TEMPERATURE + WATER LEVEL + log(TURBIDITY) + TSS | 6.40 | 0.98 | 16 | 42.40 | 0.37<br>0.14<br>0.50 |
| - SAV ~ TSS + TEMPERATURE + N/P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ WATER LEVEL + log(TURBIDITY) + TSS | 7.57 | 0.98 | 18 | 41.57 | 0.37<br>0.14<br>0.52 |
| - SAV ~ TSS + TEMPERATURE + N/P<br>- CPUE ~ SAV + GROWTH<br>- GROWTH ~ WATER LEVEL + log(TURBIDITY) | 8.65 | 0.99 | 20 | 40.65 | 0.37<br>0.14<br>0.50 |

**Table S2** (Follows)

| **STRUCTURAL EQUATION MODEL FORMULA** | **Fisher's C** | **P-value** | **df** | **AIC** | **R²** |
|---|---|---|---|---|---|
| **- SAV ~ TEMPERATURE + N/P** | | | | | **0.34** |
| **- CPUE ~ SAV + GROWTH** | **9.45** | **0.89** | **16** | **39.45** | **0.14** |
| **- GROWTH ~ WATER LEVEL + log(TURBIDITY)** | | | | | **0.50** |
| - SAV ~ N/P | | | | | 0.26 |
| - CPUE ~ SAV + GROWTH | 7.16 | 0.85 | 12 | 35.16 | 0.14 |
| - GROWTH ~ WATER LEVEL + log(TURBIDITY) | | | | | 0.50 |
| - SAV ~ N/P | | | | | 0.26 |
| - CPUE ~ SAV + GROWTH | 5.61 | 0.69 | 8 | 31.61 | 0.14 |
| - GROWTH ~ WATER LEVEL | | | | | 0.40 |

**Table S3.** Parameter estimates from the best pSEM for the main set of models (Table S1, in bold). The significant pathways are represented in bold. ~~ indicates correlated errors.

| RESPONSE | PREDICTOR | STANDARD ESTIMATE | STANDARD ERROR | P-value |
|---|---|---|---|---|
| SAV | TSS | -0.564 | 0.362 | 0.140 |
| **SAV** | **P** | **1.033** | **0.381** | **0.016** |
| CPUE | SAV | 0.279 | 0.230 | 0.244 |
| CPUE | GROWTH | 0.249 | 0.212 | 0.260 |
| **GROWTH** | **WATER LEVEL** | **-0.526** | **0.179** | **0.010** |
| GROWTH | log(TURBIDITY) | -0.382 | 0.202 | 0.078 |
| ~~log(TURBIDITY) | ~~TSS | 0.286 | NA | 0.251 |
| ~~P | ~~GROWTH | -0.140 | NA | 0.296 |

**Table S4.** Parameter estimates from the best pSEM for the alternative set of models (Table S2, in bold). The significant pathways are represented in bold. ~~ indicates correlated errors.

| **RESPONSE** | **PREDICTOR** | **STANDARD ESTIMATE** | **STANDARD ERROR** | **P-value** |
|---|---|---|---|---|
| SAV | TEMPERATURE | -0.260 | 0.206 | 0.227 |
| **SAV** | **N/P** | **-0.513** | **0.220** | **0.034** |
| CPUE | SAV | 0.279 | 0.230 | 0.244 |
| CPUE | GROWTH | 0.249 | 0.212 | 0.260 |
| **GROWTH** | **WATER LEVEL** | **-0.526** | **0.179** | **0.010** |
| GROWTH | log(TURBIDITY) | -0.382 | 0.202 | 0.078 |
| ~~N/P | ~~GROWTH | 0.407 | NA | 0.948 |

## Figures

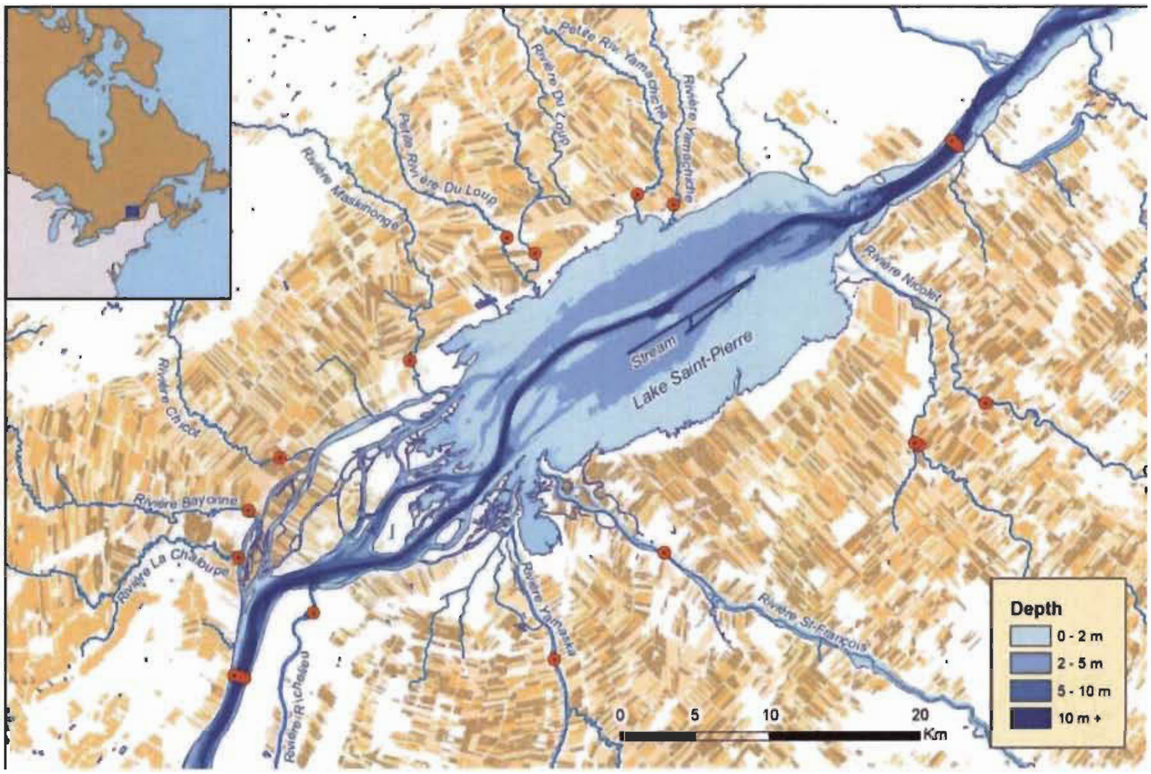

**Fig. 1.** Lake Saint-Pierre (LSP), its watershed and major tributaries, and the surrounding agricultural regions. Orange dots represent sampling stations. Information on the variables used and their calculation is provided in the section "Environmental data".

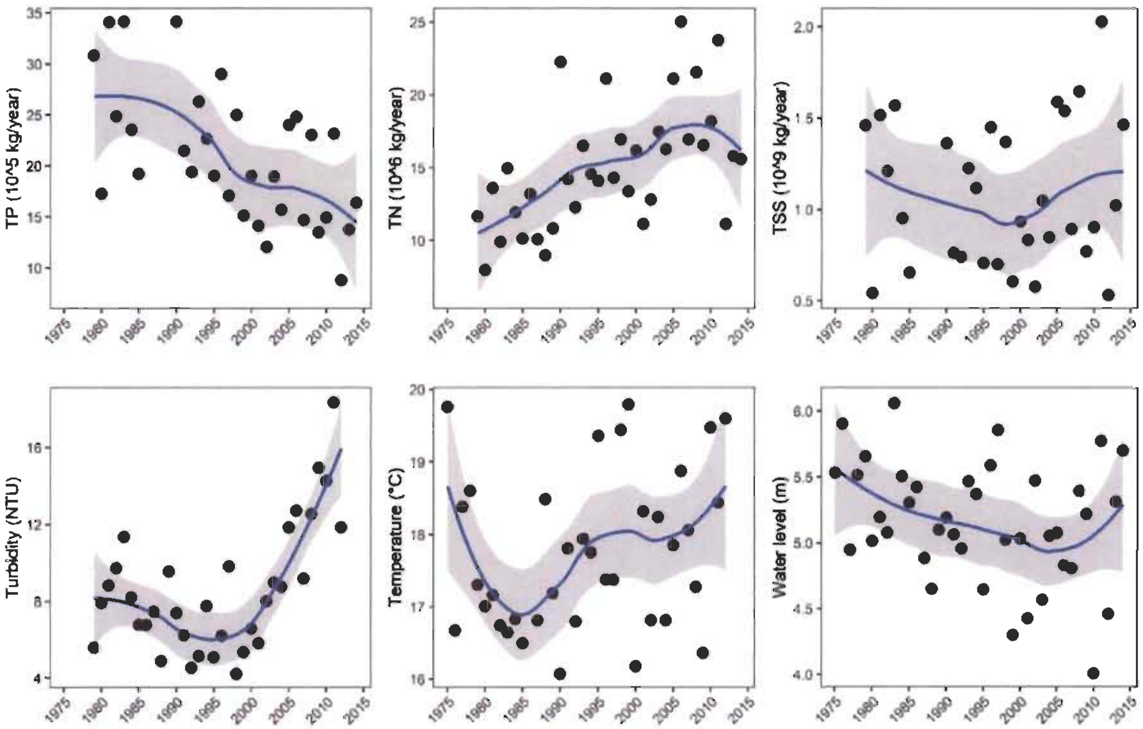

**Fig. 2.** Time series of abiotic variables (data not transformed). Upper panels from left to right: total phosphorus (TP), total nitrogen (TN), total suspended solids (TSS); lower panels: turbidity, temperature, spring water level. See the section "Environmental data" for details on variable calculations. Data are smoothed using a local polynomial regression fitting (LOESS, blue line), and the associated standard error is in the shaded grey area.

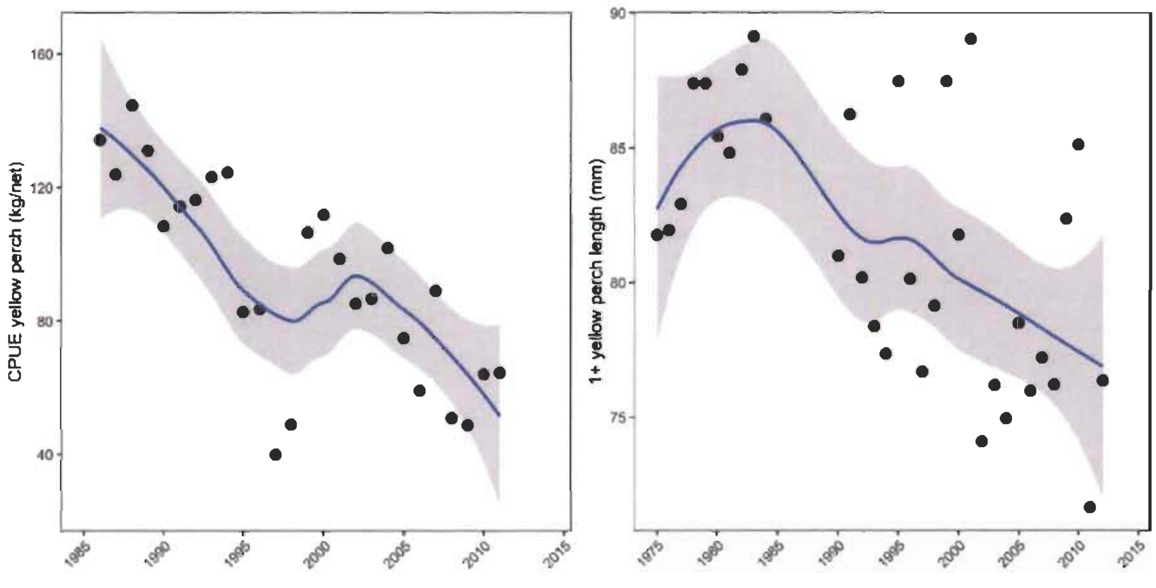

**Fig. 3.** Yellow perch commercial landings expressed as catch per unit effort (CPUE, left panel) and length of age 1+ yellow perch, back-calculated from opercula readings (right panel). See Material and Methods for details.

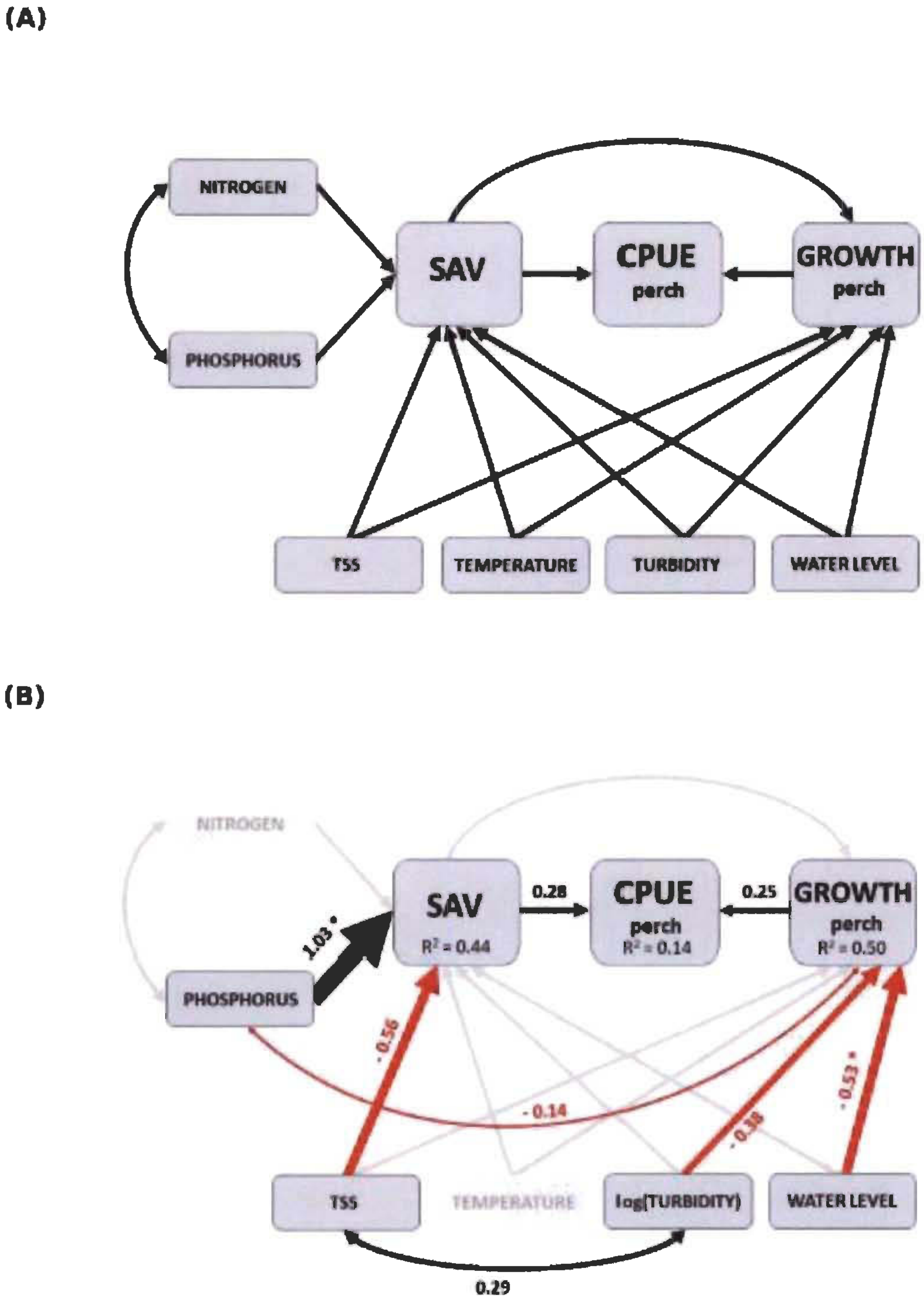

**Fig. 4.** (A) Conceptual model showing how the interactions between abiotic variables, SAV abundance, and YP growth can affect YP commercial landings with a four-year lag (CPUE). (B) Best fitting structural equation model. Boxes with black lettering joined by black or red arrows show variables and pathways that were retained during model selection; the semi-transparent boxes and grey arrows indicate variables and pathways that were not retained. Arrow width is proportional to the reported standard estimates (asterisks indicate significance at $p < 0.05$). Red and black arrows represent negative and positive relations, respectively.

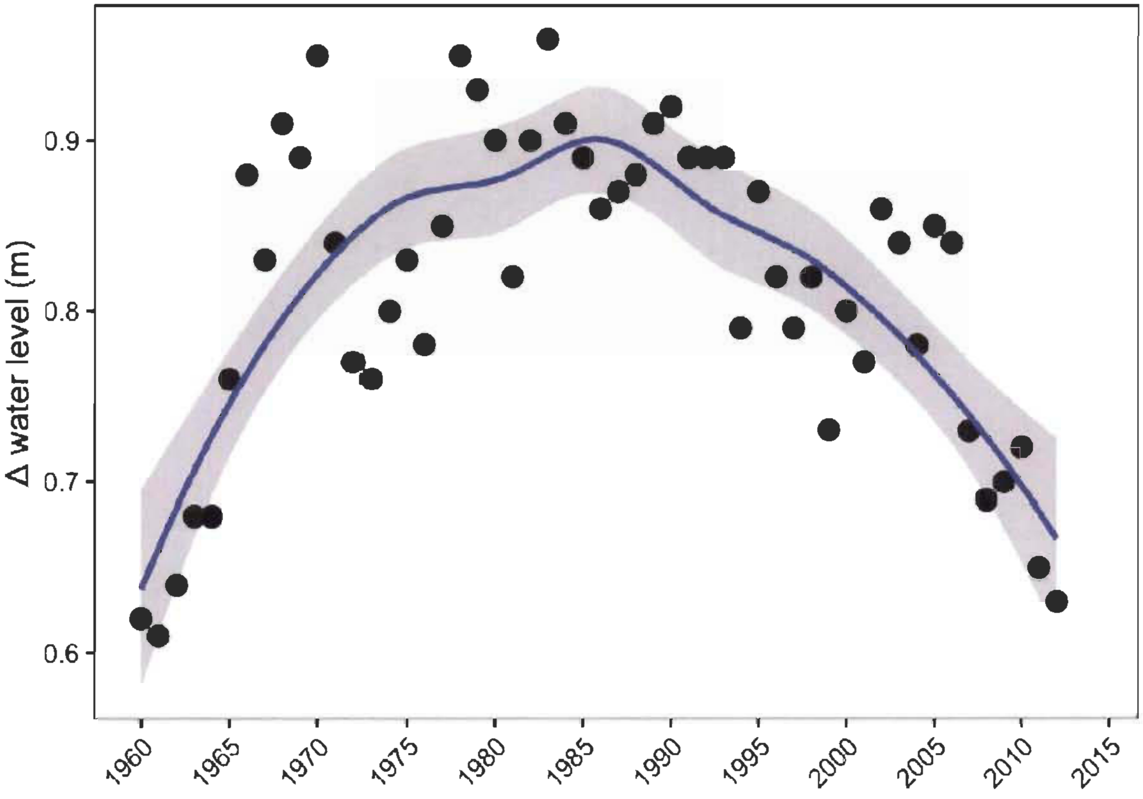

**Fig. 5.** Back-calculated SAV abundance estimated by the difference in water level between the inlet and the outlet of Lake St. Pierre (summer Δ water level). Data are smoothed by means of local polynomial regression fitting (LOESS, blue line), and the associated standard error is the shaded grey area.

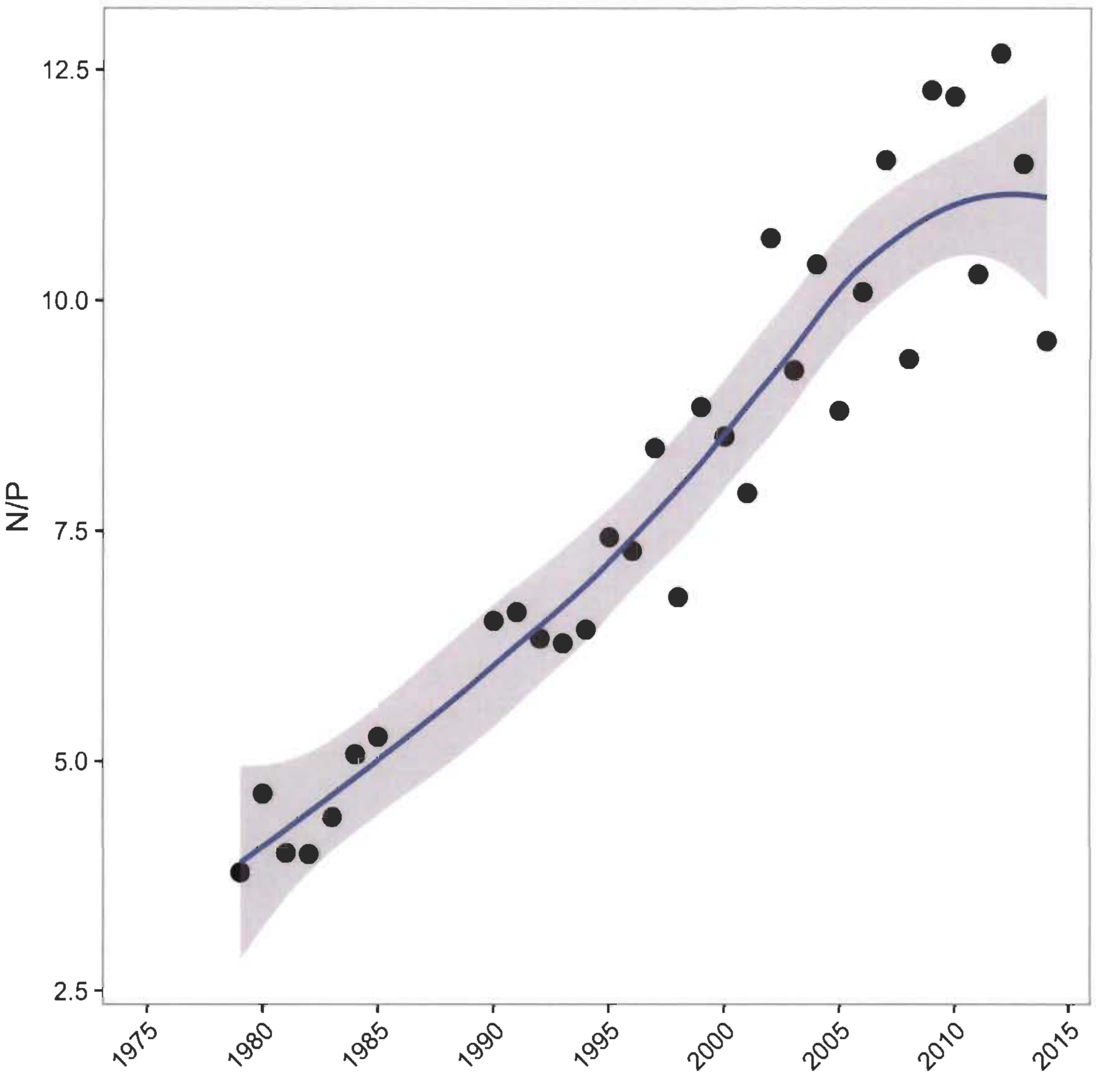

**Fig. S1.** Long-term N/P ratio calculated at seven tributaries (eight stations) in LSP tributaries (see details in the "Environmental data" section in the main text). Data are smoothed using a local polynomial regression fitting (LOESS, blue line), and the associated standard error is in the shaded grey area.

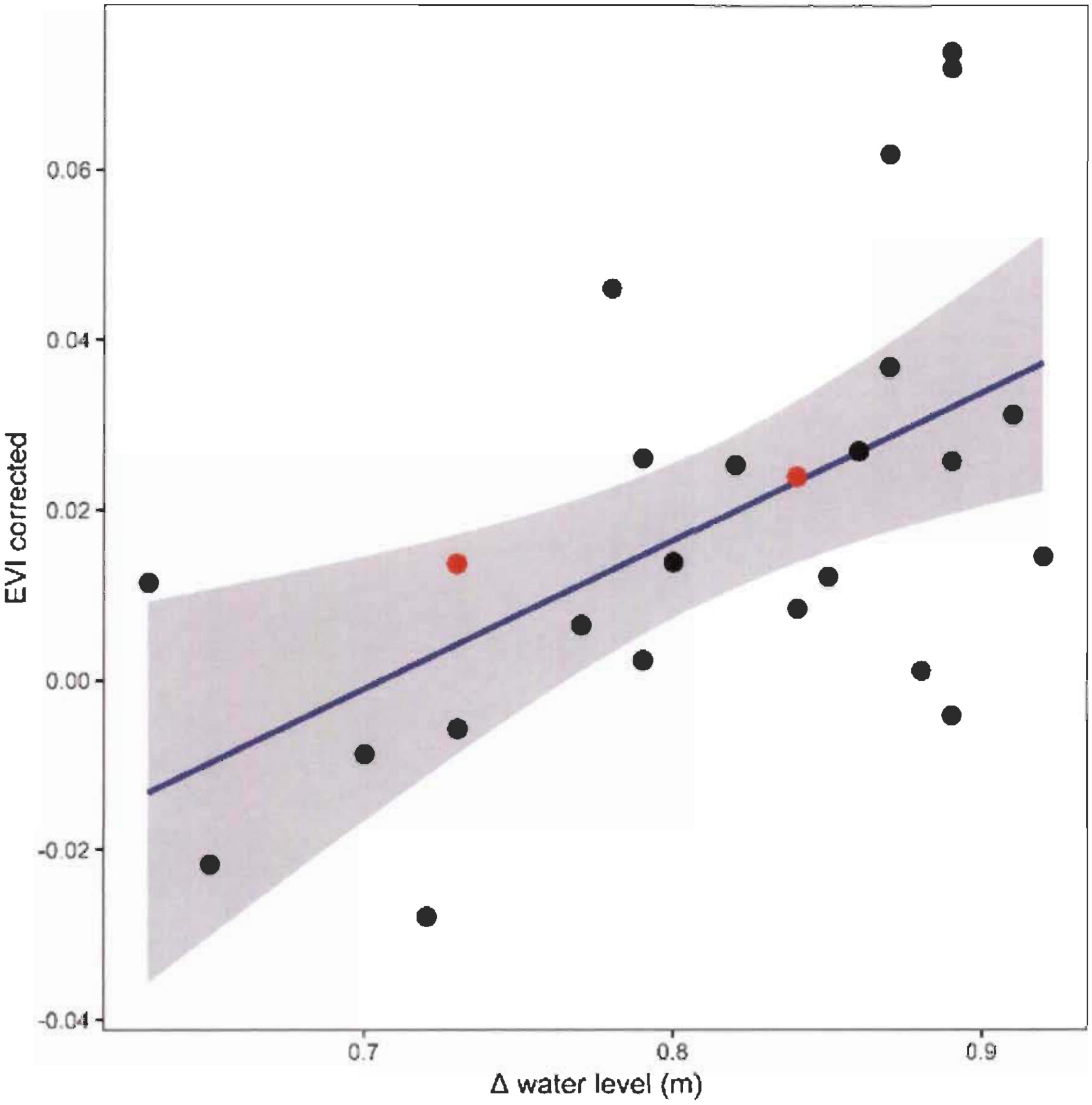

**Fig. S2.** Relationship between SAV abundance (estimated as the yearly mean August value of the proxy variable "Δ water level") and the corrected values (average residuals) of the enhanced vegetation index (EVI). EVI values were corrected using a GAMM controlling for the date on which the satellite picture was taken and for the water depth. Red dots represent years for which satellite pictures were not taken in August, at peak SAV abundance, for technical reasons. Analyses performed including either all data (Pearson correlation = 0.55) or removing these two data points (Pearson correlation = 0.56) gave similar results. Data range from 1985 to 2012. Data are fitted using a linear model (blue line), and the associated standard error is in the shaded grey area.

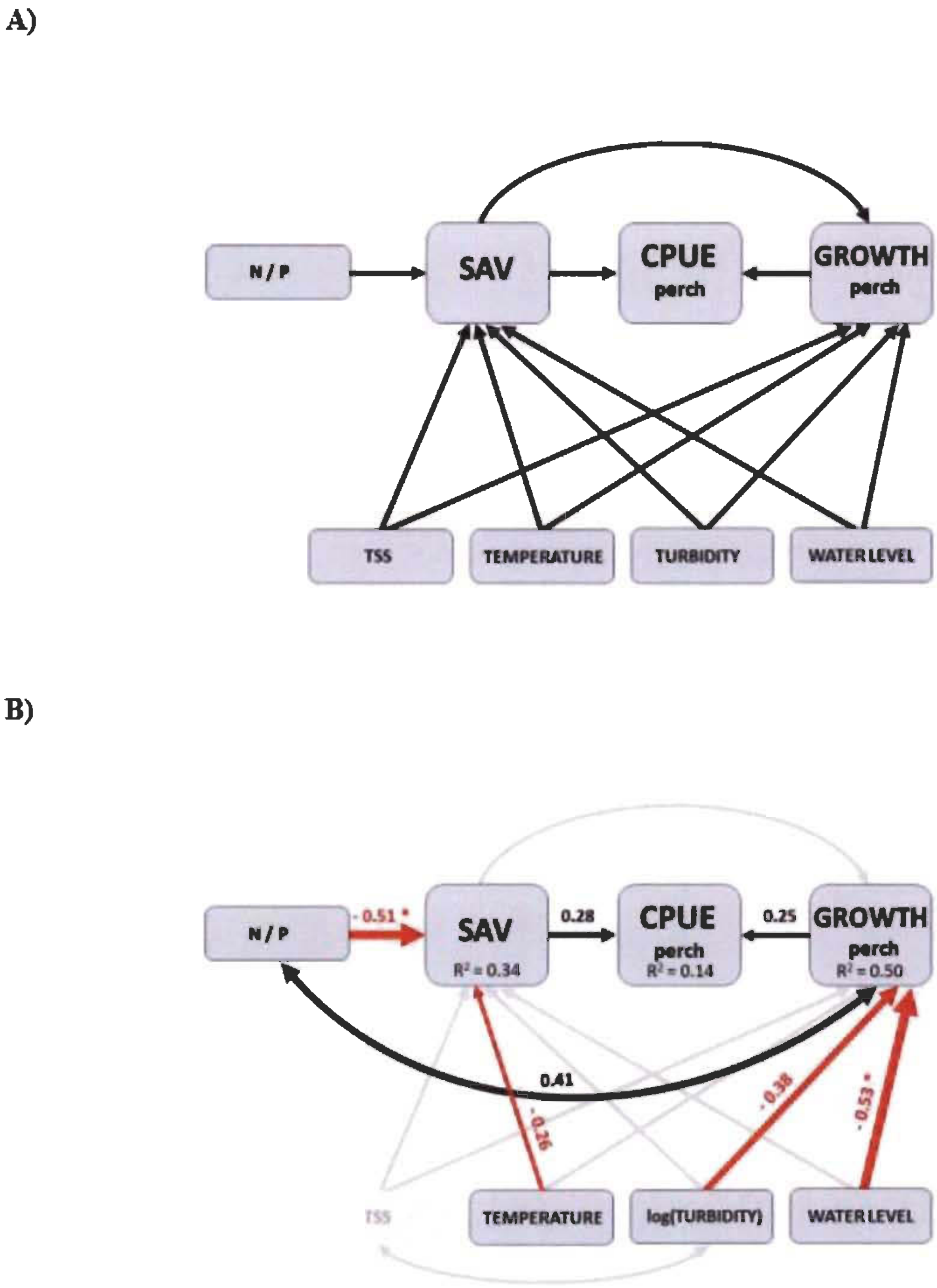

**Fig. S3.** (A) Alternative conceptual model showing how the interactions between abiotic variables, SAV abundance, and YP growth can affect YP commercial landings with a four-year lag (CPUE). Note that here N/P replaces N and P loads that were included in the main conceptual model. (B) Best fitting structural equation model. Boxes with black lettering joined by black or red arrows show variables and pathways that were retained during model selection; the semi-transparent boxes and grey arrows indicate variables and pathways that were not retained. Arrow width is proportional to the reported standard estimates (asterisks indicate significance at $p < 0.05$). Red and black arrows represent negative and positive relationships, respectively.

# CHAPTER II

# THE ROLES OF AQUATIC VEGETATION AND SOLAR RADIATION IN DRIVING YELLOW PERCH LARVAE DISTRIBUTION IN A SHALLOW FLUVIAL LAKE

This article is submitted to *Limnology and Oceanography*.

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## Author contributions

Giacomazzo M., Bertolo A., Magnan P., Brodeur P. conceived the idea. Brodeur P. provided fish data, Massicotte P. calculated light attenuation coefficients and irradiance data and Giacomazzo M. performed statistical analyses. All authors contributed critically to the drafts and gave final approval for publication.

## Abstract

Dispersal of pelagic fish larvae is deemed mainly passive, but several examples suggest that active habitat selection might be determinant for their survival. Once a suitable habitat to settle is found, larvae still need to avoid threats that reduce their fitness and exacerbate mortality risks. The aim of this study was to assess yellow perch (*Perca flavescens*) larvae distribution along two isobaths of a shallow fluvial lake in relationship with factors potentially affecting their survival: daily variations in solar irradiance, optical properties of the water column and aquatic vegetation. More precisely, we have evaluated the importance of variations in both visible and UV solar radiation, turbidity, and aquatic vegetation abundance in relationship with the vertical distribution of yellow perch larvae as proxies of larvae active behavioral habitat choice. We also assessed the importance of aquatic vegetation and UV risk in driving the differences in abundance between two different isobaths. Our results show that larvae always aggregated in the lower part of the water column (40-80 cm depth) and that aquatic vegetation (but not UV risk) apparently drove their aggregation patterns both within (i.e. on the vertical axis) and among stations. Turbidity also resulted to be a driver of larvae distribution on both the vertical and horizontal axis, being associated to higher aggregation at surface layers. Finally, after controlling for the other factors, variation in visible light irradiance was associated to a higher aggregation of larvae at surface layers, giving additional support to the view that larvae are actively selecting their habitat.

**Keywords:** Yellow perch larvae, vertical distribution, UV and visible radiation, aquatic vegetation, turbidity

## Introduction

Dispersal is a key factor for fish larvae, determining their probability of survival, settling, and ultimately contributing to drive the range of distribution of species (Sale, 2004). Many fish species begin their life as pelagic larvae with limited locomotion capabilities and therefore their dispersal mode is primarily passive and driven by currents (Leis, 2006). Given this dependence on hydrodynamic forces (e.g. wind-driven and large-scale currents; Kingsford, 1990), it is not unlikely that larvae settlement might occur in a sub-optimal habitat for their development, with potential dramatic consequences for inter-annual population recruitment (Sale, 2004). However, whereas previously considered as mainly passive particles drifted by the currents, the larvae of some fish species have been shown to be able to make active habitat choices (e.g. sheltering into reefs or vegetation), thus increasing their probability of survival (Montgomery et al., 2001; Leis, 2006). For instance, larvae can actively control their vertical position in the water column to exploit layers with different water velocities and thus ultimately change their horizontal distribution with minimum metabolic costs (Norcross and Shaw, 1984). Whereas such type of movement still has a passive component, it might be driven by an active behavioral choice (Montgomery et al., 2001). Conversely, late-stage larvae are better swimmers (Stobutzki and Bellwood 1994; Dudley et al. 2000) and can move towards suitable habitats from considerable distance (Stobutzki and Bellwood, 1998) by using ambient sound, as well as visual and/or chemosensory cues (Tolimieri et al., 2000; Lecchini et al., 2005; Wenger et al., 2011).

Whereas light is a key factor for visually oriented predators, solar radiation represents a potential stressor, because of the presence of damaging wavelengths such as UV radiation (UVR; both UV-A and UV-B; Olson et al., 2006). UVR have been shown to be deleterious for unpigmented organisms such as yellow perch larvae (Boily et al., 2011). This is particularly true in clear shallow waters, where UVR can potentially penetrate through the entire water column, thus increasing the mortality risk for fish larvae (Olson et al., 2006). UV-A are less damaging than UV-B, but they can penetrate deeper in the water column (Tedetti and Sempéré, 2006). UV-A and UV-B are known to affect larvae physiology, increasing oxidative stress, damaging DNA, inducing apoptosis (but see Provencher et al.

2014), and eventually decreasing survival (see Dahms and Lee, 2010 for an exhaustive review). Adult yellow perch can detect UVR (Williamson et al., 1997; Huff et al., 2004) and therefore one can expect that irradiance variations of these damaging wavelengths can drive yellow perch vertical distribution by affecting their behavior (i.e. avoidance phenomenon).

Depth has other potential effects on fish larvae since it can also modulate the mechanical action of waves, and, in turn, increase larvae mortality by exposing them to siltation or pushing them ashore (Stoll and Beeck, 2011). The survival of larvae is also potentially under the control of other limnological factors such as turbidity and suspended sediments, which have detrimental effects on larvae, impairing among other things their capability to detect potential settlement sites (Wenger et al., 2011). Also, variations in the concentration of the chromophoric component of dissolved organic matter (cDOM) has the potential to affect larvae survival by decreasing UVR penetration in the water column in darker waters (Kirk, 2011). Huff et al. (2004) found that adult yellow perch adjust their spawning depth in function of water color to reduce UVR exposure for eggs and embryos, even if this behavior can ultimately lead spawners to lay eggs at sub-optimal temperatures. Finally, both emerged and submerged aquatic vegetation (hereafter EAV and SAV, respectively) can also mitigate the effects of UVR, by providing shadowed areas allowing larvae to shelter.

Shallow ecosystems are compelling ecological models to get insights about larvae habitat selection in terms of vertical distribution. In these aquatic ecosystems, many of the stressors presented above may interact on a very small scale (at less than one-meter depth in some cases, as in the present study) and their effects could be amplified compared to deeper systems.

Yellow perch larvae (YPL) are among the smallest freshwater fish larvae (Houde 1994). They are pelagic, transparent and are expected to display positive phototropic behavior during the first weeks after hatching, then switching towards a negative phototropism with development (Sandström, 1999). In a shallow fluvial lake, it was suggested that

YPL dispersal was not merely a passive process, with larvae showing a clear association with AV at the whole lake scale which could not be explained entirely by large-scale directional forces (Bertolo et al., 2012; Massicotte et al., 2015). Such a relationship might be driven (at least partially) by an active habitat choice by YPL, thus mitigating the importance of drift. However, given the potential antagonistic effects between positive phototropism (surface aggregation to increase food intake in optimal light environment) and UVR avoidance (aggregation at the bottom to reduce UVR-induced mortality), it is difficult to predict the outcome of their interplay on vertical distribution of YPL in natural systems.

The goal of this study was to investigate the effect of incident solar radiation, light attenuation in the water column (mitigated by turbidity and water optical parameters), and AV on YPL distribution, both on the vertical and horizontal axis in a shallow fluvial system (Lake Saint-Pierre; hereafter LSP; St-Lawrence River; Québec, Canada). Given the shallowness of this system, we assumed that YPL vertical distribution was driven at least partly by an active behavioral habitat choice, whereas YPL distribution across sampling stations (separated by at least 500 m) could be due to a combination of factors such as passive dispersal and mortality.

We tested three hypotheses ($H_{1.1}$-$H_{1.3}$) in relationship with YPL vertical distribution in the water column by analyzing their aggregation patterns between the upper (0-0.4 m depth) and the lower portion of the water column (0.4-0.8 m depth) at the 1.2 m isobath (Fig. 1):

> $H_{1.1}$ – Positive phototropism hypothesis: i) YPL will show an overall tendency to aggregate at the water surface in response to the vertical gradient of visible light; and ii) they will aggregate ever densely when the irradiance of visible light is high.
>
> $H_{1.2}$ – UVR avoidance hypothesis: in contrast to what predicted by $H_{1.1}$, YPL will adjust their vertical position as a function of UVR penetration in the water column by aggregating towards the bottom when UVR risk is high (to shelter from UVR-induced mortality), independently from AV.

> $H_{1.3}$ – Aquatic vegetation shading hypothesis: We predict YPL will aggregate at the bottom in the presence of AV to reduce UVR and/or predation risk.

We tested two additional hypotheses ($H_{2.1}$-$H_{2.2}$) in relationship with the horizontal distribution patterns of YPL among sites by comparing their abundance at both shallow and deep sites (respectively isobaths 0.8 and 1.2 m) at the scale of the whole lake (Fig. 1):

> $H_{2.1}$ – UVR risk hypothesis. YPL will exhibit higher abundance at sites with a low UVR penetration in the water column (i.e. operationally defined by high turbidity or high UVR extinction coefficients) because of a lower risk of UVR-induced mortality. When the UVR risk is high, YPL will be more abundant at the deep isobath compared to the shallow one because of the availability of a larger refuge against UVR towards the bottom (i.e. overall lower risk of mortality). Based on previous knowledge, UVR risk at the bottom of the 120 cm depth isobath is mostly close to zero in LSP, whereas this is not always the case at the shallower sites (Frenette et al. 2006).
>
> $H_{2.2}$ – Aquatic vegetation refuge hypothesis. Similarly to the prediction at the scale of the water column, YPL will be more abundant in presence of AV. At this scale, we expect a combination of factors (behavior and mortality) as potential drivers of YPL abundance among sampling sites. Moreover, we predict YPL to be more strongly associated with AV at the shallow isobath compared to the deep one, because of the overall risk of UVR-induced mortality.

To test these hypotheses, we used a database on YPL collected each spring during a period spanning 11 years. YPL were captured yearly at more than 200 sampling sites distributed on two isobaths (60-80 and 100-120 cm depth). The larvae abundance data were modeled by using habitat variables (sampling depth or isobath; turbidity; vegetation abundance) coupled with hourly estimations of solar irradiance (both visible and UV; using an atmospheric radiative transfer model), and estimated values of light attenuation coefficients in the water column based on remote sensing calibrated on field data.

## Materials and methods

### *Study system*

LSP is the largest fluvial lake of the St. Lawrence River covering an area of approximately 400 $km^2$ (Fig. 1). LSP is a compelling ecosystem to study stressors affecting larvae distribution, given its limited depth, the absence of a typical pelagic area and the spatial variability in water optical properties (Frenette et al. 2003). LSP has a reduced water velocity ($< 0.5$ m $s^{-1}$ in most areas), is shallow (mean depth approx. 3 m), except for the artificial navigation channel that is approximately 11 m deep (Hudon and Carignan, 2008). LSP receives water from several tributaries, characterized by different physical and biogeochemical characteristics (Frenette et al., 2003; 2012). The south shore tributaries drain watersheds mainly characterized by agricultural areas, carrying high inputs of nutrients and sediments as well as a wide spectrum of contaminants, while north shore tributaries have lower nutrient concentrations and are less polluted (Simoneau, 2017). The lake's floodplain covers approximately 140 $km^2$ during spring flood, which lasts five to nine weeks, and represents an important spawning ground for yellow perch (Mailhot et al., 2015).

Once eggs hatch, YPL slowly drift offshore and along the shallow shorelines, with higher abundances in sheltered and vegetated bays (Bertolo et al., 2012). The AV represents both a feeding and a growth habitat for YPL (Paradis et al., 2014). Although eventually patchy, AV can be very abundant during the summer in LSP, eventually forming a canopy at the surface (Hudon et al., 2012). The most abundant SAV species are American eel-grass (*Vallisneria americana*) and pondweeds (*Potamogeton richardsonii* and *Stuckenia pectinata*). Emergent vegetation is mainly represented by bulrushes (*Schoenoplectus fluviatilis*, *S. lacustris*, and *S. pungens*), broad-fruited bur-reed (*Sparganium eurycarpum*), and broad-leaved arrow-leaf (*Sagittaria latifolia*) (Massicotte et al., 2015).

### *Larval sampling*

YPL were collected with push-nets (2 m long plankton nets; 500 µm mesh size; 0.4 x 0.4 square mount), pushed forward by motorized boats at a velocity of 1 m $s^{-1}$, parallel to the shoreline. Two boats were used (each equipped with two nets), one sampling along the 60-80 cm isobath (with both nets at the surface; 0-40 cm depth) and the other sampling along the 100-120 cm isobath (with one surface net at 0-40 cm depth and the other at 40-80 cm depth) (Fig. 1). These isobaths (average distance between them > 500 m) were selected based on a pilot study which detected close to zero YPL abundances outside the 50-150 cm depth range (P. Brodeur, unpubl. res.). Sampling was performed between 2005 and 2016, usually 2-3 weeks after hatching (785 stations, ca. from the end of May to half of June, i.e. before larvae develop a sufficient swimming capability to avoid sampling nets). The chosen sampling period represents a snapshot of the YPL distribution pattern during the peak of their dispersal phase (Bertolo et al., 2012). After collection, YPL were narcotized with tricaine methanesulfonate (MS-222$^{TM}$ – Sandoz) and immediately preserved in 95% ethanol for laboratory identification and measurement (at the nearest 0.01 mm) under binocular microscope.

### *Aquatic vegetation*

At each sampling site, EAV and SAV were visually estimated both at the beginning and at the end of the transect, using the following semi-quantitative scale: 0 (open water), 1 (sparse), 2 (dense, bottom visible), 3 (very dense, bottom non-visible, open water at the surface), 4 (extremely dense, bottom non-visible, canopy at the surface). Whenever values did not coincide at the beginning and at the end of the transect, we used the following conservative criterion to get a unique AV class per site: if one of the two measures was either 0 (open water) or 1 (sparse), the overall value for the transect was fixed to 1 (sparse); for all other combinations we averaged and rounded classes to the lower unit (i.e. 2 and 3 = 2; 2 and 4 = 3; 3 and 4 = 3).

### *Surface irradiance and light vertical attenuation in the water*

Surface downwelling irradiance, $E_d(0^+)$, was derived from a precomputed Look-Up-Table (LUT) generated using the Santa Barbara DISORT Atmospheric Radiative Transfer model (SBDART; Ricchiazzi et al., 1998) as described in Bélanger et al. (2013) and Laliberté et al. (2016). $E_d(0^+)$ was estimated hourly for the whole LSP area and for each sampling year with the assumption that the incoming sunlight at the surface was uniform over the study area. Moderate Resolution Imaging Spectroradiometer onboard Aqua satellite (MODISA) was used to extract the daily ozone, cloud fraction, and the cloud cover parameters needed to extract hourly $E_d(0^+)$ from the LUT between 290 and 700 nm.

### *Estimation of the vertical attenuation coefficients*

Vertical downwelling irradiance ($E_d$) profiles were obtained in LSP at 142 stations in 2015 and at 50 stations in 2016. Vertical attenuation coefficients ($K_d$) were thus calculated based on $E_d$ profiles at five different wavelengths (313, 320, 340, 443 and 550 nm) using a PUV-2500 submersible profiler radiometer (Biospherical Instruments, San Diego, CA, USA), slowly lowered into the water column. At each location, $K_d$ were calculated by using the slope of a log-linear regression between irradiance and depth. Only vertical profiles containing at least 25 observations and a coefficient of determination ($R^2$) of at least 0.9 were retained. These data were used to construct a model to predict *in situ* $K_d$ for all the stations/years at the scale of the whole LSP. This was done using satellite imagery reflectance from Landsat 7 and 8 with a pixel resolution of 30 m by 30 m. The reader is referred to https://landsat.gsfc.nasa.gov/landsat-data-continuity-mission/ for a detailed overview of the spectral and spatial characteristics of these sensors. Satellite images were selected based on their quality (i.e. with a low cloud coverage) and to temporal match with YPL sampling dates (between the 5th May and the 14th June). Pixels of the satellite images contaminated with clouds and cloud shadows were removed/masked using the Matlab *FMask* toolbox (https://github.com/GERSL/Fmask). Before matching up *in-situ* measurements and satellite reflectances, atmospheric scattering correction and conversion of sensors digital numbers to reflectances were performed using the dark object subtraction model (DOS2), as proposed by Chavez

(1996). Then, remote sensing reflectance (Rrs) for spectral bands 1 to 8 were extracted at each *in-situ* sampling. At each location of *in-situ* measurement, the closest pixel in space of the satellite image was extracted using the *nngeo* R package (Dorman, 2020). Finally, a neural network was used to predict *in-situ* $K_d$ from extracted Rrs using the *neuralnet* R package (Fritsch et al., 2019). The model was constructed with a training set containing 80% of the data and validated using the remaining 20%. The final model was then used to predict the $K_d$ of each band at each pixel location for all the selected images. Using predicted Kd, simulated $E_d(0^+)$ at each wavelength was propagated vertically in the water column at each Landsat pixel location according to the Lambert-Beer equation:

$$E_d(z) = E_d\,(0^+) * \exp\,(-K_d * z)$$

where $E_d(z)$ is the estimated irradiance at depth $z$, $E_d(0^+)$ the irradiance at surface, $K_d$ the coefficient of light attenuation estimated using in-situ vertical irradiance measurements (see next section). Based on the Lambert-Beer equation, we also estimated the depth at which irradiance was 1% of the irradiance at the surface for each station in order to have an idea of the overall optical environment across stations.

### *Turbidity*

Nephelometric turbidity (± 0.01 NTU) was measured in the laboratory on two water samples collected at each site (one at the beginning and one at the end of the transect and then turbidity measurements were averaged) with a WTW-550 turbidity meter.

### *Statistical analyses*

YPL abundance was modeled using zero-inflated models for counts, given the large number of zero values observed in the nets (Zuur et al., 2009). The model consists of two parts: a generalized linear mixed model (GLMM) following a negative binomial or Poisson distribution to model abundance counts, allowing to include random effects, and a binomial zero inflated model. We modeled the counts with a negative binomial distribution rather than a Poisson distribution because of the presence of overdispersion in the data (i.e. variance of YPL abundance is larger than the mean). Model assumptions of linearity, homoscedasticity, and outliers were visually evaluated.

Two candidate sets of models were developed to test different *a priori* hypotheses about the effects of solar radiation on YPL abundance distribution. The first set concerned the vertical aggregation patterns of YPL ($H_{1.1}$ to $H_{1.3}$; Table 1), whereas the second one was relative to their horizontal distribution patterns between the two isobaths ($H_{2.1}$ and $H_{2.2}$; Table 2). Each set of models included a null model ($M_{1.1}$ and $M_{2.1}$, respectively; see Tables 1 and 2) containing only three explanatory variables, shared with all the other models: (1) YPL body length, (2) EAV and (3) SAV (the first two were not reported in Table 1 and 2 for sake of simplicity). Larvae body length was included in the models since i) longer YPL correspond to older individuals which should display improved swimming capabilities and therefore are expected to be more efficient to avoid sampling nets and ii) body size could be partially related to YPL abundance given that older individuals have been exposed for a longer period to mortality risk. Both EAV and SAV were included because they have been shown to affect YPL abundance and distribution (Bertolo et al., 2012). Given the higher abundance of SAV compared to EAV at our sampling sites and its expected stronger structuring effect on YPL habitat, we focused on SAV in the other models. For this reason, SAV was also included in the models in interaction with other explanatory variables (see below).

### *YPL vertical aggregation patterns (hypotheses $H_{1.1}$-$H_{1.3}$)*

The first set of models, aiming to explain the vertical aggregation patterns of YPL at the 120 cm isobath (Table 1), was used to test the positive phototropism ($H_{1.1}$), the UVR avoidance ($H_{1.2}$), and the AV shading hypothesis ($H_{1.3}$). In this set of models, the irradiance was calculated hourly at the depth of each of the two nets (20 and 60 cm deep, which corresponds to the middle depth of the surface and deep nets, respectively) for the wavelengths 340 nm and 443 nm ($E_{d\,340}$ and $E_{d\,443}$; hereafter UVR and visible light, respectively, for simplicity). We expect that visible light will explain positive aggregation in the surface layers if the overall UVR risk is low in our system ($H_{1.1}$). In contrast, we expect short-term variation in solar irradiance to be related to a stronger aggregation of YPL in deep water layers in case of strong UVR risk, as predicted by $H_{1.2}$, because we expect that the risk of mortality due to exposure to UVR should be a stronger driver than the positive phototropism.

Despite UVR and visible light differ in their penetration in the water column, irradiances at depth were still strongly correlated for these two groups of wavelengths (Pearson's $r = 0.74$). To compare their contribution to the model's fit whereas at the same time avoid collinearity problems, these variables were used to build different models rather than being included in the same one. Depth, SAV, visible light, and UVR irradiance were used to build both additive ($M_{1.1}$, $M_{1.2}$, $M_{1.4}$, $M_{1.5}$, $M_{1.9}$ and $M_{1.10}$; Table 1) and interactive models ($M_{1.3}$, $M_{1.6}$-$M_{1.8}$ and $M_{1.11}$-$M_{1.13}$; Table 1). YPL vertical aggregation was analyzed by looking at both additive and interactive models including a term for depth. Models including depth as an additive term ($M_{1.2}$, $M_{1.5}$ and $M_{1.10}$) were used to test the hypothesis that YPL do aggregate, whereas models including depth in interaction with other factors ($M_{1.3}$, $M_{1.6}$-$M_{1.8}$ and $M_{1.11}$-$M_{1.13}$) were used to test the hypothesis that aggregation is modulated by other drivers. Based on $H_{1.1}$, $H_{1.2}$, and $H_{1.3}$, the effect of visible light, UVR and SAV, respectively, are in fact expected to affect larvae abundance differently depending on depth (i.e. the net depth is expected to interact with these factors in the model). We predict that YPL will respond positively to visible light irradiance if UVR risk is low, increasing their aggregation in the upper layers (i.e. interaction between visible light and depth at the intra-site scale; $H_{1.1}$). In contrast, if UVR risk is a stronger driver of YPL behavior, we expect YPL to aggregate at the bottom and adjust their vertical position as a function of UVR penetration in the water column (i.e. moving towards the bottom with high UVR risk; $H_{1.2}$). Across sites, YPL will be more abundant in the presence of SAV, while at the scale of stations, we predict YPL to be more associated with AV at the bottom, searching for shelter given the higher UVR risk (i.e. expected significant interaction between SAV and depth; $H_{1.3}$). Therefore, we expect the most complex models ($M_{1.8}$ with the depth in interaction respectively with SAV and UVR, and $M_{1.13}$ with the depth in interaction respectively with SAV and visible light) to perform better than the respective models with additive terms only ($M_{1.5}$ and $M_{1.10}$).

Given that it was not possible to calculate irradiance at depth for all the sampling stations because cloud cover prevented the estimation of $K_d$ at various pixel locations in some cases, we built an alternative set of models where the irradiance at depth was replaced by irradiance at the surface ($E_d(0^+)$). Whereas in this case we can only have a partial insight on YPL behavior because the actual light environment they experienced in the water column was not explicitly included in the models, this alternative database allowed to expand the analysis to the full data set (785 obs instead of 470). Despite some limitations, this approach allowed thus to explore more thoroughly the effects of the hourly variation of solar irradiance on YPL behavior. A full discussion of these results is given in the supplementary materials (see also Table S1 and S2).

### *YPL distribution patterns between isobaths (hypotheses $H_{2.1}$-$H_{2.2}$)*

The second set of models (Table 2) aimed to test the hypotheses $H_{2.1}$ and $H_{2.2}$ (UVR risk and AV refuge, respectively) by analyzing factors driving YPL abundance between the isobaths. In this case, the optical environment was evaluated based on the estimation of light attenuation coefficients (i.e. $K_d$) only (i.e. not accounting for the hourly variation in solar irradiance). Given that the aim here was to compare the abundance of YPL between isobaths (spaced by >500 m), we focused on $K_d$ rather than integrating hourly variations in the incident irradiance. This is because we do not expect the abundance of YPL to vary rapidly among stations (given the distance) in response to variations in either visible light or UVR, whereas it is more likely that they could be driven by longer-term exposition to such wavelengths. Therefore, we consider $K_d$ a more stable proxy of UVR risk integrated over the long-term compared to hourly variation in solar irradiance. Depth, SAV, turbidity and $K_d$ calculated at both 340 and 443 nm were used to build both additive ($M_{2.1}$, $M_{2.2}$, $M_{2.4}$, $M_{2.5}$, $M_{2.9}$, $M_{2.10}$, $M_{2.14}$ and $M_{2.15}$) and interactive models ($M_{2.3}$, $M_{2.6}$-$M_{2.8}$, $M_{2.11}$-$M_{2.13}$ and $M_{2.16}$-$M_{2.18}$) (Table 2). Interactive models were built based on the prediction that the SAV, $K_d$ and turbidity will differently affect YPL abundance depending on the isobaths. Based on our hypotheses, we expect the most complex models ($M_{2.8}$ with the isobath in interaction respectively with SAV and $K_{d\ 340}$, $M_{2.13}$ with the isobath in interaction respectively with SAV and $K_{d\ 443}$, and $M_{2.18}$ with the isobath in interaction respectively with SAV and turbidity) to perform better than the respective models with additive terms ($M_{2.5}$, $M_{2.10}$ and $M_{2.15}$). We predicted YPL to be more abundant in the deep compared to the shallow isobath at sites highly exposed to UVR because of reduced mortality risk. Moreover, we predict YPL to be more strongly associated with SAV in the shallow isobath searching for shelter given the higher UVR risk.

The zero inflated part of all models (both sets) contained SAV and EAV. Such choice was based on previous studies showing the pivotal role of vegetation in driving YPL abundance at the scale of LSP (Bertolo et al., 2012, Massicotte et al. 2015). YPL abundance in the first set of models were expressed as number of individuals per $m^3$, whereas in the second set of models their abundance was expressed per unit surface (individuals per $m^2$) to standardize data between isobaths.

While dealing with time series, spatio-temporal autocorrelation may be problematic because most of the statistics assume independence of the data. To cope with this issue, we included an exponential term of autocorrelation on sampling sites coordinates. Time has been accounted for by using nested random effects as follows: for the first set of models, we included two random effects representing, respectively, the station nested into the year and the day of the year nested into the year; for the second set of models, we included the year as random effect, whereas the day of the year was nested into the year. The time series spanned from 2005 to 2016, but 2008 was excluded because of very few data points.

Sampling effort was standardized by considering the transect length as offset covariable. Continuous variables were scaled by their standard deviation. The variables SAV and EAV were coded as ordinal, meaning that we imposed a hierarchy among classes, namely 0 (open water) < 1 (sparse) < 2 (dense) < 3 (very dense) < 4 (extremely dense). Orthogonal polynomial coding was used to transform ordinal variables prior to modeling. This approach allows to look for linear, quadratic, and cubic trends (as many as the number of categories -1) between a categorical ordered variable and the dependent variable. Each component of the polynomial is orthogonal and can be interpreted independently of the others.

The Akaike information criterion (AIC) was used to compare and rank our models based on *a-priori* hypotheses (Burnham and Anderson, 2002). AIC is based on the principle of parsimony, helping to identify the model that accounts for the most variation with the fewest variables. Models were ranked using ΔAICc, i.e., the difference in AICc between a candidate model and the model with the lowest (best) AICc (Burnham and Anderson, 2002). The larger the ΔAIC, the less plausible the model: models with $\Delta AIC < 2$ are highly plausible and can be considered as equivalent, those with $2 < \Delta AIC < 4$ are plausible, those where $4 < \Delta AIC < 7$ are plausible but have considerably less support, while those with $\Delta AIC > 10$ have essentially no support (Burnham and Anderson, 2002). Similarly, the inclusion of an additional variable in a model is recognized to improve its plausibility only when it is associated with a reduction of more than two units of the AIC (Burnham and Anderson, 2002).

All statistical analyses were performed using the R language environment (version 3.6.0). Models were fitted using the R package glmmTMB (version 1.0.1, Magnusson et al., 2020). The DHARMa package (version 0.3.2.0, Hartig, 2020) was used to inspect residuals (observed vs expected; standardized residuals vs predicted values).

## Results

### *Light attenuation in the water column*

Our estimates of the 1% irradiance depth for visible light showed that, across all stations and years, the first 40 cm of the water column (i.e. the portion corresponding to the surface net) were always well lit despite a relatively large variability in the attenuation of the 443 nm wavelength (Fig. 2). In 75% of cases, the 1% irradiance depth for the 443 nm wavelength was deeper than 60 cm and in nearly 50% of cases penetrated beyond the deeper sampling net (i.e. 80 cm; Fig. 2). Estimations for UVR 1% irradiance depth measured at 340 nm showed that in most cases UVR penetrated deeper than the first 40 cm of the water column (Fig. 2), with the 40-80 cm layer (i.e. the portion corresponding to the surface sampling net) showing a great deal of variability. In only few cases the UVR 1% irradiance depth was deeper than 1 m (Fig. 2).

### ***YPL vertical aggregation patterns (hypotheses $H_{1.1}$-$H_{1.3}$)***

Model comparison for the first set of models (470 obs.) showed that ten models ($M_{1.2}$, $M_{1.3}$, $M_{1.5}$-$M_{1.8}$, $M_{1.10}$-$M_{1.13}$) can be considered plausible, with the others having no support ($\Delta$AIC > 10; Table 1). Models including the interaction between UVR and depth ($M_{1.6}$ and $M_{1.8}$; i.e. the only two models testing $H_{1.2}$) were in all cases outperformed by their additive version ($M_{1.5}$ and $M_{1.7}$), giving no support to the UVR avoidance hypothesis ($H_{1.2}$). Moreover, all models including UVR were outcompeted by those including visible light, with the former showing $\Delta$AIC > 4 for all models (Table 1). Among the five models that included visible light, four were plausible and three competed as best ($M_{1.10}$, $M_{1.12}$ and $M_{1.13}$), given that all had a $\Delta$AIC < 2. Between these three best models, model $M_{1.10}$ was retained based on the parsimony criterion. In addition to YPL body length and EAV (both terms present in all the models), this model included visible light, Net and SAV, but no interaction term (Table 1). As predicted, YPL body length was significantly associated with a reduction of YPL abundance (Table 3). The abundance of YPL was significantly associated to the variable Net, but in contrast to our predictions based on $H_{1.1}$, larvae were more aggregated in the deeper than in the surface layer (Table 3). YPL abundance was not significantly associated with SAV within this set of models (i.e. none of the terms of the polynomials were significant; Table 3). Despite YPL abundance was significantly associated with visible light irradiance among stations (Fig. 3, Table 3), there was no evidence within this set of models of any effect modulating the relative proportion of larvae in the bottom vs the surface net within stations (i.e. no significant interaction between the Net and the other variables). Therefore, this result did not support the positive phototropism hypothesis ($H_{1.1}$). The best model did not include the interaction between SAV and Net, suggesting that the SAV sheltering hypothesis ($H_{1.3}$) was not supported either. Furthermore, none of the AV (neither SAV nor EAV) categorical ordered terms was significantly related to YPL abundance among stations (Table 3).

The alternative set of models for hypotheses $H_{1.1}$-$H_{1.3}$ expanded these results, since they confirmed the significant roles of the variables body length and net in driving YPL abundance, but they also showed that all the interaction terms including the variable Net were significant (see Supp. Mat.). The interaction between SAV and net showed that YPL aggregated in the deeper layer when SAV was more abundant, supporting the AV shading hypothesis ($H_{1.3}$), whereas the interaction between depth and turbidity showed that YPL aggregated in the upper part of the water column when turbidity was higher, in accordance with the predictions of the UVR avoidance hypothesis ($H_{1.2}$; Table S2). The interaction between the irradiance of visible light at the surface and the variable Net showed that larvae increased their aggregation at the surface when solar radiation was more intense, in accordance with the positive phototropism hypothesis ($H_{1.1}$; Table S2).

### *YPL distribution patterns between isobaths (hypotheses $H_{2.1}$-$H_{2.2}$)*

Model comparison for the second set of models (553 obs.) showed that 14 over 18 models were plausible ($\Delta$AIC < 10; Table 2). Among these, only three had a $\Delta$AIC < 4, ($M_{2.6}$, $M_{2.16}$, $M_{2.18}$), with model $M_{2.16}$ being clearly the best (the only having a $\Delta$AIC < 2). This model included EAV and YPL body length (both terms present in all the models), together with SAV and the interactions between turbidity and isobath (Table 2), meaning that the effect of turbidity on YPL abundance is expected to change in function of the isobath. More specifically, while we found on average a higher YPL abundance associated with the deeper isobath (Table 3), turbidity reduced this effect, by increasing the abundance of YPL in the shallow isobath, in accordance with the hypothesis $H_{2.1}$ (negative interaction term between turbidity and the shallow isobath; Table 3; Fig. 4). Moreover, despite the best model did not include the interaction between the isobath and SAV, YPL abundance was positively associated with SAV at both isobaths (Fig. 4), supporting the AV refuge hypothesis ($H_{2.2}$).

## Discussion

By combining 11 years of extensive sampling effort (ca. 200 sampling stations per year) under varying environmental conditions, both in space and time, our results show that the vertical distribution of YPL in LSP is not random. Whereas there was a great deal of variability in our data and our main hypotheses received some mixed support, our results consistently indicate that YPL avoid the surface layers in the water column by aggregating at the bottom and that different factors (SAV, visible light irradiance at the surface and turbidity) could modulate this pattern. In contrast, none of the results about the vertical aggregation patterns included a term explicitly related to UVR (either $E_{d\,340}$ or $E_{0\,340}$). However, we cannot rule out a potential role of UVR in determining the vertical aggregation patterns of YPL since these latter clearly avoided the surface layers which are the riskiest in terms of UVR (Fig. 2). Moreover, YPL tended to reduce their use of deep layers when turbidity was higher (Fig. S1b). Our results also suggested a potential role of UVR in driving the distribution patterns between isobaths since YPL proportion was higher at the shallow isobath in correspondence with higher turbidity. Whereas we cannot state that the factors analyzed here are strong drivers of YPL aggregation patterns in either the vertical or the horizontal axis, our results confirm the potential for these organisms to actively select their habitat.

### *YPL vertical aggregation patterns (hypotheses $H_{1.1}$-$H_{1.3}$)*

#### *$H_{1.1}$ – Positive phototropism hypothesis*

Contrary to our predictions, our models did not support the positive phototropism hypothesis (Fig. 3c). Despite a relatively large variability, the proportion of YPL in the bottom net was always higher compared to the surface, indicating a consistent non-random pattern. This could mean that at the time of sampling, about two weeks after hatching, YPL already switched toward a negative phototropism behavior, a well-known phenomenon in percids (Sandström, 1999). The non-random aggregation pattern on the vertical axis supports the hypothesis of a potential active habitat choice by YPL, which broaden the findings in Bertolo et al. (2012) and Massicotte et al. (2015) based on the large-scale YPL distribution in LSP. On the other hand, whereas we did not find any effect of visible light irradiance at depth, we found a positive effect of visible light irradiance at the surface (Fig. S1) on YPL aggregation in the surface layers, thus providing some support to the positive phototropism hypothesis. This result suggests a potential behavioral response to the underwater light environment, with larvae searching for well-lit water layers. Albeit this might seem in contradiction with the fact that YPL larvae aggregated at the bottom layers, it is reasonable to think that larvae, while showing an overall tendency to avoid the surface layers, may modulate their vertical position during the day depending on the hourly variation in solar irradiance at the surface. Whereas YPL are well adapted to a wide spectrum of visible light intensities, variations in the light environment could affect some feeding traits such as prey selection (Martin et al. 2012), feeding efficiency and predator avoidance (Dabrowski and Jewson, 1984; Blaxter, 1986; Keenan et al., 2007), thus explaining the observed pattern.

### *$H_{1.2}$ – UVR avoidance hypothesis*

Surprisingly, despite that larvae tended to avoid the surface layers (Fig. 3c), we did not find any direct relationship between variation in UVR irradiance and YPL vertical aggregation patterns. However, since the first 40 cm from the surface showed in most cases a clearly higher UVR penetration compared to the 40-80 cm layer (Fig. 2), aggregating at these depths *de facto* reduced UVR risk for YPL. It is possible that YPL larvae adjusted their vertical position mostly within the 40-80 cm depth layer (i.e. the layer where UVR risk varied most; Fig. 2) and the size of our sampling gears did not allow to detect finer patterns.

Some indirect support to the UVR avoidance hypothesis comes from the significant interaction we found between the depth of the sampling net and turbidity, with YPL being less aggregated at the bottom in more turbid waters. Whereas there is huge variation associated with this prediction and these results should be taken cautiously, this response of YPL deserves more attention in the future. Turbidity is in fact deemed to have primarily negative effects on yellow perch (e.g. Giacomazzo et al. 2020) and its role in modulating

UVR risk should also be taken into account to have a more complete picture of its effects on YP populations.

UVR are high-energy wavelengths, known to induce damage to aquatic biota (Zagarese and Williamson, 2001; Bancroft et al. 2007). These wavelengths are known to harm DNA and proteins, inducing oxidative stress by generating reactive oxygen species, phototoxicity and photosensitization (Zagarese and Williamson, 2001). Negative effects of UVR have been demonstrated on both physiology and immunology of YPL (e.g. oxidative stress, DNA fragmentation, neurotransmitter impairment) as well as on YPL mortality (Boily et al., 2011; Provencher et al., 2014; Paquet-Walsh et al., 2019). Whereas published results suggest that YP can detect UVR from the larval (Browman et al. 1993) to the adult stage (Williamson et al., 1997; Huff et al., 2004), it has been shown that YPL progressively lose their UV photoreceptors with ontogeny (Browman et al., 1993). Such a reduction of photoreception range is associated to a shift from a pelagic to a benthic habitat (Loew et al., 1993), usually associated to a diet shift towards benthic preys, which could be another mechanism behind the observed vertical distribution of YPL. Whereas our results are not conclusive on this point, they stress the need to carry experimental and/or comparative approaches to explore the potential of larval behavior to cope with UVR risk in natural systems.

### $H_{1.3}$ – *AV sheltering hypothesis*

The positive relationship observed between SAV and larvae aggregation in the bottom layers gives an extra support to the view that YPL display an active habitat choice in LSP (Fig. S1; see Supp. Mat. for more details). Whereas our results confirm the association between YPL and AV, previously shown at the scale of the whole lake (Bertolo et al. 2012, Massicotte et al., 2015), they also show that the presence of AV seems to affect YPL habitat choice in the vertical axis at the small scale (Fig. S1). This interaction between SAV and Net can be clearly seen in our analysis conducted on the whole data set (i.e. on the alternative set of models; Table S2). For these reasons, we feel confident to conclude that AV was associated with a denser aggregation of YPL towards the bottom.

It has been shown that YPL tend to associate with overwintering and/or AV of the year at the scale of the LSP, presumably looking for shelter and invertebrate resources (Bertolo et al. 2012, Paradis et al., 2014; Massicotte et al., 2015). Whereas it has been argued that YPL show an active habitat choice, at least partially, and do not disperse passively (Bertolo et al., 2012; Massicotte et al., 2015), we still lack a more direct evidence of this behavior. In this context, our results contribute to support the hypothesis that YPL perform an active habitat choice by confirming the pivotal role of AV in structuring YPL distribution in the LSP, on the vertical axis.

### ***YPL distribution patterns between isobaths (hypotheses $H_{2.1}$-$H_{2.2}$)***

#### *$H_{2.1}$ – UVR risk hypothesis*

Whereas turbidity showed only a marginally significant negative relationship with YPL abundance (Table 3), suggesting a potential negative effect on larvae, our results show a significant, albeit weak, interaction between turbidity and isobath on YPL abundance. More specifically, we found that higher turbidity was associated with higher YPL abundances at the shallower isobath only, which is consistent with the hypothesis $H_{2.1}$ (Fig. 4a). Coupled with the result about the vertical distribution patterns, this suggests that turbidity allows YPL to occupy water layers close to the surface, at both the deep and the shallow isobaths. The consistently higher abundance of larvae at the deep isobath and their aggregation towards the bottom suggest a potential role of depth as a refuge habitat.

Turbidity affects the light environment both by attenuating light penetration in the water column and by scattering light (Gallegos et al. 1990), thus potentially reducing the UVR risk. Reduced transparency has been associated with a lower need of photoprotection in yellow perch (i.e. lower dermis melanin concentration; Rheault et al., 2015), suggesting a potential link with UVR risk. Therefore, in turbid waters, UVR risk is potentially lower and YPL may increase the use of the upper layers and better cope with mortality risk in high-UV risk shallow waters. Despite that none of the models including $K_{d\,340}$ were considered plausible, the observed significant interaction between isobath and turbidity indirectly corroborates the idea that UVR might shape YPL abundance but deserves more attention in the future is deserved on this point.

### *$H_{2.2}$ – AV refuge hypothesis*

As for the hypothesis $H_{1.3}$, our results confirmed the positive association between YPL abundance and aquatic vegetation already observed in LSP (Bertolo et al. 2012; Paradis et al. 2014; Massicotte et al. 2015). However, the best model (Table 3) did not contain the interaction between isobath and AV, meaning that the association between YPL abundance and AV was similar for the two isobaths. This result does not give support to the view that YPL larvae used AV as a refuge against UVR. In contrast, taken together, the results from the two sets of models confirm the key role of aquatic vegetation in driving YPL abundance both at the local scale (i.e. the water column) and at the scale of the whole lake, suggesting that, at least at the smaller scale, YPL do operate an active habitat choice in the presence of SAV.

### **Body length**

The expected negative relationship between body length and YPL abundance (consistent among all sets of models) is in accordance with the idea that YPL had the swimming ability to make an active habitat choice at the time of our sampling. The ability to counteract currents and make active movements increase during larvae ontogeny making larger larvae more able to potentially avoid push nets. Unfortunately, a strong conclusion about this point could only be made by disentangling the relative roles of mortality and swimming abilities to better explain the negative relationship between body size and YPL abundance.

## Conclusion

Taken together, our results give additional support to the hypothesis that YPL can perform active habitat selection, changing their vertical position based on habitat features (i.e. SAV) and the light environment. Our results shed a new light on YPL ecology contributing to disentangle the role of key factors such as aquatic vegetation, visible light, UVR and turbidity. They also suggest that, even in very shallow water bodies, the vertical distribution of fish larvae can show non-random patterns. Whereas with the data at hand it has not been possible to explain the aggregation of larvae at the bottom, nor the mechanism behind their response to turbidity, these results suggest that both the vertical and the light gradient should be taken into account to understand patterns in larvae distribution at different scales.

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## References

Bancroft A, Baker NJ, Blaustein AR 2007 Effects of UV-B radiation on marine and freshwater organisms: a synthesis through meta-analysis. *Ecology Letters*, 10:332-345.

Bélanger S, Babin M & Tremblay JÉ 2013 Increasing cloudiness in Arctic damps the increase in phytoplankton primary production due to sea ice receding. *Biogeosciences*, 10:4087-4101. https://doi.org/10.5194/bg-10-4087-2013

Bertolo A, Blanchet FG, Magnan P, Brodeur P, Mingelbier M, Legendre P. 2012 Inferring processes from spatial patterns: The role of directional and non–directional forces in shaping fish larvae distribution in a freshwater lake system. *PLoS ONE*, 7(11): e50239. (doi:10.1371/journal.pone.0050239).

Blaxter JHS. 1986 Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*, 115: 98-114.

Boily V, Bertolo A, Magnan P, Martinoli MG, Thérien HM. 2011 The effects of UVR irradiance and spectral composition on yellow perch (*Perca flavescens*) larvae survival. *Aquatic Sciences*, 73: 345-354. (doi: 10.1007/s00027-011-0182-y).

Browman HI, Novales-Flamarique I, Hawryshyn C. 1993 Ultraviolet photoreception contributes to prey search behavior in two species of zooplanktivorus fishes. *Journal of Experimental Biology*, 186: 187-198.

Burnham KP, Anderson DR. 2002 Model Selection and multimodel inference: A practical information–theoretic approach. Springer-Verlag, New York, NY.

Chavez Jr PS. 1996 Image-based atmospheric corrections revisited and improved. *Photogrammetric Engineering and Remote Sensing*, 62 (9): 1025-1036. (URL http://www.asprs.org/wp-content/uploads/pers/1996journal/sep/1996_sep_1025-1036.pdf).

Dabrowski KR, Jewson DH. 1984 The influence of light environment on depth of visual feeding by larvae and fry of *Coregonus pollan* (Thompson) in Lough Neagh. *Journal of fish biology*, 25(2): 173-181.

Dahms HU, Lee JS. 2010 UV radiation in marine ectotherms: Molecular effects and responses. *Aquatic Toxicology,* 97: 3-14. (doi:10.1016/j.aquatox.2009.12.002).

Dorman M. 2020 nngeo: k-Nearest Neighbor Join for Spatial Data. R package version. 0.3.8. https://CRAN.R-project.org/package=nngeo

Dudley B, Tolimieri N, Montgomery J. 2000 Swimming ability of the larvae of some reef fishes from New Zealand waters. *Marine and Freshwater Research*, 51, 783-787.

Frenette JJ, Arts MT, Morin J. 2003 Spectral gradients of downwelling light in a fluvial lake (Lake Saint-Pierre, St-Lawrence River). *Aquatic Ecology,* 37: 77-85.

Frenette JJ, Arts MT, Morin J, Gratton D, Martin C. 2006 Hydrodynamic control of the underwater light climate in fluvial Lac Saint-Pierre. *Limnology and Oceanography,* 51(6), 2632-2645.

Frenette JJ, Massicotte P, Lapierre JF. 2012 Colorful niches of phytoplankton shaped by the spatial connectivity in a large river ecosystem: A riverscape perspective. *PLoS ONE,* 7(4): e35891. (doi:10.1371/journal.pone.0035891).

Fritsch S, Guenther F and Wright MN. 2019 Neuralnet: Training of Neural Networks. R package version 1.44.2. https://CRAN.R-project.org/package=neuralnet

Gallegos CL, Correll DL, Pierce JW. 1990 Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. *Limnology and Oceanography*, 35: 1486-1502. (doi: 10.4319/lo.1990.35.7.1486).

Hartig F. 2020 DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. https://cran.r-project.org/web/packages/DHARMa/index.html.

Houde ED. 1994 Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science*, 51(1): 91-7. (doi: 10.1006/jmsc.1994.1008).

Hudon C, Carignan R. 2008 Cumulative impacts of hydrology and human activities on water quality in the St. Lawrence River (Lake Saint-Pierre, Quebec, Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 1165-1180. (doi:10.1139/F08-069).

Hudon C, Cattaneo A, Tourville Poirier AM, Brodeur P, Dumont P, Mailhot Y, Amyot JP, Despatie SP, de Lafontaine Y. 2012 Oligotrophication from wetland epuration alters the riverine trophic network and carrying capacity for fish. *Aquatic Science*, 74: 495-511. (doi: 10.1007/s00027-011-0243-2).

Huff DD, Grad G, Williamson CE. 2004 Environmental constraints on spawning depth of yellow perch: The roles of low temperature and high solar ultraviolet radiation. *Transactions of the American Fisheries Society*, 133: 718-726.

Keenan SF, Benfield MC, Blackburn JK. 2007 Importance of the artificial light field around offshore petroleum platforms for the associated fish community. *Marine Ecology Progress Series*, 331: 219-231.

Kingsford MJ. 1990 Linear oceanographic features: A focus for research on recruitment processes. *Australian Journal of Ecology*, 15: 341-401.

Kirk JTO. 2011 Light and photosynthesis in aquatic ecosystems. Cambridge University Press.

Laliberté J, Bélanger S, Frouin R. 2016 Evaluation of satellite-based algorithms to estimate photosynthetically available radiation (PAR) reaching the ocean surface at high northern latitudes. *Remote Sensing of Environment*, 184: 199-211. (doi: 10.1016/j.rse.2016.06.014).

Lecchini D, Shima J, Banaigs B, Galzin R. 2005 Larval sensory abilities and mechanisms of habitat selection of a coral reef fish during settlement. *Oecologia,* 143: 326-334. (doi: 10.1007/s00442-004-1805-y).

Leis JM. 2006 Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology,* 51: 59-141.

Loew EH, McFarland WN, Mills EL, Hunter D. 1993 A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. *Canadian Journal of Zoology*, 71: 384-386.

Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Bentham K, bolker B, Sadat N, Lüdecke D, Lunth R, O'Brien J, Brooks M. 2020 Generalized Linear Mixed Models using Template Model Builder. https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf

Mailhot Y, Dumont P, Paradis Y, Brodeur P, Vachon N, Mingelbier M, Lecomte F, Magnan P. 2015 Yellow perch (*Perca flavescens*) in the St. Lawrence River (Québec, Canada): Population dynamics and management in a river with contrasting pressures. Biology of Perch, eds Couture P, Pyle G (CRC Press), pp. 101-147.

Martin BT, Wahl DH, Czesny SJ. 2012 Effect of light intensity, prey density, and ontogeny on foraging success and prey selection of larval yellow perch (*Perca flavescens*). *Ecology of Freshwater Fish*, 21:588-596. (doi: 10.1111/j.1600-0633.2012.00580.x).

Massicotte P, Bertolo A, Brodeur P, Hudon C, Mingelbier M, Magnan P. 2015 Influence of the aquatic vegetation landscape on larval fish abundance. *Journal of Great Lakes Research*, 41: 873-880. (doi: http://dx.doi.org/10.1016/j.jglr.2015.05.010).

Montgomery JC, Tolimieri N, Haine OS. 2001 Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries*, 2: 261-277.

Norcross BL, Shaw RF. 1984 Oceanic and Estuarine Transport of Fish Eggs and Larvae: A Review. *Transactions of the American Fisheries Society*, 113 (2): 153-165. (doi: 10.1577/1548-8659(1984)113<153:OAETOF>2.0.CO;2).

Olson MH, Colip MR, Gerlach JS, Mitchell DL. 2006 Quantifying ultraviolet radiation mortality risk in bluegill larvae: effects of nest location. *Ecological Applications*, 16(1): 328-338.

Paquet-Walsh A, Bertolo A, Landry C, Deschamps L, Boily M. 2019 Interactive effects of neonicotinoids and natural ultraviolet radiation on yellow perch (*Perca flavescens*) larvae. *Science of the Total Environment*, 685: 690-701. (doi: 10.1016/j.scitotenv.2019.05.113).

Paradis Y, Bertolo A, Mingelbier M, Brodeur P, Magnan P. 2014 What controls distribution of larval and juvenile yellow perch? The role of habitat characteristics and spatial processes in a large, shallow lake. *Journal of Great Lakes Research*, 40 (1): 172-178 (doi: 10.1016/j.jglr.2013.12.001).

Provencher C, Bertolo A, Magnan P, Martinoli MG. 2014 Modulation of specific apoptotic DNA fragmentation after short term exposure to natural UVR in fish larvae. *Open Journal of Apoptosis*, 3: 39-51. (doi: 10.4236/ojapo.2014.33005).

Rheault G, Langevin M, Cabana G, Glémet H. 2015 Dermal melanin concentration of yellow perch *Perca flavescens* in relation to water transparency. *Journal of Fish Biology*, 87: 1248-1253. (doi:10.1111/jfb.12780).

Ricchiazzi P, Yang S, Gautier C, Sowle D 1998 SBDART: A research and teaching software tool for plane-parallel radiative transfer in the Earth's atmosphere. *Bulletin of the American Meteorological Society*, *79:*2101-2114.

Sale PF. 2004 Connectivity, recruitment variation, and the structure of reef fish communities. *Integrative and Comparative Biology*, 44: 390-399.

Sandström A. 1999 Visual ecology of fish – a review with special reference to percids. *Fiskeriverket Rapport*, 2: 45-80.

Simoneau M. 2017 Qualité de l'eau des tributaires du lac Saint-Pierre : évolution temporelle 1979-2014 et portrait récent 2012-2014. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques. Direction générale du suivi de l'état de l'environnement, ISBN 978-2-550-76229-4 (PDF), 54 p. 33+ 13 ann. (http://www.mddelcc.gouv.qc.ca/eau/lac-st-pierre/qualite-eau-tributaires.pdf). Bibliothèque et Archives nationales du Québec.

Stobutzki IC, Bellwood DR. 1994 An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. *Journal of Experimental Marine Biology and Ecology*, 175: 275-286.

Stobutzki IC, Bellwood DR. 1998 Nocturnal orientation to reefs by late pelagic stage coral reef fishes. *Coral Reefs,* 17: 103-110.

Stoll S, Beeck P. 2011 Post-release stranding rates of stocked allis shad (*Alosa alosa*) larvae exposed to surface wave action. *Journal of Applied Ichthyology*, 27: 41-44. (doi: 10.1111/j.1439-0426.2011.01879.x).

Tedetti M, Semperé R. 2006 Penetration of Ultraviolet Radiation in the Marine Environment. A Review. *Photochemistry and Photobiology*, 82: 389-397. (doi:10.1562/2005-11-09-IR-733).

Tolimieri N, Jeffs A, Montgomery JC. 2000 Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Marine Ecology Progress Series,* 207: 219-224.

Urho L. 1996 Habitat shifts of perch larvae as survival strategy. *Annales Zoologici Fennici,* 33:329-340.

Wenger AS, Johansen JL, Jones GP. 2011 Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. *Coral Reefs,* 30: 879-887. (doi: 10.1007/s00338-011-0773-z).

Williamson CE, Stemberger RS, Morris DP, Frost TM, Paulsen SG. 1996 Ultraviolet radiation in North American lakes: Attenuation estimates from DOC measurements and implications for plankton communities. *Limnology and Oceanography*, 41(5), 1024-1034.

Williamson CE, Metzgar SL, Lovera PA, Moeller RE. 1997 Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens. Ecological Applications,* 7(3): 1017-1023.

Zagarese HE, Williamson CE. 2001 The implications of solar UV radiation exposure for fish and fisheries. *Fish and Fisheries*, 2: 250-260.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009 Mixed effects models and extensions in ecology with R. Springer New York, New York, NY. (URL http://link.springer.com/10.1007/978-0-387-87458-6).

## Supplementary material

In the alternative set of models explaining the YPL vertical distribution patterns (785 obs., Table S1), solar radiation is expressed as the instant dose estimated at the surface, at the time of sampling (a proxy of radiation damage potential at the station). Irradiance at the surface was calculated for the wavelengths 340 nm and 443 nm (hereafter called UVR and visible light). Given that solar irradiation intensity is a function of photon irradiance, irradiance at surface correlates highly for close wavelengths (e.g. UVR and visible light). It is thus not surprising that our data show a nearly perfect correlation between the irradiance at the surface for UVR and visible light (Pearson correlation = 0.998). For this reason, we could not test the effect of both UVR and visible light irradiance on YPL abundance in the same model. Therefore, we present only the results for visible light. Within this alternative set of models, we tested the ($H_{1.1}$) positive phototropism and the ($H_{1.3}$) sheltering hypotheses. This set of models included a null model ($M_{1.1.b}$; Table S1) containing only three explanatory variables, shared with all the other models: YPL body length, emerged (EAV) and submerged aquatic vegetation (SAV). The variables SAV, visible light irradiance, turbidity and depth were used to build both additive ($M_{1.1.b}$, $M_{1.2.b}$, $M_{1.4.b}$, $M_{1.5.b}$, $M_{1.9.b}$, $M_{1.10.b}$, Table S1) and interactive ($M_{1.3.b}$, $M_{1.6.b}$-$M_{1.8.b}$, $M_{1.11.b}$-$M_{1.15.b}$; Table S1) models, because the effect of the SAV, visible light irradiance and turbidity are expected to affect differently YPL abundance depending on depth. Based on our hypotheses, we expect that the most complex model (with net in interaction respectively with SAV, visible light, and turbidity; $M_{1.15.b}$) to perform better than the respective model with additive terms ($M_{1.14.b}$).

Model comparison based on the ΔAIC showed that only four models ($M_{1.8.b}$, $M_{1.13.b}$, $M_{1.14.b}$ and $M_{1.15.b}$) can be considered plausible within this set of models, with all the others having a ΔAIC > 10 (Table S1). Moreover, among these four models, none can be considered as a strong competitor for the best model ($M_{1.15.b}$), given that all the others had a ΔAIC > 4. Thus, besides being the most complex, model $M_{1.15.b}$ resulted to be the best. Model $M_{1.15.b}$ included EAV and YPL body length (both terms present in all the models) together with the interactions between net and the following variables: i) SAV, ii) (log) turbidity and iii) visible light (Table S1). This result agrees with our predictions about the effect of these variables on YPL abundance, which is expected to change in function of depth. As predicted, YPL body length was significantly inversely associated with YPL abundance (Table S2). As for the first set of models, we confirmed that YPL are more abundant at the bottom. As predicted by the AV shading hypothesis ($H_{1.3}$), YPL abundances were positively associated with SAV (Fig. S3, S4; significant linear term, $SAV^1$), a relationship that was even stronger in deeper than shallow nets (Table S2; significant interaction term between SAV ($SAV^4$) and the deep net). No significant effect of EAV was found. The significant interaction between depth and SAV, (log) turbidity and PAR (Table S2), show that the consistently higher YPL abundance found in the bottom net is nevertheless modulated by these variables, therefore changing the relative proportion of larvae in the two nets. The interaction between PAR and net was significant, and the negative coefficient for PAR x bottom net showed that higher PAR irradiances were associated with lower YPL abundances at the bottom (Fig. S3, S4). The negative effect of PAR irradiance measured at the surface on YPL abundances at the bottom of the water column might suggest that YPL respond to light by moving towards better illuminated layers closer to the surface. If enough light reaches the bottom, then larvae tend to move off the bottom. On the other hand, when PAR surface radiation intensity is low (and so, there is a weak driver for phototaxis for YPL at the bottom), YPL do not move significantly towards the surface and are thus more abundant in the bottom net. For these reasons, despite YPL are clearly aggregated in the deeper part of the water column, they still seem to show a positive phototactic behavior at the time of sampling, given their response to visible light.

Similarly to PAR, the interaction between turbidity and the bottom net was significant, with less larvae at the bottom with higher turbidity values (Fig. S3, S4). The negative effect of turbidity on YPL abundance in the water column (less abundant YPL at the bottom), might be seen again as a support for the hypothesis that YPL look for well illuminated water layers. It is thus not surprising that higher turbidity values are associated with lower YPL abundances at the bottom given their tendency to occur in well illuminated water layers. The negative effects of turbidity on early yellow perch ontogenetic stages (e.g. age 1 +, Giacomazzo et al., 2020) has often been ascribed to an impaired visual foraging (Radke and Gaupisch, 2005; Wellington et al., 2010) or gills clogging, affecting growth, and ultimately increasing starvation mortality and cohort strength (Manning et al., 2014). Finally, we confirmed the expected negative relationship between YPL body length and abundance.

## Supplementary references

Giacomazzo M, Bertolo A, Brodeur P, Massicotte P, Goyette JO, Magnan P. 2020 Linking fisheries to land use: How anthropogenic inputs from the watershed shape fish habitat quality. *Science of the Total Environment*, 717, 135377. (doi: 10.1016/j.scitotenv.2019.135377).

Manning NF, Bossenbroek JM, Mayer CM, Bunnell DB, Tyson JT, Rudstam LG, Jackson JR. 2014 Modeling turbidity type and intensity effects on the growth and starvation mortality of age-0 yellow perch. *Canadian Journal of Fisheries and Aquatic Sciences,* 71: 1544-1553. (doi: 10.1139/cjfas-2013-0528).

Radke R.J, Gaupisch A, 2005. Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): Possible implications for fish community structure in lakes. *Naturwissenschaften*, 92: 91-94. https://doi.org/10.1007/s00114-004-0596-7.

Wellington CG, Mayer CM, Bossenbroek J.M, Stroh NA. 2010 Effects of turbidity and prey density on the foraging success of age 0 year yellow perch *Perca flavescens*. *Journal of Fish Biology*, 76: 1729-1741. https://doi.org/10.1111/j.1095-8649.2010.02612.x.

## Tables

**Table 1.** Set of models predicting the YPL vertical aggregation patterns (hypotheses $H_{1.1}$ to $H_{1.3}$). For this set of models, UVR risk and visible light intensity experienced by the larvae in the water column were estimated by calculating the solar irradiance (at 340 and 443 nm, respectively) at the depth corresponding to the sampling nets (i.e. in their middle point). Yellow perch larvae abundance was modeled as a function of the following variables: submerged aquatic vegetation (SAV); depth of the sampling net (Net); 340 nm ($E_{d\ 340}$) and 443 nm ($E_{d\ 443}$) irradiance at depth. The variables emerged aquatic vegetation (EAV) and body length were included in all models but have not been reported for the sake of clarity. The best model is indicated in bold. The first column indicated the hypothesis related to a given model: models for which the hypothesis is not specified are used as null models for more complex ones in the same group (models grouped by line). N obs. = 470. See text for more details.

| Hypothesis | Model candidate | Independent variables | AIC | Δ AIC | Df. resid |
|---|---|---|---|---|---|
| | $M_{1.1}$ | SAV | 4530.1 | 101.6 | 448 |
| $H_{1.1}$ | $M_{1.2}$ | SAV + Net | 4434.0 | 5.5 | 447 |
| $H_{1.3}$ | $M_{1.3}$ | SAV * Net | 4432.5 | 4 | 443 |
| | $M_{1.4}$ | SAV + $E_{d\ 340}$ | 4476.3 | 47.8 | 447 |
| | $M_{1.5}$ | SAV + $E_{d\ 340}$ + Net | 4435.8 | 7.3 | 446 |
| $H_{1.2}$ | $M_{1.6}$ | SAV + $E_{d\ 340}$ * Net | 4437.6 | 9.1 | 445 |
| $H_{1.3}$ | $M_{1.7}$ | SAV * Net + $E_{d\ 340}$ | 4434.2 | 5.7 | 442 |
| $H_{1.2}$ $H_{1.3}$ | $M_{1.8}$ | SAV * Net + $E_{d\ 340}$ * Net | 4436.1 | 7.6 | 441 |
| | $M_{1.9}$ | SAV + $E_{d\ 443}$ | 4473.6 | 45.1 | 447 |
| | $M_{1.10}$ | **SAV + $E_{d\ 443}$ + Net** | **4429.7** | **1.2** | **446** |
| $H_{1.1}$ | $M_{1.11}$ | SAV + $E_{d\ 443}$ * Net | 4430.9 | 2.4 | 445 |
| $H_{1.3}$ | $M_{1.12}$ | SAV * Net + $E_{d\ 443}$ | 4428.5 | 0 | 442 |
| $H_{1.1}$ $H_{1.3}$ | $M_{1.13}$ | SAV * Net + $E_{d\ 443}$ * Net | 4429.9 | 1.4 | 441 |

**Table 2.** Set of models predicting the distribution patterns of YPL between isobaths (hypotheses $H_{2.1}$ and $H_{2.2}$). For this set of models, UVR risk and visible light penetration in the water column were estimated by calculating the light attenuation coefficients ($K_d$) estimated at each station (at 340 and 443 nm, respectively). Yellow perch larvae abundance was modeled in function of the following variables: submerged aquatic vegetation (SAV); Isobath, a categorical variable referring either to the shallow or deep isobath; $K_{d\,340}$ and $K_{d\,443}$ are the light attenuation coefficients calculated respectively at 340 and 443 nm; Turb, the logarithm of turbidity measured in nephelometric units (NTU). The variables emerged aquatic vegetation and yellow perch length were included in all the models but have not been reported for sake of clarity. Models $M_{2.9}$-$M_{2.13}$ (i.e. those including $K_d$ for visible light) serve as comparison for models $M_{2.4}$-$M_{2.8}$ (i.e. those including $K_d$ for UVR). The best model is indicated in bold. N obs. = 553. See table 1 and text for more details.

| Hypothesis | Model candidate | Independent variables | AIC | Δ AIC | Df. resid |
|---|---|---|---|---|---|
| | $M_{2.1}$ | SAV | 5224.3 | 48.7 | 529 |
| | $M_{2.2}$ | SAV + Isobath | 5181.8 | 6.2 | 528 |
| $H_{2.2}$ | $M_{2.3}$ | SAV * Isobath | 5182.2 | 6.6 | 524 |
| | $M_{2.4}$ | SAV + $K_{d\,340}$ | 5224.9 | 49.3 | 528 |
| | $M_{2.5}$ | SAV + $K_{d\,340}$ + Isobath | 5183.8 | 8.2 | 527 |
| $H_{2.1}$ | $M_{2.6}$ | SAV + $K_{d\,340}$ * Isobath | 5179.5 | 3.9 | 526 |
| $H_{2.2}$ | $M_{2.7}$ | SAV * Isobath + $K_{d\,340}$ | 5184.2 | 8.6 | 523 |
| $H_{2.1}$ $H_{2.2}$ | $M_{2.8}$ | SAV * Isobath + $K_{d\,340}$ * Isobath | 5181.2 | 5.6 | 522 |
| | $M_{2.9}$ | SAV + $K_{d\,443}$ | 5225.3 | 49.7 | 528 |
| | $M_{2.10}$ | SAV + $K_{d\,443}$ + Isobath | 5182.0 | 6.4 | 527 |
| | $M_{2.11}$ | SAV + $K_{d\,443}$ * Isobath | 5182.9 | 7.3 | 526 |
| $H_{2.2}$ | $M_{2.12}$ | SAV * Isobath + $K_{d\,443}$ | 5182.6 | 7 | 523 |
| $H_{2.2}$ | $M_{2.13}$ | SAV * Isobath + $K_{d\,443}$ * Isobath | 5182.9 | 7.3 | 522 |
| | $M_{2.14}$ | SAV + Turb | 5225.6 | 50 | 528 |
| | $M_{2.15}$ | SAV + Turb + Isobath | 5183.6 | 8 | 527 |
| **$H_{2.1}$** | **$M_{2.16}$** | **SAV + Isobath * Turb** | **5175.6** | **0** | **526** |
| $H_{2.2}$ | $M_{2.17}$ | SAV * Isobath + Turb | 5183.9 | 8.3 | 523 |
| $H_{2.1}$ $H_{2.2}$ | $M_{2.18}$ | SAV * Isobath + Turb * Isobath | 5179.4 | 3.8 | 522 |

**Table 3.** Slope coefficients and associated standardized errors for the variables in the best model for the first and second sets of models (solar irradiance calculated at depth and light attenuation coefficients calculated at each site, respectively). Significant variables (P-value < 0.05) are in bold. SAV: submerged aquatic vegetation; EAV: emerged aquatic vegetation. Exponents for SAV and EAV refer to the linear, quadratic, cubic, and the fourth power trends of the categorical ordered variable. For the first set of models, the coefficient for the term Net refers to the deeper net relatively to the shallow. For the second set of models, the coefficient for the term Isobath refers to the shallow isobath relatively to the deep.

| Variable | Estimate | Std. Error | Z value | P-value |
|---|---|---|---|---|
| **First set of models** | | | | |
| **Intercept** | -2.32 | 0.38 | -6.08 | **> 0.001** |
| **SAV$^1$** | 1.25 | 0.67 | 1.88 | 0.061 |
| **SAV$^2$** | -0.14 | 0.51 | -0.28 | 0.779 |
| **SAV$^3$** | -0.39 | 0.35 | -1.11 | 0.265 |
| **SAV$^4$** | -0.14 | 0.20 | -0.69 | 0.492 |
| **EAV$^1$** | 0.59 | 0.55 | 1.07 | 0.285 |
| **EAV$^2$** | -0.42 | 0.40 | -1.05 | 0.292 |
| **EAV$^3$** | 0.16 | 0.22 | 0.74 | 0.462 |
| **E$_{d\ 443}$** | 0.42 | 0.17 | 2.53 | **0.011** |
| **Net** | 2.13 | 0.30 | 7.18 | **> 0.001** |
| **Body length** | -0.49 | 0.13 | -3.73 | **> 0.001** |
| **Second set of models** | | | | |
| **Intercept** | -0.83 | 0.35 | -2.37 | **0.018** |
| **SAV$^1$** | 1.79 | 0.38 | 4.73 | **> 0.001** |
| **SAV$^2$** | -0.27 | 0.26 | -1.04 | 0.300 |
| **SAV$^3$** | -0.24 | 0.20 | -1.22 | 0.223 |
| **SAV$^4$** | 0.08 | 0.14 | 0.61 | 0.541 |
| **EAV$^1$** | -0.41 | 0.58 | -0.71 | 0.478 |
| **EAV$^2$** | -1.06 | 0.44 | -2.40 | **0.016** |
| **EAV$^3$** | -0.10 | 0.30 | -0.32 | 0.746 |
| **EAV$^4$** | 0.01 | 0.18 | 0.08 | 0.933 |
| Body length | -0.15 | 0.13 | -1.15 | 0.249 |
| Turbidity | -0.27 | 0.14 | -1.92 | 0.055 |
| **Isobath** | -1.26 | 0.18 | -7.11 | **> 0.001** |
| **Turbidity * Isobath** | 0.46 | 0.15 | 3.17 | **0.002** |

**Table S1.** Results of model comparison for the alternative set of models to predict the vertical aggregation patterns of yellow perch larvae (YPL; hypotheses $H_{1.1}$-$H_{1.3}$). Here, solar irradiance is calculated at the surface of each station (and not at depth, as in the first set of models). YPL abundance was modeled in function of the following variables: SAV: submerged aquatic vegetation; Net: categorical variable referring either to shallow or deep net; visible light: surface irradiance measured at 443 nm; Turb: the logarithm of turbidity measured in nephelometric units (NTU). The variables emerged aquatic vegetation (EAV) and yellow perch body length are present in all the models and have not been reported in the table for sake of clarity. The best model is indicated in bold. N obs. = 785. See text for more details.

| **Model candidate** | **Independent variables** | **AIC** | **Δ AIC** | **Df. resid** |
|---|---|---|---|---|
| $M_{1.1.b}$ | SAV | 7617.3 | 166.1 | 763 |
| $M_{1.2.b}$ | SAV + Net | 7478.8 | 27.6 | 762 |
| $M_{1.3.b}$ | SAV * Net | 7463.6 | 12.4 | 758 |
| $M_{1.4.b}$ | SAV + PAR | 7618.2 | 167 | 762 |
| $M_{1.5.b}$ | SAV + PAR + Net | 7480.3 | 29.1 | 761 |
| $M_{1.6.b}$ | SAV + PAR * Net | 7467.9 | 16.7 | 760 |
| $M_{1.7.b}$ | SAV * Net + PAR | 7465.1 | 13.9 | 757 |
| $M_{1.8.b}$ | SAV * Net + PAR * Net | 7456.2 | 5 | 756 |
| $M_{1.9.b}$ | SAV + Turb | 7617.8 | 166.6 | 762 |
| $M_{1.10.b}$ | SAV + Turb + Net | 7479.5 | 28.3 | 761 |
| $M_{1.11.b}$ | SAV + Turb * Net | 7466.7 | 15.5 | 760 |
| $M_{1.12.b}$ | SAV * Net + Turb | 7464.2 | 13 | 757 |
| $M_{1.13.b}$ | SAV * Net + Turb * Net | 7458.4 | 7.2 | 756 |
| $M_{1.14.b}$ | SAV + Turb * Net + PAR * Net | 7457.7 | 6.5 | 758 |
| $M_{1.15.b}$ | **SAV * Net + Turb * Net + PAR * Net** | **7451.2** | **0** | **754** |

**Table S2.** Coefficients and associated standardized errors for the variables in the best model ($M_{1.15.b}$) for the alternative set in which irradiance is calculated at the surface ($E_{0\,443}$) Significant variables (P-value <0.05) are in bold. SAV: submerged aquatic vegetation; EAV: emerged aquatic vegetation. Exponents for SAV and EAV refer to the linear, quadratic, cubic, and the fourth power trends of the categorical ordered variable. The coefficients for the term Net refer to the deeper net relatively to the shallow.

| **Variable** | **Estimate** | **Std. Error** | **Z value** | **P-value** |
|---|---|---|---|---|
| **Intercept** | 1.88 | 0.35 | 5.40 | > **0.001** |
| **SAV$^1$** | 2.01 | 0.49 | 4.07 | > **0.001** |
| **SAV$^2$** | 0.35 | 0.36 | 0.98 | 0.338 |
| **SAV$^3$** | -0.13 | 0.28 | -0.45 | 0.651 |
| **SAV$^4$** | -0.30 | 0.20 | -1,47 | 0.141 |
| **Net** | 1.20 | 0.13 | 9.38 | > **0.001** |
| **EAV$^1$** | 0.49 | 0.39 | 1.25 | 0.210 |
| **EAV$^2$** | 0.01 | 0.27 | 0.05 | 0.964 |
| **EAV$^3$** | 0.05 | 0.17 | 0.33 | 0.744 |
| Turbidity | 0.02 | 0.14 | 0.16 | 0.873 |
| PAR | 0.11 | 0.14 | 0.77 | 0.444 |
| **Body lenght** | -0.33 | 0.12 | -2.86 | **0.004** |
| **SAV$^1$ * Net** | -0.26 | 0.38 | -0.70 | 0.484 |
| **SAV$^2$ * Net** | -0.49 | 0.31 | -1.58 | 0.115 |
| **SAV$^3$ * Net** | 0.09 | 0.26 | 0.03 | 0.973 |
| **SAV$^4$ * Net** | 0.49 | 0.20 | 2.49 | **0.013** |
| **Turbidity * Net** | -0.29 | 0.11 | -2.77 | **0.006** |
| **$E_{0\,443}$ * Net** | -0.33 | 0.10 | -3.31 | **0.001** |

## Figures

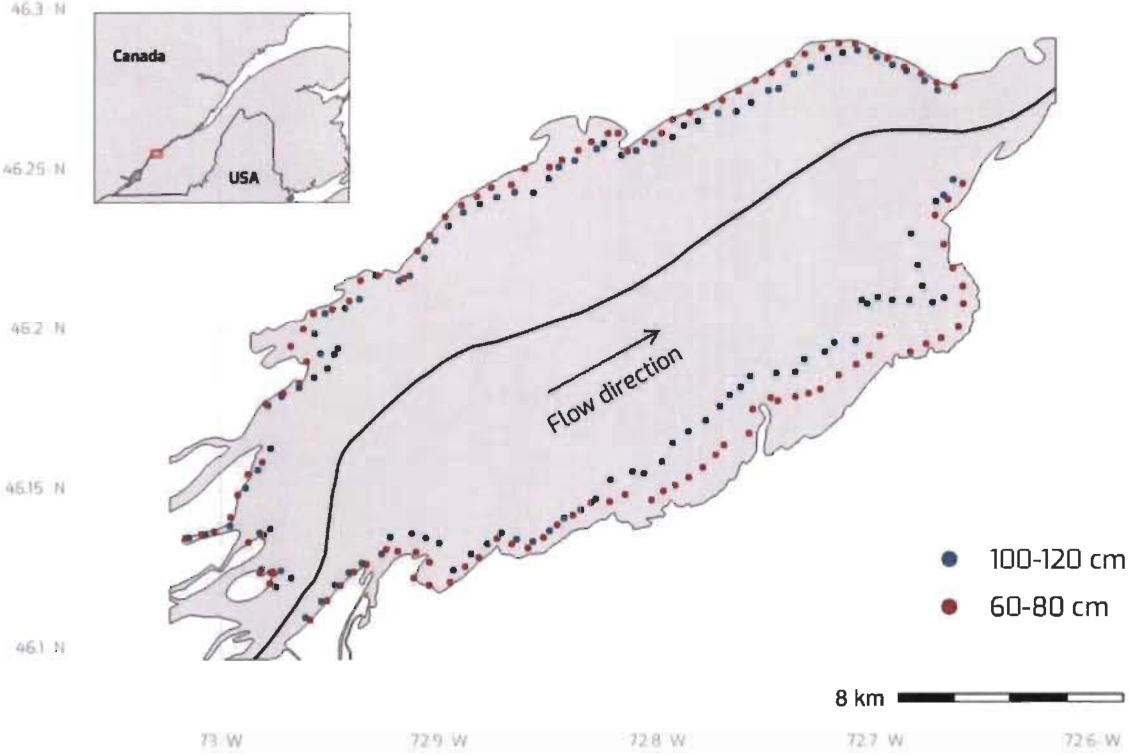

**Fig. 1.** Sampling sites in the Lake Saint-Pierre (Québec, Canada). Red and blue dots show, respectively, the location of sites at the isobaths 60-80 cm and 100-120 cm. The continuous line in the middle of the lake represents the man-made navigation channel (250 m wide, > 11 m deep). All the areas outside the navigation channel have a depth < 3.5 m. Due to inter-annual changes in water levels, the exact position of each sampling site was adjusted each year standardizing sampling at the two isobaths depths. Further details are reported in the section 'Study system' in Materials and Methods.

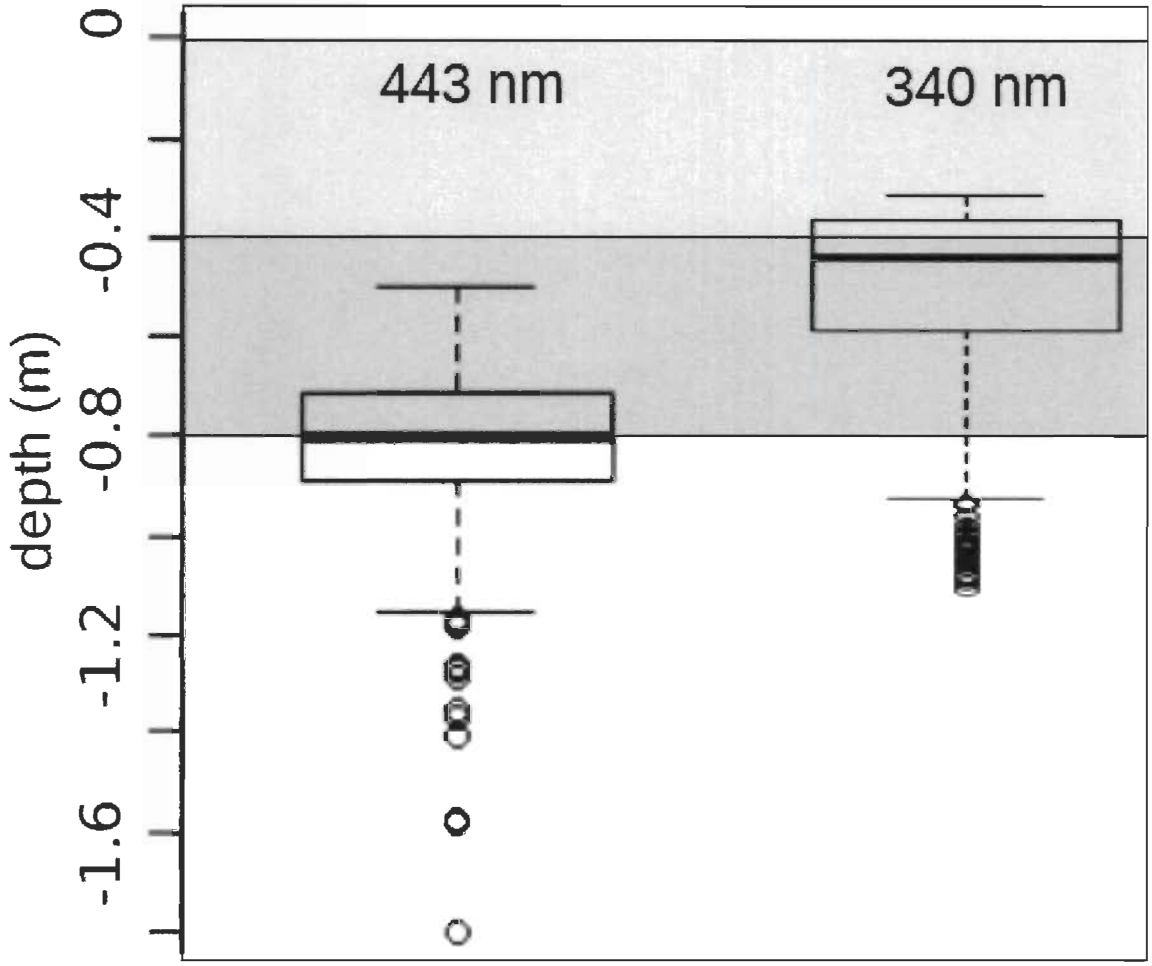

**Fig. 2.** Light penetration in the water column for the wavelengths 443 and 340 nm, expressed as the 1% irradiance depth for the sites sampled in the Lake Saint-Pierre. The shaded areas correspond to the depths sampled by the surface and bottom nets (light and dark gray, respectively).

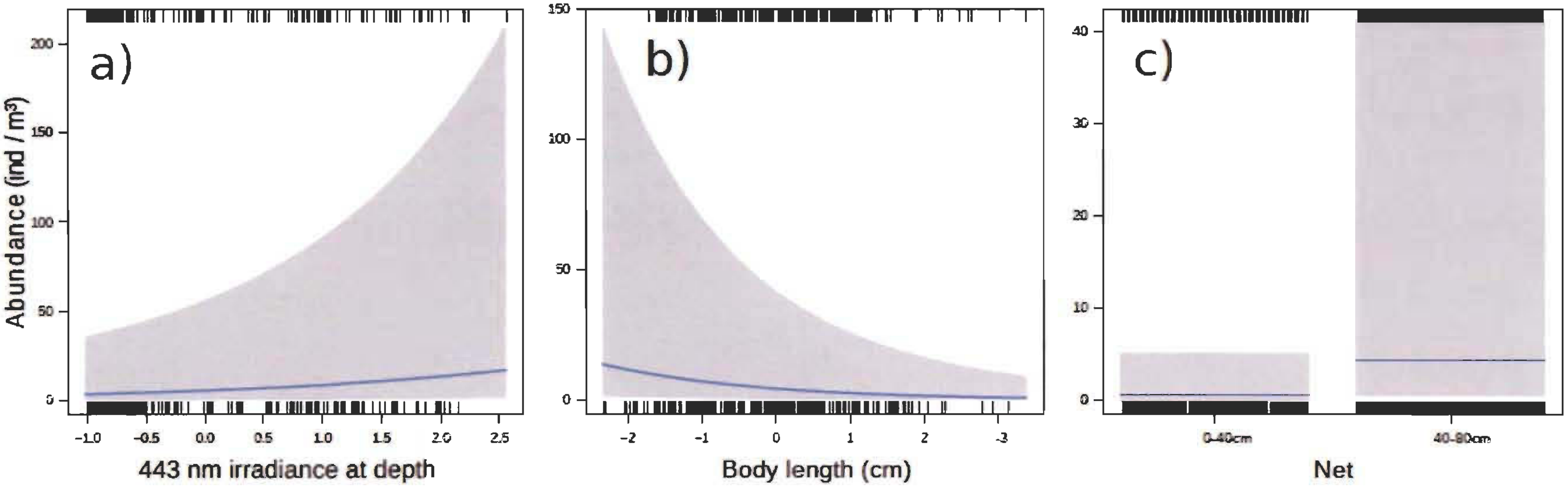

**Fig. 3.** Predicted values from the best model on the YPL vertical aggregation patterns (hypotheses $H_{1.1}$ to $H_{1.3}$) after controlling for all other variables in the model: a) 443 nm irradiance at depth (mW $m^{-2}$), b) body length (cm) and c) net (shallow and deep), on yellow perch larvae abundance. Note that continuous values on the x-axis are standardized (i.e. centered to zero and divided by their standard deviation). The blue line represents the mean predicted value whereas the grey area represents the 95% CI. Vertical bars on the horizontal axis are the observed values, respectively larger (above) or smaller (below) than the average. See text for details.

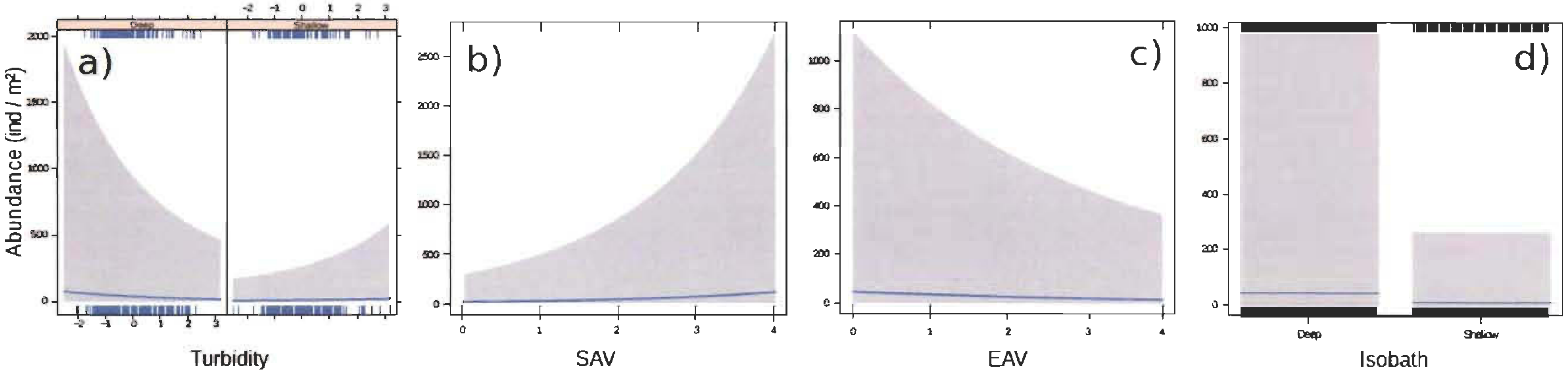

**Fig. 4.** Predicted values from the best model on the distribution pattern of YPL between isobaths (hypotheses $H_{2.1}$ and $H_{2.2}$) after controlling for all other variables in the model: a) turbidity, b) SAV, c) EAV and d) isobath, on yellow perch larvae abundance. For SAV and EAV, respectively, the predictions refer to the linear and quadratic terms of the orthogonal polynomial coding (see Table 3). See Fig. 3 for more details.

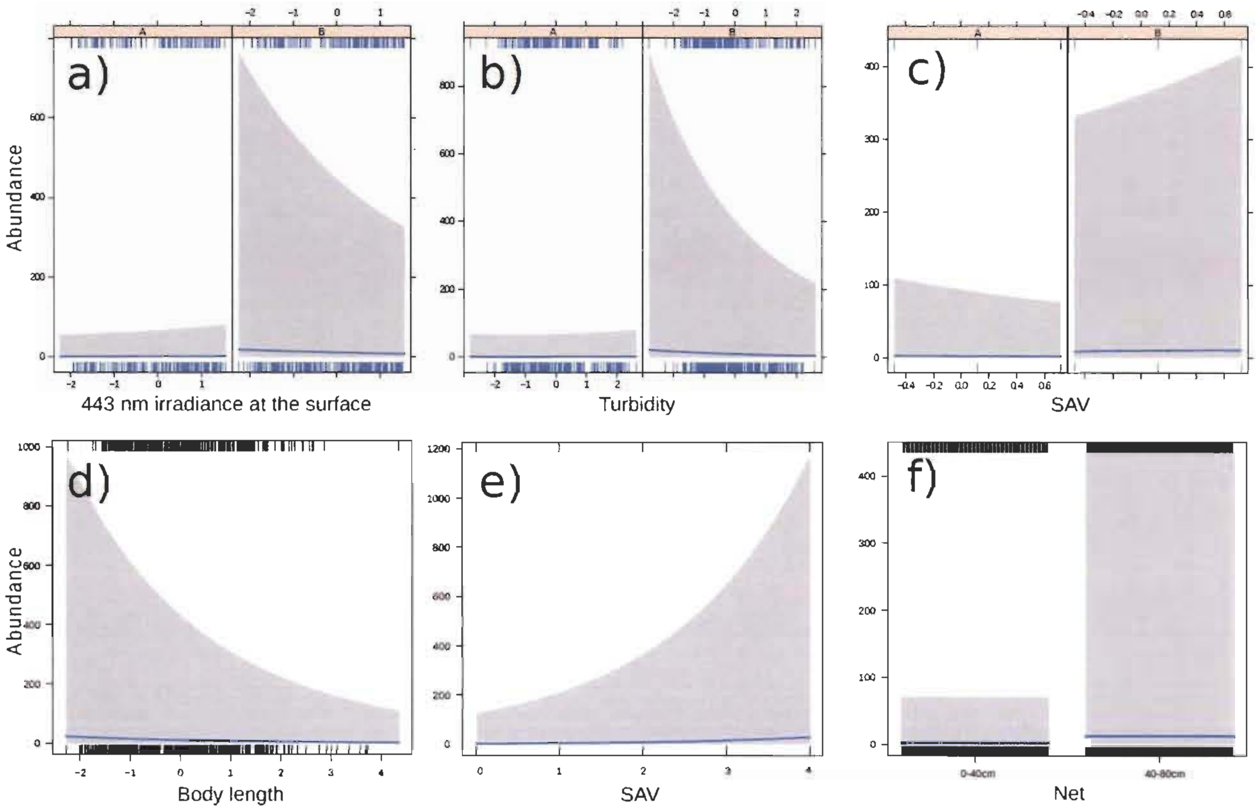

**Fig. S1.** Relative contribution of the variables visible light (a), turbidity (b), submerged aquatic vegetation (c) in interaction with Net and yellow perch body length (d), submerged aquatic vegetation (e) and net (f) on the yellow perch larvae abundance after controlling for all other variables in the model, based on the best model of the alternative set ($M_{1.15.b}$, solar radiation calculated at the surface; see Table S1). For panels a-c, A indicated the shallow and B the deep net. In panels c and e, respectively, SAV is expressed as the fourth power and linear term, respectively (i.e. $SAV^4$ and $SAV^1$ of the orthogonal polynomial coding; see the section 'Statistical analyses' and Table S2 for more details). Note that continuous values on the x-axis are standardized (i.e. centered to zero and divided by their standard deviation). The blue line represents the mean predicted value whereas the grey area represents the 95% CI. Vertical bars on the horizontal axis are the observed values, respectively larger (above) or smaller (below) than the average. See text for details.

# CHAPTER III

# THE RELATIONSHIP BETWEEN SUBMERGED AQUATIC VEGETATION, TURBIDITY, AND FISH DISTRIBUTION IN A LARGE SHALLOW FLUVIAL LAKE

This article will be submitted to *Hydrobiologia*.

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## Author contributions

Giacomazzo M., Bertolo A., Magnan P., Brodeur P. conceived the idea. Brodeur P. provided data. Giacomazzo M. performed statistical analyses. All authors contributed critically to the manuscript and gave final approval for publication.

## Abstract

Aquatic ecosystems are exposed to many stressors affecting their integrity. Increases in water turbidity and extensive macrophyte beds losses are examples of two phenomena of concern at the global scale. These factors are often causally linked, potentially leading to regime shifts if system-specific thresholds are exceeded. Given that species assemblages reflect both habitat quality and availability, such changes in water properties and habitat features can affect the relative abundance of species in the community or the composition of ecological guilds, with potential consequences of the whole trophic network. Here, we estimate the relationship between fish species and key habitat features in Lake Saint-Pierre (Québec, Canada), a shallow fluvial lake of the St. Lawrence River. During the last 30 years this lake experienced an increase in turbidity with a decline in the abundance of aquatic vegetation. To explain the association between the fish community and environmental variables, we performed multiple linear regressions on fish abundance, species richness, and Shannon diversity calculated at 133 stations, along a gradient of turbidity, temperature, and the abundance aquatic vegetation as well as canonical correspondence analysis (CCA) to estimate the relationship between dominant fish species and environmental variables. As expected, we found that both species richness and fish abundance (especially for phytophile species), were positively related with aquatic vegetation. Surprisingly, turbidity was also positively related to both Shannon diversity and species richness. Given the global trend of increase in turbidity and loss of aquatic vegetation, quantifying the association between fish species and habitat features might help to understand mechanisms structuring fish communities in changing environments.

**Keywords:** species diversity, species richness, abundance, fish community, submerged aquatic vegetation, turbidity.

## Introduction

Aquatic ecosystems are subjected to several anthropogenic stressors affecting water quality and their ecological integrity (Brinson and Malvárez, 2002; Lotze et al., 2006). Water quality degradation is a major issue worldwide, affecting all types of water bodies, from marine to freshwater (Brinson and Malvárez, 2002; Lotze et al., 2006). Global trends show important increases in pollutants (Schwarzenbach et al., 2010), nutrients (Howarth 2008, Liu et al., 2012), and turbidity (Miguel-Chinchilla et al., 2019) loads, particularly in freshwater and coastal regions. Especially for nutrients and turbidity inputs, the main anthropogenic sources are sewage treatment plants, farming, and intensive agricultural land use (Howarth 2008; Liu et al., 2012), the latter involving the use of fertilizers and soil labour. Most fertilizers are constituted of nitrogen and phosphorous compounds and once discharged into an aquatic ecosystem they tend to increase its eutrophication level. Land labour is often associated to soil erosion (García-Ruiz et al. 2015), leading to an increase in sedimentary turbidity concentrations in the rivers draining agricultural-dominated watersheds. Besides altering the trophic status of aquatic systems, these stressors also affect aquatic macrophytes (Giacomazzo et al., 2020), with potential for regime shifts if nutrients and turbidity thresholds are exceeded (Scheffer et al., 1993; Hilt et al., 2018). Aquatic macrophyte loss is another worldwide alarming trend (Zhang et al., 2017), especially regarding submerged aquatic vegetation (hereafter SAV). SAV is disappearing in many freshwater (e.g., Hilt et al., 2006; Zhang et al., 2017) as well as in marine and brackish (e.g., Orth et al., 2010; Shafer & Bergstrom, 2010) ecosystems. Not surprisingly, water quality degradation and SAV abundance are strictly connected. The most important cause of SAV loss is the degradation of the water-column optical environment, exerted both by sedimentary turbidity and phytoplankton growth (this latter boosted by fertilizers-induced eutrophication) (Sand-Jensen and Borum, 1991; Scheffer et al., 1993, Hidding et al., 2016). The interplay between these stressors might result in a regime shift towards a turbid, non-vegetated, plankton-dominated state (Scheffer et al., 1993, Hilt et al., 2018.), which is associated to an array of ecosystem services loss (e.g., water purification, coastal protection, fish habitat; Barbier et al., 2011).

In addition to the effects mentioned above, a decline in habitat complexity due to SAV loss implies a habitat degradation for many invertebrate and vertebrate species (e.g., Chow-Fraser et al., 1998; Bolduc et al., 2020), which is expected to be mirrored by a rearrangement of relative abundances, potentially leading to species losses. For instance, in Cootes Paradise March (Ontario, Canada), decreases in water clarity and increases in nutrients concentration due to sewage effluent pollution, induced a marked decline in SAV species diversity and coverage, which resulted in long-term changes in planktonic, benthic and fish community's composition (Chow-Fraser et al., 1998). Other studies showed that a reduction in SAV abundance induced a decline in benthic invertebrates' abundance (e.g., Caires et al., 2013, Whatley et al., 2013) and a rearrangement of fish assemblages (Sheppard et al., 2011). In New Zealand, the trophic network of lakes that undergone regime shifts towards turbid states and SAV loss has been affected both in terms of food chain length and food web complexity (Kelly & Schallenberg, 2019). To make predictions about the potential long-term effects of these threats on aquatic ecosystems, we first need to understand how communities respond to the different stressors in the short term.

Here, we evaluate the association between fish species, SAV abundance, turbidity, and water temperature in the Lake Saint-Pierre (Québec, Canada; hereafter LSP), the largest fluvial lake of the St. Lawrence River. The LSP undergone major environmental changes over the last 50 years. Water temperature gradually increased since the beginning of the century, and especially regarding the SAV growing season, temperature increased from 13.5 °C in 1972 to 18.1 °C in 2016 (Hudon et al., 2018). Starting from the 1960s, the agricultural lands surrounding the LSP have been converted from perennial to intensive annual crops (Dauphin and Jobin, 2016), releasing high inputs of phosphorous, nitrogen and sedimentary turbidity into the rivers draining the watershed, ultimately entering the LSP (Simoneau 2017, Giacomazzo et al., 2020). Turbidity loads had a negative effect on SAV abundance, which started declining since the mid-1990s (Giacomazzo et al., 2020). Given that SAV is a high-quality habitat for both invertebrates and fish species, we expect that a reduction in SAV habitat availability will be mirrored by a change in fish species assemblage and distribution within LSP. We compared data from 133 stations across the lake (from 2002 and 2007), within a gradient of SAV abundance and turbidity, to forecast changes in the relative abundance and species diversity following a scenario of increase in turbidity and a decrease submerged aquatic vegetation. We predicted that: i) higher SAV abundance will sustain locally a higher overall fish abundance, species richness and diversity because of high quality habitat; ii) higher turbidity will be negatively associated to the overall fish abundance, species richness and diversity, because narrowing the niche for clear water/visual species, iii) phytophile species will be more abundant in vegetated stations.

## Materials and Methods

### *Study area*

LSP (Fig. 1) is the largest fluvial lake of the St. Lawrence River covering an area of approximately 400 km$^2$. LSP has a slow water velocity (< 0.5 m s-1), is shallow (mean depth approx. 3 m), except for the artificial navigation channel that is approximately 11 m deep (Hudon & Carignan, 2008). LSP receives water from several tributaries, characterized by different physical and biogeochemical characteristics (Frenette et al., 2003; 2012), and is therefore heterogeneous concerning water optical properties (Frenette et al. 2003). The south shore tributaries drain watersheds mainly characterized by agricultural areas, carrying high inputs of nutrients and sediments as well as a wide spectrum of contaminants, while north shore tributaries have lower nutrient concentrations and are less polluted (Simoneau 2017).

SAV can be abundant during the summer in LSP, eventually forming a canopy at the surface (Hudon et al., 2012). However, especially in the last decades, SAV showed very heterogenous patterns, alternating from densely vegetated patches to almost bare substrate. The most abundant SAV species are American eelgrass (*Vallisneria americana*) and pondweeds (*Potamogeton richardsonii* and *Stuckenia pectinata*). Emergent vegetation is mainly represented by bulrushes (*Schoenoplectus fluviatilis*, *S. lacustris*, and *S. pungens*), broad-fruited bur-reed (*Sparganium eurycarpum*), and broad-leaved arrow-leaf (*Sagittaria latifolia*) (Massicotte et al., 2015). The SAV is expected to represent a good quality habitat for many fish species, both for feeding and growing (Rozas and Odum,1988; Paradis et al., 2014).

### *Fish sampling*

A standardized fish sampling survey of the fluvial section of the St. Lawrence River has been conducted by Québec governmental authorities since 1995 (1995, 1997, 2002, 2007, 2009, 2011, 2013) in late summer/early fall with the objective to assess the health of the LSP fish community and the temporal changes in relative abundances. Fish were sampled at 72 stations for each year (Fig. 1). Stations were systematically distributed at each km of shore including the flats in the center of the river (La Violette et al., 2002; 2007). Sampling has been performed by means of seine nets (4 m height, 12.5 m long, mesh 3.2 mm, with upper floaters and lead sinkers at the bottom) to be selective for juvenile fish. Here, we analyzed data from 2002 (19th-30th August; 66 stations) and 2007 (21st-28th August; 67 stations) sampling campaigns, the years for which we have complete information on turbidity. This data set contains a total of 51 fish species, belonging to different families (Table S1). After collection, fish were narcotized with tricaine methanesulfonate (MS-222TM – Sandoz) and immediately preserved in 10% formaldehyde for laboratory species identification.

The temperature (± 0.1 °C) was measured at each station with an YSI 556 MPS Multiprobe System. Water samples were collected and brought to the laboratory to measure nephelometric turbidity (± 0.01 NTU) with a WTW-550 turbidity meter.

### *SAV estimation*

We estimated SAV abundance by using two different measures, aiming to estimate SAV cover at two different scales. *In situ* measures were meant to depict the very local spatial scale at the level of the seine sampling, whereas satellite imagery was used to describe the SAV abundance at a larger scale (90 x 90 m). These two methods represent two different scales at which fish perceive their habitat and could show different abilities in predicting fish abundance.

*In situ* measures were taken at each fish sampling station. SAV was visually estimated using the following semi-quantitative scale: 1 (absent), 2 (sparse), 3 (dense, bottom visible), 4 (very dense, bottom non-visible, open water at the surface), 5 (extremely dense, bottom non-visible, canopy at the surface).

Satellite imagery from Landsat 5 and 7 was used to estimate the SAV abundance by calculating the enhanced vegetation index (EVI). The EVI index is very sensitive to dense vegetation, especially in cases of high biomass and surface canopy (Gao et al., 2000; Huete et al., 2002), and was shown in LSP to correlate with quantitative SAV biomass samples collected *in situ* (Massicotte et al., 2015). Mean EVI values on a 90 x 90 m (3 x 3 pixels) buffer were calculated for 2002 and 2007, to spatially match the fish sampling stations. Satellite data were extracted at the summer peak of SAV abundance (7th September 2002 and 28th August 2007), also matching with the fish sampling campaign. The calibration, correction, and treatment for atmospheric effects on satellite images were performed as in Massicotte et al. (2013).

To account for the fact that water levels might have differed between the date of fish sampling and the date of the satellite pictures, EVI rough values were corrected as in Giacomazzo et al. (2020). Water levels can change quickly in LSP, and they can affect the detection of SAV by remote sensing, because of variations in the height of the water column above SAV canopy. EVI data from 1995 to 2012 were thus modelled by means of a generalized additive mixed model (GAMM) including the year, the day of the year of the satellite pictures and depth (these two latter as smoothed fixed effects), and the station as random effect. EVI residuals from the GAMM for 2002 and 2007 were then extracted and used as explanatory variable for statistical analyses. EVI residuals were validated by comparison with semi-quantitative measures taken at each sampling station (Fig. S1).

### *Statistical analyses*

At each station we calculated: i) total fish abundance, as the total number of individuals of all species per sampling station; ii) species richness, as the count of the number of species per station; and iii) Shannon diversity (defined as H = - sum $p_i$ log($b$) $p_i$, where $p_i$ is the proportional abundance of species $i$ and $b$ is the base of the logarithm), according to the *diversity()* function in the *vegan* R cran package (Oksanen et al., 2020). Linear models coupled with a multi-model inference approach (Burnham and Anderson 2002) were used to explore the best set of independent predictors of the dependent variables. To evaluate the relationships between the above-mentioned response variables and the explanatory variables SAV abundance (both EVI or *in situ* SAV cover), temperature, turbidity, and depth we performed multiple general linear regression models. Shannon diversity data were modelled with a Gaussian distribution whereas both species richness and total abundance were modelled with a Poisson distribution. A total of 66 and 67 observations were used for the years 2002 and 2007, respectively.

Model assumptions were visually evaluated for normality, linearity, homoscedasticity, and outliers. Residuals of linear models were screened for autocorrelation and partial autocorrelation with the functions *acf()* and *pacf()* in the R environment (R core team version 3.6.0).

Multi-model inference was conducted by using the R package *MuMIn* (Barton, 2012). Dependent data were standardized before analysis to allow direct comparison of the strength of the relationship between independent and dependent variables. The available variables were used to build all the possible models with the *dredge()* function whereas the *model.avg()* function was thereafter used to extract model-averaged estimates. Models were ranked based on Akaike information criterium corrected for small sample size, which provides a relative strength of evidence to each model ($AIC_C$, Burnham and Anderson, 2002b). Akaike weights ($w_i$) were calculated based on $AIC_C$ to estimate the relative importance of each model and of each variable. A 95% confidence interval set of models was calculated based on the cumulative $w_i$ and used to make model averaging of the coefficients of the parameters and their 95% CI. Those parameters whose 95% CI did not include the zero values were considered significant. To get an estimate of the percent variation explained by the models, we calculated the adjusted determination coefficient of the most parsimonious model based on $AIC_C$ values.

To quantify the association between dominant fish species in the community (relative species abundance > 1% of the total abundance) and explanatory variables, we performed canonical correspondence analyses (CCA). This choice was motivated to reduce the relative importance of rare species, which tend to be overemphasized in CCA. CCA is a widely used multivariate analysis to quantify the relationships between species and environmental variables (ter Braak & Verdonschot, 1995). CCA is also suited for large datasets with species showing a unimodal response to environmental variables (ter Braak & Verdonschot, 1995). The effect of time (year of sampling) was integrated in the CCA as conditional variable to control for the non-independency of the data within a given year. The 11 fish species analyzed by means of the CCA were classified into three guilds based on the predilection for spawning in SAV habitats (La Violette et al. 2003), namely phytophiles, non-phytophiles and facultative-phytophiles (i.e., which can spawn both on SAV and/or other substrates). Phytophile species are the banded killifish (*Fundulus diaphanous)*, bridle shiner (*Notropis bifrenatus*), and the golden shiner (*Notemigonus crysoleucas*). Non-phytophile species are the brown bullhead (*Ameiurus nebulosus*), tessellated darter (*Etheostoma olmstedi*), emerald shiner (*Notropis antherinoides*), and the bluntnose minnow (*Pimephales notatus*). Facultative phytophile species are the brook silverside (*Labidesthes sicculus*), pumpkinseed (*Lepomis gibbosus*), mimic shiner (*Notropis volucellus*), and the yellow perch (*Perca flavescens*). CCA was performed with the ‘vegan’ R package.

All statistical analyses were performed using the R language environment (version 3.6.0; R core team 2019).

## Results

EVI estimated with satellite imagery correlated with SAV measured *in situ* (Fig. S1), despite not perfectly because of a relatively high error spread in the EVI values, leading to some overlap, especially for the SAV categories associated to lower abundances.

For Shannon diversity, multi-model inference showed that, within the 32 possible models built with the variables at hand, 15 can be considered plausible (i.e., having a $\Delta$AICc < 10) whereas eight can be included in the 95% CI set of models to be used for inference (Table 1a). The best of these models explained 16.1% of the variation in the data, as based on its $R_{adj}^2$. Depth, turbidity, temperature, and year had large Akaike weights (1, 0.97, 0.86 and 0.75, respectively), with EVI showing lower weight (0.26). Shannon diversity was significantly positively related to both turbidity (averaged estimate = 0.104; CI = 0.031/0.178) and depth (averaged estimate = 0.112; CI = 0.042/0.183), and negatively related to temperature (averaged estimate = -0.094; CI = -0.172/-0.0154) (Table 1a). We also found a significant effect of the year on Shannon diversity (averaged estimate = 0.156; CI = 0.003/0.310) with a higher diversity observed in 2007 compared to 2002. EVI did not show any significant relationship with Shannon diversity (averaged estimate = 0.013; CI = -0.063/0.089) (Table 1a).

For species richness, multi-model inference showed that eight models can be considered as plausible and, among these, five can be included in the 95% CI set of models to be used for inference (Table 1b). The best of these models explained 22.0% of the variation in the data, as based on its $R_{adj}^2$. Species richness was positively related to EVI (averaged estimate = 0.068; CI = 0.006/0.131), turbidity (averaged estimate = 0.069; CI 0.014/0.125) and depth (averaged estimate = 0.109; CI =0.058/0.160), and negatively related to temperature (averaged estimate = -0.155; CI = -0.220/-0.090) (Table 1b). For species richness, depth, temperature, turbidity and EVI had large Akaike weights (1, 1, 0.93 and 0.81, respectively), with year having a somewhat lower weight (0.69). No significant effects of year were found on species richness (averaged estimate = 0.124; CI = - .006/0.253).

Within all the possible models to explain total fish abundance, multi-model inference showed that only the one including all the variables can be considered as plausible (Table 1c), with the second-best model having a ΔAICc > 130. Despite such a low uncertainty in model selection, this model explained only 4.1% of the variation in the data. Total abundance was positively related to both EVI (estimate = 0.274; CI = 0.264/0.285) and depth (estimate = 0.203; CI = 0.195/0.211), whereas it was negatively related to both turbidity (estimate = -0.231; CI = -0.245/-0.216) and temperature (estimate = -0.348; CI = -0.360/-0.336) (Table 1c). We also found a significant effect of the year on total abundance, with higher values in 2007 compared to 2002 (estimate = 0.130; CI = 0.108/0.152). Since all these variables were included in the only model retained in the 95% CI set of models, they all have an Akaike weight equal to 1.

Models including the categorical variable SAV measured *in situ* gave overall similar results for the three modelled variables, with the exception of the model for Shannon diversity, for which SAV also resulted to be a significant predictor (see Table S2).

The CCA showed that the variables EVI, temperature, turbidity, and depth explained together 14.6% of the total variation in the dominant fish species abundance data with the year explaining the 3.3% (Fig. 2). Both the first two axes were significant and explained respectively the 8.7% and 5.1% of the total variance. The first axis of the CCA represents a gradient of EVI, turbidity and temperature. The variables EVI and turbidity were negatively correlated to this axis, whereas temperature and turbidity were positively correlated. The abundance of phytophile species was positively associated to EVI, and negatively to turbidity and temperature. Non-phytophile species tended to be positively associated to turbidity and temperature, and despite some overlap, negatively associated to EVI. Facultative-phytophile species were located around the centroid (closer to phytophile rather than non-phytophile species), on the average of the EVI, temperature, and turbidity gradient. The CCA including the variable SAV measured *in situ* gave similar results and explained 20.3% of the total variation in fish abundance data (Fig. S2).

## Discussion

Overall, our results agree with the expectation that SAV has a positive effect on fish abundance and species richness/diversity. Depth and temperature also showed interpretable patterns, with higher abundance and diversity at both deeper and cooler stations, suggesting a potential role of thermal stress in driving species distribution within the lake. In contrast, it is more difficult to interpret the results on turbidity since this variable was negatively related to total fish abundance as predicted (despite the low variation explained by the model), although positively related to both species richness and diversity. On the other end, it is worth noting that we were able to explain only a relatively small fraction of the variation in fish abundance, species richness, and diversity, suggesting that, at the scale of our study, the relationship between fish species distribution of and the features of their habitat are relatively weak.

Even though *in situ* SAV estimates tended to explain somewhat more variation in the data, models including the variables EVI and SAV measured *in situ* gave very comparable results. This suggests that remote sensing can give reasonable estimates of SAV in LSP, despite the differences in the scale analyzed between the two methods. Therefore, it seems that both measures depict a spatial scale that these fish can exploit. Given the similarity in the results we will only discuss the models including the variable EVI and refer the reader to the 'Supplementary material' for models built with SAV measured *in situ*.

Both species richness and abundance are the result of the interplay between biotic and abiotic factors. Biotic factors such as predation, competition, mutualism, and interference play a major role in driving species assemblage in the community (Pianka, 1994). Since such mechanisms are difficult to measure, historically, abiotic factors have been some of the most studied variables in community ecology, providing an indication on species habitat utilization along environmental gradients. Here, we specifically focused on key environmental variables structuring fish habitat, both biotic (i.e., SAV abundance) and abiotic (i.e., turbidity, temperature, and depth), which are expected to drive fish species richness, diversity, and abundance. Whereas we are aware that our models explained a relatively low fraction of the variation in the data ($R^2$ from 0.04 to 0.22), probably because key biotic interactions within the fish community were not accounted for, this fraction was non-negligible for many models, providing information on habitat features selected by these fish species.

Albeit Shannon diversity was not correlated to EVI, SAV abundance evaluated *in situ* (semi-quantitatively) was significantly related to this descriptor (see Table S2). Therefore, all the three response variables responded to a different degree to SAV, as suggested by a large body of literature. Bryan and Scarnecchia (1992), for example, sampled fish along a lake with natural and urban-altered shorelines (i.e., with SAV removed), and found that SAV abundance was the key variable affecting both young-of-the-year total abundance and fish species richness, supporting our findings. In shallow habitats, SAV provides a fundamental habitat for the establishment of a juvenile fish community, especially during their first year of growth (Bryan and Scarnecchia, 1992). SAV represents a good habitat quality for many fish species, providing shelter from predators and invertebrate food resources. For instance, Rozas and Odum (1988) conducted field experiments to disentangle the relative roles of refuges from predators and food availability to explain fish abundance in a freshwater marsh. Their tethering experiments revealed that the relative predation pressure was significantly higher in areas without SAV (Rozas and Odum, 1988). Moreover, fish confined in a vegetated habitat was found to enhance their foraging profitability, increasing prey intake or size, depending on fish species (Rozas and Odum, 1988).

In LSP, Hudon et al. (2012) found that invertebrate biomass was ninefold lower in low-vegetated sites compared to highly vegetated ones. Accordingly, fish biomass showed the same pattern, with small/young fish being threefold less abundant (and large fish 1.5-fold) in low SAV biomass sites. It is worth mentioning that several studies in LSP showed that SAV is a key variable for fish populations at the scale of the whole lake. For example, yellow perch is known to be strongly associated with SAV, from larval (Bertolo et al. 2012, Paradis et al., 2014; Massicotte et al., 2015) to young-of-the year and adult stages (Giacomazzo et al., 2020). Given that our sampling gear targeted small fish, the fish community in our samples is mainly composed by juveniles and invertebrate feeders, and it is reasonable to assume that SAV offered both a refuge from predators while enhancing prey availability (higher fish carrying capacity in the SAV). Taken together, these mechanisms could lead to an increased fish survival and niche availability and sustain a higher total abundance and species richness.

We found an unexpected positive effect of turbidity on Shannon diversity and species richness, but a negative, albeit weak, relation with total fish abundance. These results might reflect the fact that turbid waters could exert opposite pressures on different species, depending on their ontogenetic stage and ecology. For instance, turbid waters can hide prey from predation, or, in contrast, could favor predators which might be more difficult to detect by preys (Utne-Palm 2002). Visual predators could be less efficient in turbid waters, whereas predators using chemo-sensorial cues (e.g., ictalurids) might be advantaged (Rodríguez and Lewis 1997). However, a tethering study conducted in LSP showed that prey fish mortality due to predation was overall higher at low transparency, even though predation risk was species-specific and possibly depending on preys' colour and morphology (Laplante-Albert et al., 2010). These findings support our results on the negative relationship between fish abundance and turbidity, a relationship that may hide a different predation pressure depending on water clarity. On the other hand, higher predation might turn into a lower interspecific competition, allowing the co-existence of a higher number of species locally (Paine 1966; Parrish and Saila, 1970; Menge et Sutherland, 1976). For instance, predators may affect the relationships between preys (e.g., anti-predator behaviour), allowing a weaker competitor to co-occur with stronger ones (Jermacz et al., 2015). This predation-competition scenario might underlie the increase in both species richness and Shannon diversity observed at more turbid stations in our study, but this post-hoc hypothesis should be validated by more targeted studies.

Temperature was negatively correlated with Shannon diversity, species richness, and total abundance. Given the shallowness of this temperate fluvial lake, and the lack of a deep thermal refuge, high temperatures are likely to lead to a reduction in the number of species able to tolerate these habitats. Even though fish might react to an increase in temperature by finding a more suitable area (e.g., refreshing currents or deeper zones), summer fish mortality phenomena have been reported in LSP (R. Bacon, MFFP, pers. comm.). Moreover, competitive ability for each fish species is known to be temperature dependent (Taniguchi et al., 1998), and some species might have been outcompeted from warmer stations. Therefore, given all these reasons, it is not surprising that higher temperatures are associated to lower fish abundances and diversity.

Our results also show a positive relationship between depth and Shannon diversity, species richness, and total abundance. Despite the depth gradient is relatively small among our sampling stations (ca. from 0.5 to 1 m), this still potentially represents a biologically significant gradient for juveniles and small fish species. By modelling yellow perch larvae vertical distribution in the LSP, Giacomazzo et al., (in prep.) showed that higher larvae abundances were systematically close to the bottom and at the deeper isobath (more larvae at 1.2 m isobath than the 0.8 m isobath), a very consistent pattern detected over 11 years and hundreds of stations. This pattern was deemed behavioural and explained as a form of habitat selection (i.e., closer match with SAV), and probably a form of UVR-avoidance in very shallow, high UV-risk waters (Giacomazzo et al., in prep.). Here, the positive effect of depth on fish abundance, Shannon diversity, and species richness might underlie different mechanisms, like an increased number of thermal niches (probably increasing richness and diversity), but we cannot exclude a potential effect mediated by UVs (i.e., reduced mortality at lower UV risk and therefore higher total fish abundance).

Sampling year was also included as covariable in the model to control for eventual inter-annual differences in the response variables albeit we do not have specific predictions about it.

Despite the overall trend in decreasing SAV observed during the last decade in LSP, we did not find significant differences in overall SAV abundances between the two study years (results not shown). Therefore, we cannot interpret the significant differences between the two years in the Shannon diversity, species richness and total abundance (all higher in 2007 compared to 2002) as an effect of SAV. Among factors behind this result, we could hypothesize spring floods, which could affect inter-annual recruitment of many fish species and which is highly variable in LSP. Flooded areas provide suitable spawning grounds for many species (Mailhot et al., 2015), as well important sources of invertebrate preys, which represent high quality resources for young fish larvae. In LSP, littoral juvenile fish have been found to strongly rely on these food resources, to the point that fish stable isotopic signature was consistent with invertebrates coming from the floodplain (Farly et al., 2019). Therefore, due to annual variations in environmental conditions, it is possible that spawning and recruitment were better in 2007 compared to 2002.

Results from the CCA showed that the variables depth, SAV, temperature, and turbidity explained a relatively small, albeit not trivial, fraction, of the total variance (14.6 %). We are aware that environmental variables can explain only partly the species community structure since key biotic interactions among species (e.g., competition, predation) were not specifically accounted for in our study. Therefore, our goal here was not to maximize the explanation of the total variance, but rather to predict the abundance of dominant species based on key environmental variables known to structure the fish community. As expected, SAV abundance estimated with the EVI was positively associated with phytophile species and negatively with non-phytophile species. Therefore, SAV can be considered a relatively good predictor of dominant fish species (or at least guilds) abundance. However, this grouping into guilds was based on information about spawning preferences and might have missed some important species traits in relationship with the SAV habitat summer use. Most fish species in LSP spawn in late winter – early summer, when SAV is dormant or starting to grow. Therefore, the species' spawning preferences are not directly related to the summer habitat use. Nevertheless, most species spawning in the early SAV beds are also abundant in vegetated areas during the summer, and therefore we consider spawning guilds as a proxy of the species likeliness to generally exploit SAV.

Facultative phytophile species were closely grouped around the centroid, suggesting that they did not respond to the environmental gradient of SAV abundance, temperature, and turbidity. Non-phytophile species showed the most distinctive responses relatively to the other species and were negatively associated to SAV. This suggests that non-phytophile spawners are less associated to SAV also during the summer and not only during the reproductive season. These species were positively associated to turbidity, in contrast to facultative and phytophile species. In LSP, turbidity has been shown to negatively affect SAV abundance, shaping on the long-term the extent of SAV beds, mostly because of the degradation of the light environment of the water column (Giacomazzo et al., 2020). In the CCA, this negative relationship was clear, with SAV abundance and turbidity being negatively correlated on the first axis. Interestingly, temperature and turbidity correlated positively, possibly because suspended particles absorb and scatter sunlight, increasing water temperature (Paaijmans et al., 2008). However, other local factors associated with the presence of water masses in the LSP with different physico-chemical properties cannot be excluded (Frenette et al. 2003). Non-phytophile species were positively correlated to both turbidity and temperature, but it is not clear if all these species have an affinity for warm turbid water habitats or if they simply react to the SAV gradient selecting the extreme with lower SAV abundance. Such preferences are certainly species specific, with species such as brown bullhead (*Ameiurus nebulosus*) which is a chemo-sensorial species known for its adaptations to low oxygen concentrations and warm, turbid waters (Scott and Crossman, 1974). The low proportion of variation explained by the CCA might also be due to the relatively small spatial scale accounted for, because fish could move between different habitats, weakening the strength of the relation between species and environmental variables.

In a global change scenario, SAV is deemed to further decrease while eutrophication, turbidity, and water temperature to increase. Estimating the association between fish species and habitat features is key to infer future environmental changes. If these trends continue, the fish community may react by restructuring the species relative abundance, eventually leading to a loss of non-adapted species. Our study showed that the above-mentioned environmental variables drive species richness, diversity and abundance, and that fish spawning guilds based on the preferred spawning substrate, use different gradients of SAV and turbidity/temperature.

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## References

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier & B. R. Silliman, 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs 81: 169-193.

Barton, K., 2012. CRAN - Package MuMIn. R package version.

Bertolo, A., F. G. Blanchet, P. Magnan, P. Brodeur, M. Mingelbier, P. Legendre, 2012. Inferring processes from spatial patterns: The role of directional and non–directional forces in shaping fish larvae distribution in a freshwater lake system. PLoS ONE 7: e50239.

Bolduc, P., A. Bertol, C. Hudon & B. Pinel-Alloul, 2020. Submerged aquatic vegetation cover and complexity drive crustacean zooplankton community structure in a large fluvial lake: An *in situ* approach. Journal of Great Lakes Research 46: 767-779.

Brinson, M. M. & A. I. Malvárez, 2002. Temperate freshwater wetlands: types, status, and threats. Environmental Conservation 29: 115-133.

Bryan, M. D. & D. L. Scarnecchia, 1992. Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake. Environmental Biology of Fishes 35: 329-341.

Burnham, K. P. & D. R. Anderson, 2002. Model selection and multimodel inference: a practical information-theoretic approach. Ecological Modelling. Springer Science & Business Media.

Burnham, K. P. & D. R. Anderson, 2002b. Formal inference from more than one model: multimodel inference (MMI). In Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag.

Caires, A. M., S. Chandra, B. L. Hayford & M. E. Wittmann, 2013. Four decades of change: dramatic loss of zoobenthos in an oligotrophic lake exhibiting gradual eutrophication. Freshwater Science 32: 692-705.

Chow-Fraser, P., V. Lougheed, V. Le Thiec, B. Crosbiel, L. Simser & J. Lord, 1998. Long-term response of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. Wetlands Ecology and Management 6: 19-42.

Dauphin, D. & B. Jobin, 2016, Changements de l'occupation du sol dans la plaine inondable du lac Saint-Pierre entre les années 1950 et 1997. Le Naturaliste canadien 140: 42-52.

Farly, L., C. Hudon, A. Cattaneo & G. Cabana, 2019. Seasonality of a floodplain subsidy to the fish community of a large temperate river. Ecosystems 22: 1823-1837.

Frenette, J. J., M. T. Arts & J. Morin, 2003. Spectral gradients of downwelling light in a fluvial lake (Lake Saint-Pierre, St-Lawrence River). Aquatic Ecology 37: 77-85.

Frenette, J-J, P. Massicotte, J. F. Lapierre, 2012. Colorful Niches of Phytoplankton Shaped by the Spatial Connectivity in a Large River Ecosystem: A Riverscape Perspective. PLoS ONE 7(4): e35891.

Gao, X., A. R. Huete, W. Ni & T. Miura, 2000. Optical-biophysical relationships of vegetation spectra without background contamination. Remote Sensing of Environment 74: 609-620.

García-Ruiz, J. M., S. Beguería, E. Nadal-Romero, J. C. González-Hidalgo, N. Lana-Renault & Y. Sanjuán, 2015. A meta-analysis of soil erosion rates across the world. Geomorphology 239: 160-173.

Giacomazzo, M., A. Bertolo, P. Brodeur, P. Massicotte, J. O. Goyette & P. Magnan, 2020. Linking fisheries to land use: How anthropogenic inputs from the watershed shape fish habitat quality. Science of the Total Environment 717: 135377.

Hidding, B., E. S. Bakker, M. J. M. Hootsmans & S. Hilt, 2016. Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. Oikos 125: 1489-1495.

Hilt, S., E. M. Gross, M. Hupfer, H. Morscheid, J. Mählmann, A. Melzer, J. Poltz, S. Sandrock, E. V. Scharf, S. Schneider & K. van de Weyer, 2006. Restoration of submerged vegetation in shallow eutrophic lakes – A guideline and state of the art in Germany. Limnologica 36: 155-171.

Hilt, S., M. M Alirangues Nuñez, E. S. Bakker, I. Blindow, T. A. Davidson, M. Gillefalk, L. A. Hansson, J. H. Janse, A. B. G. Janssen, E. Jeppesen, T. Kabus, A. Kelly, J. Köhler, T. L. Lauridsen, W. M. Mooij, R. Noordhuis, G. Phillips, J. Rücker, H. H. Schuster, M. Søndergaard, S. Teurlincx, K. van de Weyer, E. van Donk, A. Waterstraat, N. Willby & C. D. Sayer, 2018. Response of submerged macrophyte communities to external and internal restoration measures in north temperate shallow lakes. Frontiers in Plant Science 9: 194.

Howarth, R. W., 2008. Coastal nitrogen pollution: A review of sources and trends globally and regionally. Harmful Algae 8: 14-20.

Hudon, C. & R. Carignan, 2008, Cumulative impacts of hydrology and human activities on water quality in the St. Lawrence River (Lake Saint-Pierre, Quebec, Canada). Canadian Journal of Fisheries and Aquatic Sciences 65: 1165-1180.

Hudon, C., A. Cattaneo, A. M. Tourville Poirier, P. Brodeur, P. Dumont, Y. Mailhot, J. P. Amyot, S. P. Despatie & Y. de Lafontaine, 2012. Oligotrophication from wetland epuration alters the riverine trophic network and carrying capacity for fish. Aquatic Sciences 74: 495-511.

Hudon, C., M. Jean & G. Létourneau, 2018. Temporal (1970–2016) changes in human pressures and wetland response in the St. Lawrence River (Québec, Canada). Science of the Total Environment 643: 1137-1151.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao & L. G. Ferreira, 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83: 195-213.

Jermacz, L., A. Dzierżyńska, T. Kakareko, M. Poznańska & J. Kobaka, 2015. The art of choice: predation risk changes interspecific competition between freshwater amphipods. Behavioral Ecology 26: 656-664.

Kelly, D. J. & M. Schallenberg, 2019. Assessing food web structure in relation to nutrient enrichment, macrophyte collapse and lake resilience in shallow lowland lakes. New Zealand Journal of Marine and Freshwater Research 53: 603-619.

La Violette N. et al., 2002. Protocole d'échantillonnage terrain et laboratoire. Réseau de suivi ichtyologique du fleuve Saint-Laurent : lac Saint-Pierre 2002. Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, Québec. 23 p + 31 annexes.

La Violette N., P. Brodeur & Y. Mailhot, 2007. Protocole d'échantillonnage du Réseau de suivi ichtyologique du fleuve Saint-Laurent : lac Saint-Pierre 2007. Ministère des Ressources naturelles et de la Faune, Faune Québec, Direction de la recherche sur la faune et Direction générale de la Mauricie et du Centre-du-Québec, Québec. 35 p + 36 annexes.

La Violette, N., D. Fournier, P. Dumont, & Y. Mailhot, 2003. Caractérisation des communautés de poissons et développement d'un indice d'intégrité biotique pour le fleuve Saint-Laurent, 1995-1997. Faune et Parcs Québec, Direction de la recherche sur la faune, Québec.

Laplante-Albert, K. A., M. A. Rodríguez & P. Magnan, 2010. Quantifying habitat-dependent mortality risk in lacustrine fishes by means of tethering trials and survival analyses. Environmental Biology of Fishes 87: 263-273.

Liu, C., C. Kroeze, A. Y. Hoekstra & W. Gerbens-Leenes, 2012. Past and future trends in grey water footprints of anthropogenic nitrogen and phosphorus inputs to major world rivers. Ecological Indicators 18: 42-49.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, J. B. C. Jackson, 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312: 1806-1809.

Mailhot, Y., P. Dumont, Y. Paradis, P. Brodeur, N. Vachon, M. Mingelbier, F. Lecomte & P. Magnan, 2015. Yellow perch (Perca flavescens) in the St. Lawrence River (Québec, Canada): Population dynamics and management in a river with contrasting pressures. Biology of Perch, eds Couture P, Pyle G (CRC Press), pp. 101-147.

Massicotte, P., ABertolo, P. Brodeur, C. Hudon, M. Mingelbier & P. Magnan, 2015. Influence of the aquatic vegetation landscape on larval fish abundance. Journal of Great Lakes Research. 41: 873-880.

Massicotte, P., D. Gratton, J. J. Frenette & A. A. Assani, 2013. Spatial and temporal evolution of the St. Lawrence River spectral profile: A 25-year case study using Landsat 5 and 7 imagery. Remote Sensing of Environment 136: 433-441.

Menge B. A. & J. P. Sutherland, 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. The American Naturalist 110: 351-369.

Miguel-Chinchilla L., E. Heasley, S. Loiselle & I. Thornhill, 2019. Local and landscape influences on turbidity in urban streams: a global approach using citizen scientists. Freshwater Science. 38: 303-320.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, 2020. Package 'vegan', Community Ecology Package, R CRAN.

Orth, R.J., M. R. Williams, S. R. Marion, D. J. Wilcox, T. J. B. Carruthers, K. A. Moore, W. M. Kemp, W. C. Dennison, N. Rybicki, P. Bergstrom & R. A. Batiuk, 2010. Longterm trends in submersed aquatic vegetation (SAV) in Chesapeake Bay, USA, related to water quality. Estuaries and Coasts 33: 1144-1163.

Paaijmans, K. P., W. Takken, A. K. Githeko, & A. F. G. Jacobs, 2008. The effect of water turbidity on the near-surface water temperature of larval habitats of the malaria mosquito *Anopheles gambiae.* International Journal of Biometeorology: 52: 747-753.

Paine, R. T., 1966. Food web complexity and species diversity. The American Naturalist 100: 65-75.

Paradis, Y., A. Bertolo, M. Mingelbier, P. Brodeur, P. Magnan, 2014. What controls distribution of larval and juvenile yellow perch? The role of habitat characteristics and spatial processes in a large, shallow lake. Journal of Great Lakes Research 40: 172-178.

Parrish, J. D., & S. B. Saila, 1970. Interspecific competition, predation and species diversity. Journal of Theoretical Biology 27: 207-220.

Pianka, E. R., 1994. Evolutionary Ecology. HarperCollins College Publishers, New York: 486 pp.

R Core Team (2019) R: A Language and Environment for Statistical Computing. https://www.R-project.org/

Rodríguez, M. A. & W. M. Jr. Lewis, 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs 67: 109-128.

Rozas, L. P., & W. E. Odum, 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77: 101-106.

Sand-Jensen, K. & J. Borum, 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. Aquatic Botany 41: 137-175.

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8: 275-279.

Schwarzenbach, R. P., T. Egli, T. B. Hofstetter, U. von Gunten & B. Wehrli, 2010. Global water pollution and human health. Annual Review of Environment and Resources 35: 109-136.

Scott, W. B., & E. J. Crossman, 1973. Freshwater fishes of Canada. Bulletin – Fisheries Research Board of Canada, 184: pp. 1-966.

Shafer, D. & P. Bergstrom, 2010. An introduction to a special issue on large-scale submerged aquatic vegetation restoration research in the Chesapeake Bay: 2003-2008. Restoration Ecology 18: 481-489.

Sheppard, J. N., N. C. James, A. K. Whitfield & P. D. Cowley, 2011. What role do beds of submerged macrophytes play in structuring estuarine fish assemblages? Lessons from a warm-temperate South African estuary. Estuarine, Coastal and Shelf Science 95, 145-155.

Simoneau, M., 2017. Qualité de l'eau des tributaires du lac Saint-Pierre : évolution temporelle 1979-2014 et portrait récent 2012-2014. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques. Direction générale du suivi de l'état de l'environnement, ISBN 978-2-550-76229-4 (PDF), 54 p. + 13 ann. (http://www.mddelcc.gouv.qc.ca/eau/lac-st-pierre/qualite-eau-tributaires.pdf). Bibliothèque et Archives nationales du Québec.

Taniguchi, Y., F. J. Rahel, D. C. Novinger & K. G. Gerow, 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences 55: 1894-1901.

ter Braak, C. J. F., P. F. M. Verdonschot, 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57: 255-289.

Utne-Palm, A. C., 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Marine and Freshwater Behaviour and Physiology 35: 111-128.

Whatley M. H., E. E. van Loon, H. van Dam, J. A. Vonk, H. G. van der Geest & W. Admiraal, 2014. Macrophyte loss drives decadal change in benthic invertebrates in peatland drainage ditches. Freshwater Biology 59: 114-126.

Zhang, Y., E. Jeppesen, X. Liu, B. Qin, K. Shi, Y. Zhou, S. M. Thomaz, J. Deng, 2017. Global loss of aquatic vegetation in lakes. Earth-Science Reviews 173: 259-265.

## Supplementary material

This section presents the results of the multi-model inference in which the explanatory variable enhanced vegetation index (EVI) has been replaced by the semiquantitative measures of submerged aquatic vegetation (SAV) measured *in situ* (see Materials and Methods).

For the Shannon diversity, multi-model inference showed that, within the 32 possible models built with the variables at hand, 14 can be considered plausible (i.e., having a $\Delta$AICc < 10), whereas eight can be included in the 95% CI set of models to be used for inference (Table S2a). The best of these models explained 22% of the variation in the data, based on its $R_{adj}^2$. Turbidity, depth, temperature, year and SAV measured *in situ* had large Akaike weights (1, 0.83, 0.82, 0.79, and 0.72 respectively). Shannon diversity was significantly positively related to turbidity (averaged estimate = 0.124; CI = 0.050/0.198), depth (averaged estimate = 0.089; CI = 0.013/0.165) and to the SAV categories associated to lower abundances (average estimate for SAV2 = 0.295; CI = 0.066/0.523 and for SAV 3 = 0.358; CI = 0.126/0.590), and negatively related to temperature (averaged estimate = -0.083; CI = -0.161/-0.005) (Table 1a). We also found a significant effect of the year on Shannon diversity (averaged estimate = 0.153; CI = 0.009/0.297), with a higher diversity observed in 2007 compared to 2002. The SAV categories 4 and 5 were non-significant (average estimate for SAV4 = 0.397; CI = - .068/0.861 and for SAV5 = 0.191; CI = - .233/0.615) (Table S2a).

For species richness, multi-model inference showed that four models can be considered as plausible and among these, three can be included in the 95% CI set of models to be used for inference (Table S2b). The best of these models explained 32.0% of the variation in the data, based on its $R_{adj}^2$. Species richness was positively related to turbidity (averaged estimate = 0.103; CI = 0.049/0.159), depth (averaged estimate = 0.068; CI =0.049/0.159), and all SAV categories (estimates and CI are reported for each category; SAV2 = 0.391; 0.159/0.622; SAV 3 = 0.596; 0.368/0.825; SAV4 = 0.596; 0.174/0.965; SAV5 = 0.580; 0.213/0.947), and negatively related to temperature (averaged estimate = -0.128; CI = - .193/-0.064) (Table S2b). No significant effects of year were found on species (averaged estimate = 0.034; CI = -0.089/0.157). For species richness, SAV category, turbidity, temperature, and depth had large Akaike weights (1, 1, 1 and 0.83, respectively), with year having a somewhat lower weight (0.22).

Within all the possible models to explain total fish abundance, multi-model inference showed that only the one including all the variables can be considered as plausible (Table S2c), with the second-best model having a $\Delta$AICc > 113. Despite such low uncertainty in model selection, this model explained only 11% of the variation in the data. Total abundance was positively related to all the SAV categories (estimates and CI are reported for each category; SAV2 = 1.059; 0.975/0.1.144; SAV 3 = 2.318; 2.237/2.400; SAV4 = 2.238; 2.144/2.334; SAV5 = 0.2.721; 2.633/2.812) and depth (estimate = 0.069; CI = 0.058/0.079), whereas it was negatively related to both turbidity (estimate = -0.071; CI = -0.085/-0.058) and temperature (estimate = -0.303; CI = -0.315/-0.290) (Table S2c). We also found a significant effect of the year on total abundance, with lower values in 2007 compared to 2002 (estimate = -0.220; CI = -0.241/-0.199).

## Tables

**Table 1.** Summary of the models retained with a ΔAICc $< 10$ for a) Shannon diversity, b) species richness and c) total fish abundance. Models included in the 95% confidence interval (CI) sets are in bold. The coefficients are shown for each of the explanatory variables together with the degrees of freedom (df), $\Delta AIC_c$ values associated with the model and their Akaike weight ($w_i$). The inclusion of the categorical variable "Year" in the model is indicated by "+". The models are ranked based on their $AIC_c$ value.

| | Depth | EVI | Turbidity | Temperature | Year | df | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|---|
| a) | **0.111** | **-** | **0.106** | **-0.088** | + | **6** | **0** | **0.413** |
| | **0.116** | **-** | **0.108** | **-0.111** | - | **5** | **1.7** | **0.176** |
| | **0.110** | **0.018** | **0.109** | **-0.087** | + | **7** | **2.0** | **0.152** |
| | **0.115** | **-** | **0.085** | **-** | + | **5** | **3.2** | **0.083** |
| | **0.116** | **-0.005** | **0.107** | **-0.111** | - | **6** | **3.9** | **0.060** |
| | **0.114** | **0.023** | **0.089** | - | + | **6** | **5.0** | **0.034** |
| | **0.111** | **-** | **-** | **-0.060** | + | **5** | **6.4** | **0.017** |
| | **0.114** | **-** | **-** | **-** | + | **4** | **6.7** | **0.014** |
| | - | - | 0.106 | -0.094 | + | 5 | 7.6 | 0.009 |
| | 0.116 | - | - | -0.083 | - | 4 | 8.1 | 0.007 |
| | 0.124 | - | 0.079 | - | - | 4 | 8.5 | 0.006 |
| | 0.111 | 0.003 | - | -0.060 | + | 6 | 8.6 | 0.006 |
| | 0.113 | 0.009 | - | - | + | 5 | 8.8 | 0.005 |
| | - | 0.021 | 0.109 | -0.092 | + | 6 | 9.5 | 0.004 |
| | 0.116 | -0.020 | - | -0.08 | - | 5 | 10.0 | 0.003 |
| b) | **0.107** | **0.075** | **0.072** | **-0.151** | + | **6** | **0** | **0.500** |
| | **0.111** | **0.053** | **0.071** | **-0.169** | - | **5** | **2.0** | **0.185** |
| | **0.112** | **-** | **0.062** | **-0.164** | - | **4** | **3.3** | **0.098** |
| | **0.110** | **-** | **0.060** | **-0.152** | + | **5** | **3.8** | **0.074** |
| | **0.108** | **0.063** | **-** | **-0.134** | + | **5** | **4.1** | **0.066** |
| | **0.111** | **0.041** | **-** | **-0.151** | - | **4** | **5.9** | **0.026** |
| | 0.112 | - | - | -0.150 | - | 3 | 5.9 | 0.026 |
| | 0.110 | - | - | -0.138 | + | 4 | 6.2 | 0.023 |
| c) | **0.203** | **0.274** | **-0.231** | **-0.348** | + | **6** | **0** | **1** |

**Table S1.** List of common and scientific names for the 51 fish species sampled in 2002 and 2007, together with the corresponding guilds based on the preferred substrate for spawning (see Materials and Methods section for details). Dominant species (relative species abundance > 1% of the total abundance) are in bold.

| **Common name** | **Scientific name** | **Spawning guild** |
|---|---|---|
| Alewife | *Alosa pseudoharengus* | Facultative phytophile |
| American shad | *Alosa sapidissima* | Non phytophile |
| **Brown bullhead** | ***Ameiurus nebulosus*** | **Non phytophile** |
| Eastern sand darter | *Ammocrypta pellucida* | Non phytophile |
| Rock bass | *Ambloplites rupestris* | Facultative phytophile |
| Longnose sucker | *Catostomus catostomus* | Non phytophile |
| White sucker | *Catostomus Commersonii* | Non phytophile |
| Quillback | *Carpiodes cyprinus* | Non phytophile |
| Carp | *Cyprinus carpio* | Phytophile |
| Spotfin shiner | *Cyprinella spiloptera* | Facultative phytophile |
| Pike | *Esox lucius* | Phytophile |
| Muskellunge | *Esox masquinongy* | Phytophile |
| Iowa darter | *Etheostoma exile* | Facultative phytophile |
| Johnny darter | *Etheostoma nigrum* | Non phytophile |
| **Tessellated darter** | ***Etheostoma olmstedi*** | **Non phytophile** |
| **Banded killifish** | ***Fundulus diaphanus*** | **Phytophile** |
| Mooneye | *Hiodon tergisus* | Non phytophile |
| Eastern silvery minnow | *Hybognathus regius* | Facultative phytophile |
| Channel catfish | *Ictalurus punctatus* | Non phytophile |
| **Brook silverside** | ***Labidesthes sicculus*** | **Facultative phytophile** |
| **Pumpkinseed** | ***Lepomis gibbosus*** | **Facultative phytophile** |
| Longnose gar | *Lepisosteus osseus* | Phytophile |
| Smallmouth bass | *Micropterus dolomieu* | Phytophile |
| Largemouth bass | *Micropterus salmoides* | Phytophile |
| White perch | *Morone americana* | Facultative phytophile |
| Silver redhorse | *Moxostoma anisurum* | Non phytophile |

| **Common name** | **Scientific name** | **Spawning guild** |
|---|---|---|
| Shorthead redhorse | *Moxostoma macrolepidotum* | Non phytophile |
| Round goby | *Neogobius melanostomus* | Non phytophile |
| **Emerald shiner** | ***Notropis atherinoides*** | **Non phytophile** |
| **Bridle shiner** | ***Notropis bifrenatus*** | **Phytophile** |
| **Golden shiner** | ***Notemigonus crysoleucas*** | **Phytophile** |
| Tadpole madtom | *Noturus gyrinus* | Non phytophile |
| Blackchin shiner | *Notropis heterodon* | Phytophile |
| Blacknose shiner | *Notropis heterolepis* | Non phytophile |
| Spottail shiner | *Notropis hudsonius* | Non phytophile |
| Rosyface shiner | *Notropis rubellus* | Non phytophile |
| Sand shiner | *Notropis stramineus* | Non phytophile |
| **Mimic shiner** | ***Notropis volucellus*** | **Facultative phytophile** |
| Rainbow smelt | *Osmerus mordax* | Non phytophile |
| Logperch | *Percina caprodes* | Non phytophile |
| Channel darter | *Percina copelandi* | Non phytophile |
| **Yellow perch** | ***Perca flavescens*** | **Facultative phytophile** |
| Trout-perch | *Percopsis omiscomaycus* | Non phytophile |
| **Bluntnose minnow** | ***Pimephales notatus*** | **Non phytophile** |
| Fathead minnow | *Pimephales promelas* | Non phytophile |
| Black crappie | *Pomoxis nigromaculatus* | Phytophile |
| Sauger | *Sander canadensis* | Non phytophile |
| Walleye | *Sander vitreus* | Non phytophile |
| Fallfish | *Semotilus corporalis* | Non phytophile |
| Tench | *Tinca tinca* | Phytophile |
| Central mudminnow | *Umbra limi* | Phytophile |

**Table S2.** Summary of the models retained with a ΔAICc < 10 for a) Shannon diversity, b) species richness and c) total fish abundance. Models included in the 95% confidence interval (CI) sets are in bold. The coefficients are shown for each of the explanatory variables together with the degrees of freedom (df), $\Delta AIC_c$ values associated with the model and their Akaike weight ($w_i$). The inclusion of the categorical variable "Year" in the model is indicated by "+". The models are ranked based on their $AIC_c$ value.

| | **Depth** | **SAV** | **Turbidity** | **Temperature** | **Year** | **df** | **ΔAICc** | **$w_i$** |
|---|---|---|---|---|---|---|---|---|
| a) | **0.080** | + | **0.130** | **-0.069** | + | **10** | **0** | **0.254** |
| | **0.101** | - | **0.107** | - | + | **6** | **0.3** | **0.219** |
| | **0.083** | + | **0.118** | - | + | **9** | **1.3** | **0.132** |
| | **0.086** | + | **0.136** | **-0.085** | - | **9** | **1.4** | **0.126** |
| | - | + | **0.137** | **-0.07** | + | **9** | **2.2** | **0.086** |
| | **0.107** | - | **0.109** | **-0.120** | - | **5** | **3.6** | **0.042** |
| | - | + | **0.125** | - | + | **8** | **3.8** | **0.038** |
| | - | + | **0.143** | **-0.090** | - | **8** | **4.2** | **0.032** |
| | 0.092 | + | 0.121 | - | - | 8 | 4.8 | 0.023 |
| | 0.105 | - | 0.084 | - | + | 5 | 4.9 | 0.022 |
| | - | - | 0.107 | -0.100 | + | 5 | 7.1 | 0.007 |
| | 0.101 | - | - | -0.066 | + | 5 | 7.6 | 0.006 |
| | - | + | 0.129 | - | - | 7 | 8.1 | 0.004 |
| | 0.104 | - | - | - | + | 4 | 8.9 | 0.003 |
| b) | **0.068** | + | **0.103** | **-0.129** | - | **8** | **0** | **0.561** |
| | **0.067** | + | **0.101** | **-0.124** | + | **9** | **2** | **0.206** |
| | - | + | **0.108** | **-0.132** | - | **7** | **2.5** | **0.160** |
| | - | + | 0.106 | -0.127 | + | 8 | 4.3 | 0.066 |
| c) | **0.069** | + | **-0.071** | **-0.303** | + | **9** | **0** | **1** |

## Figures

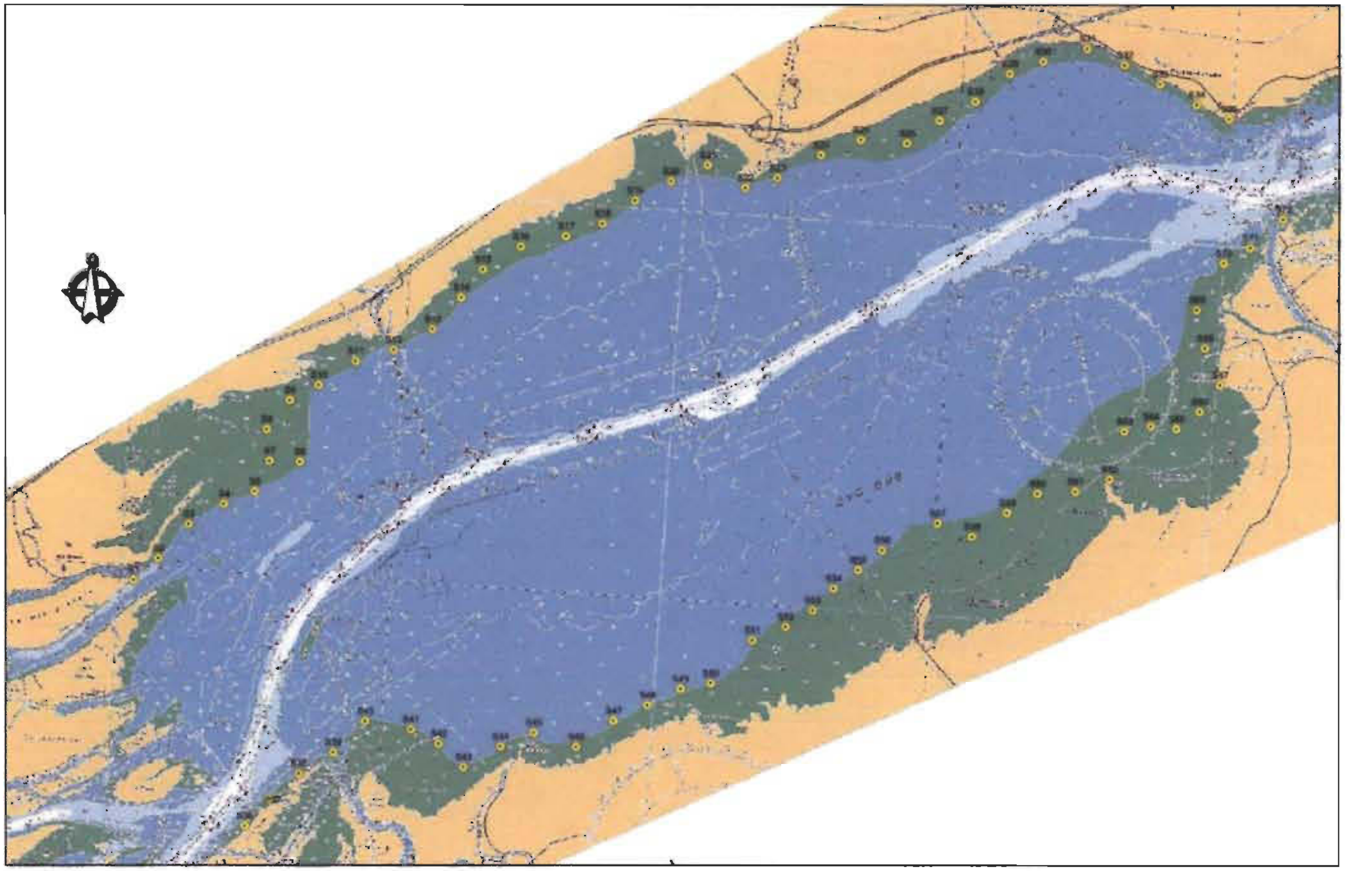

**Fig. 1.** Lake Saint-Pierre (LSP), a fluvial lake of the St. Lawrence River (Québec, Canada). Yellow dots show the location of the sampling stations. In the middle of the lake, the man-made navigation channel is 250 m wide, ~ 11 m deep. All the areas outside the navigation channel have a depth < 3.5m. The description of the study area and further details on sampling procedures are reported in Materials and Methods.

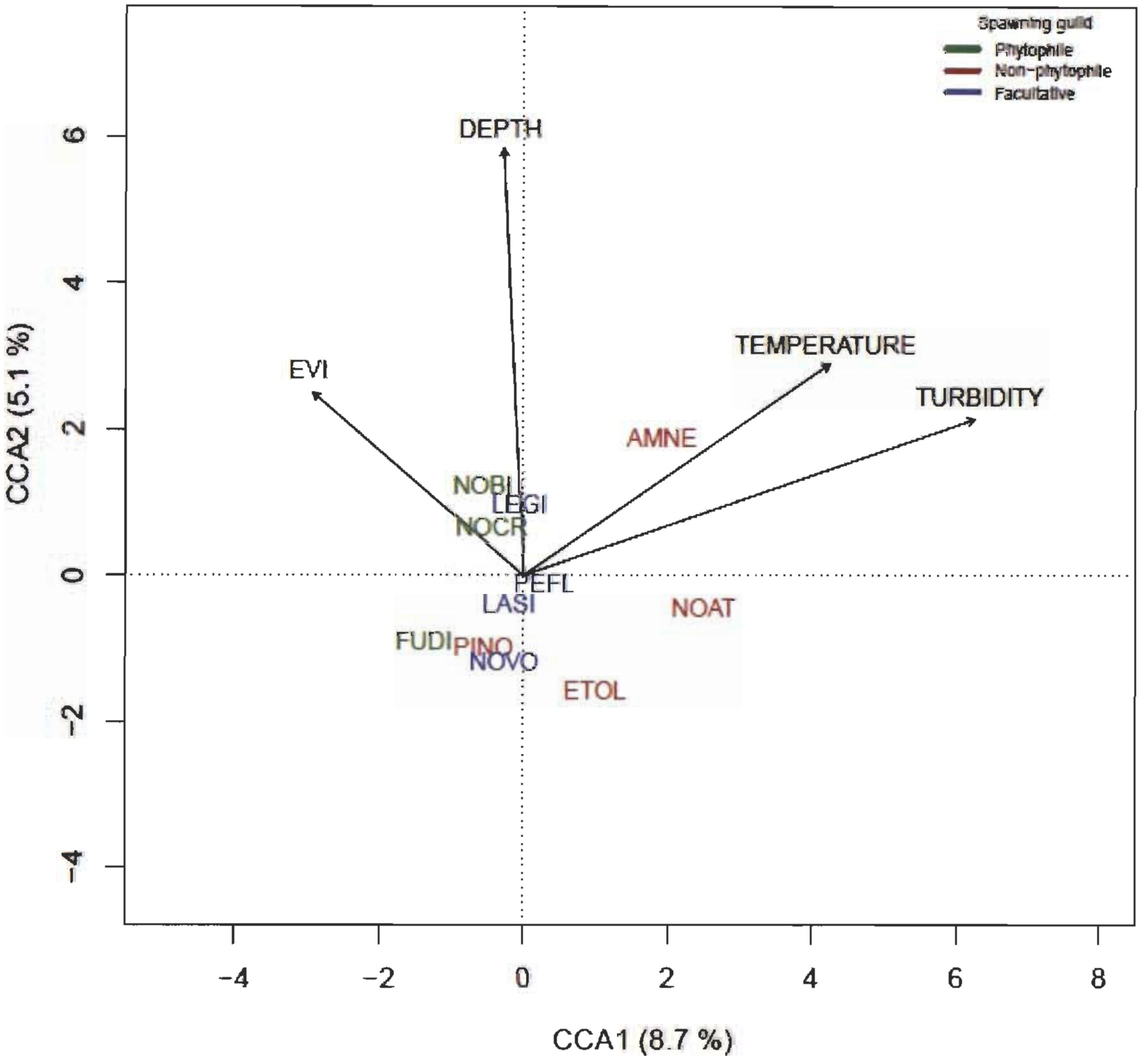

**Fig. 2.** Canonical correspondence analysis (CCA) on dominant fish species (relative abundance > 1% of the total abundance) in the community and submerged aquatic vegetation (SAV) abundance estimated with the enhanced vegetation index (EVI), turbidity, temperature, and depth. Phytophile species (in green) are the banded killifish (*Fundulus diaphanous*; FUDI), bridle shiner (*Notropis bifrenatus*; NOBI), and the golden shiner (*Notemigonus crysoleucas*; NOCR). Non-phytophile species (in brown) are the brown bullhead (*Ameiurus nebulosus*; AMNE), tessellated darter (*Etheostoma olmstedi*; ETOL), emerald shiner (*Notropis antherinoides*; NOAT), and the bluntnose minnow (*Pimephales notatus*; PINO). Facultative phytophile species (in blue) are the brook silverside (*Labidesthes sicculus*; LASI), pumpkinseed (*Lepomis gibbosus*; LEGI), mimic shiner (*Notropis volucellus*; NOVO), and the yellow perch (*Perca flavescens*; PEFL).

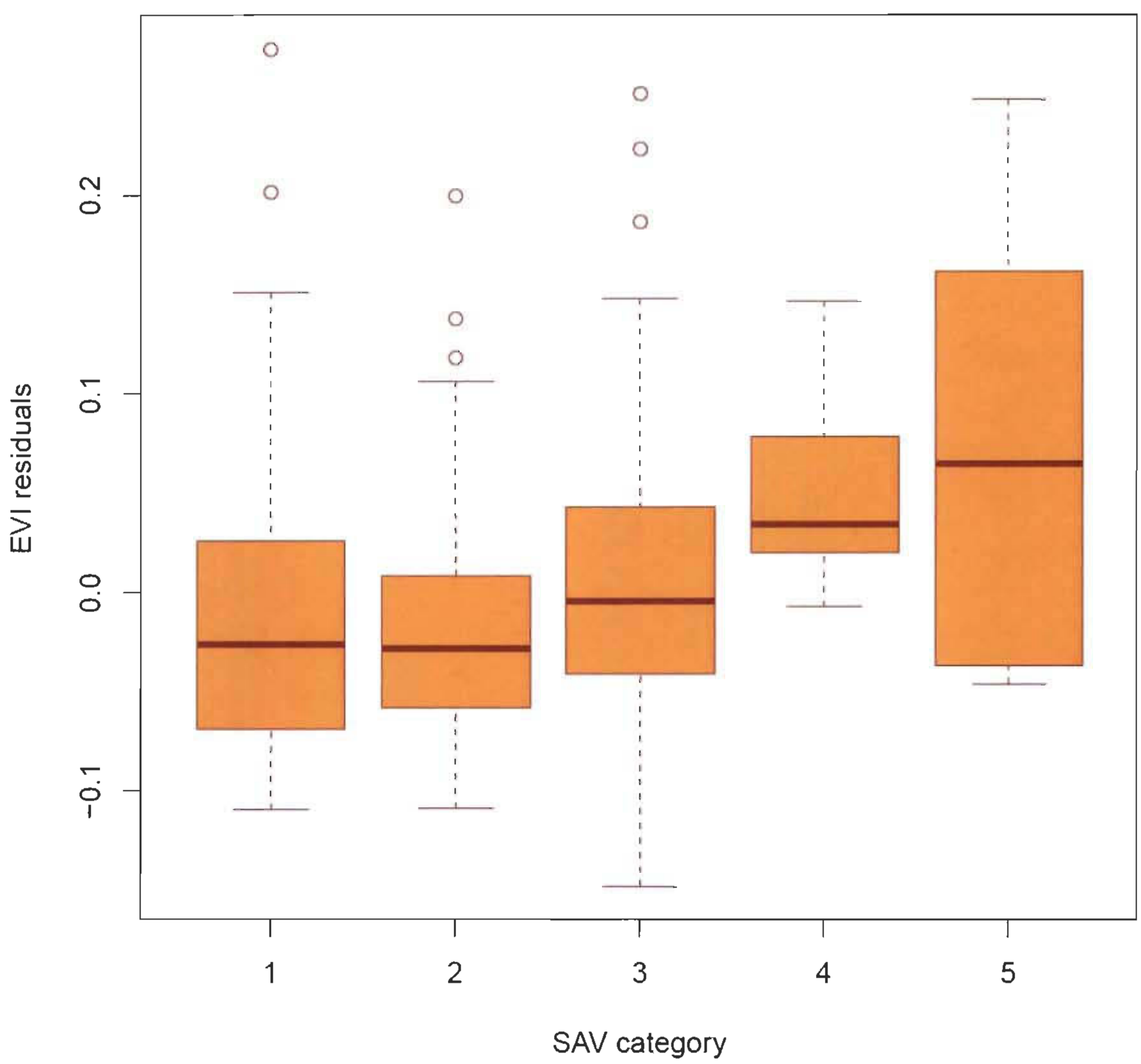

**Fig. S1.** Boxplots showing the correlation between two measures of SAV. SAV categories on the x-axis were visually estimated *in situ* (semiquantitative scale from 1 to 5); EVI residuals on the y-axis refer to the residuals of the generalized additive mixed model (GAMM) in which the EVI values extracted from satellite imagery were corrected by accounting for the year, the day of the year, and depth (these two latter as smoothed fixed effects), and the site as random effect. See Materials and Methods section for details.

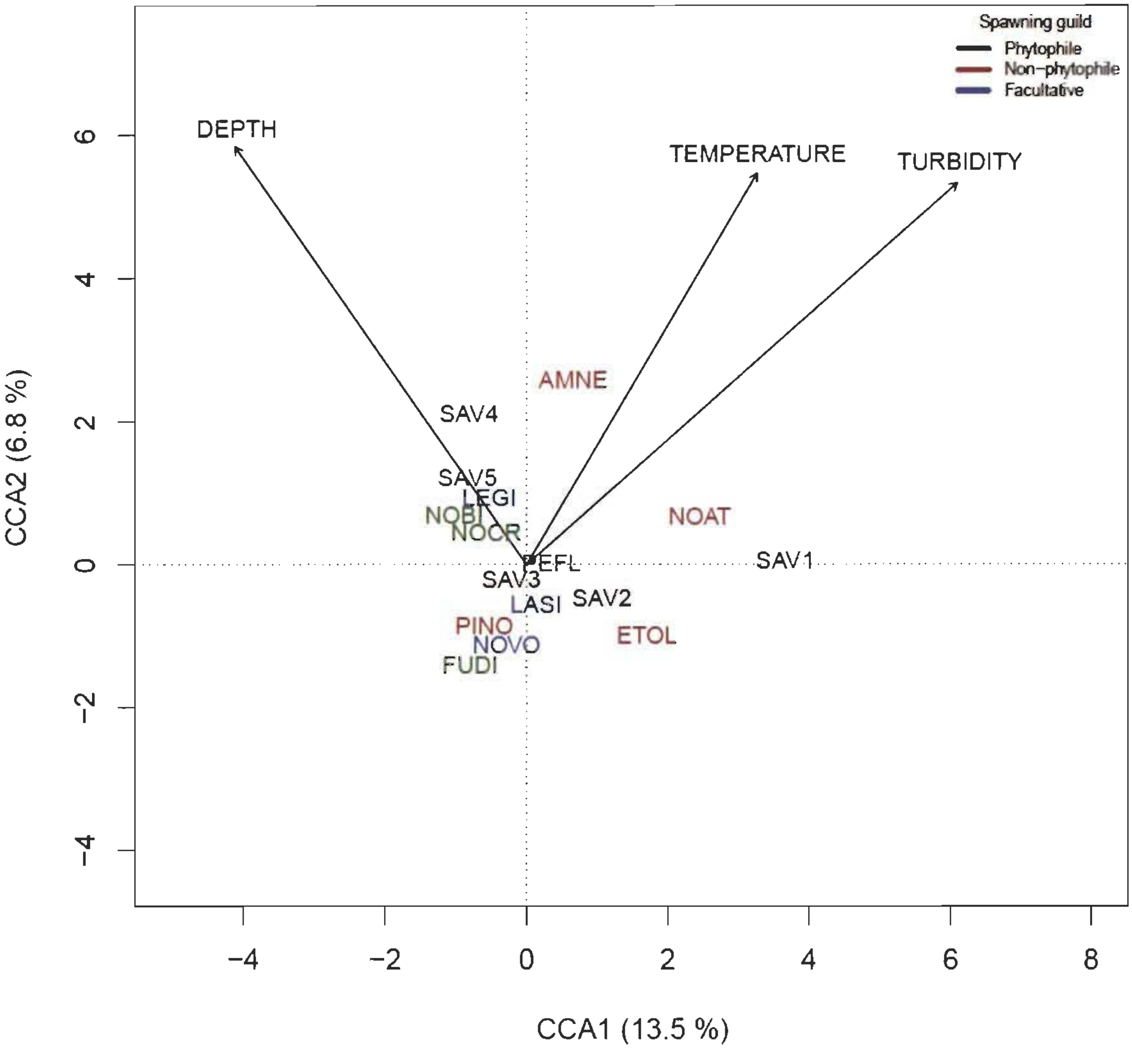

**Fig. S2.** Canonical correspondence analysis (CCA) on dominant fish species in the community and SAV abundance visually estimated *in situ* (semiquantitative scale from 1 to 5), turbidity, temperature, and depth. Phytophile species (in green) are the banded killifish (*Fundulus diaphanous*; FUDI), bridle shiner (*Notropis bifrenatus*; NOBI), and the golden shiner (*Notemigonus crysoleucas*; NOCR). Non-phytophile species (in brown) are the brown bullhead (*Ameiurus nebulosus*; AMNE), tessellated darter (*Etheostoma olmstedi*; ETOL), emerald shiner (*Notropis antherinoides*; NOAT), and the bluntnose minnow (*Pimephales notatus*; PINO). Facultative phytophile species (in blue) are the brook silverside (*Labidesthes sicculus*; LASI), pumpkinseed (*Lepomis gibbosus*; LEGI), mimic shiner (*Notropis volucellus*; NOVO), and the yellow perch (*Perca flavescens*; PEFL). See Materials and Methods section for details.

# GENERAL DISCUSSION

## Synthesis and scientific contribution of the thesis

This dissertation represents the synthesis of our research on the ecology of the yellow perch (YP) and on the fish community of the Lake Saint-Pierre (LSP). Our main objective was to shed light on the declining dynamics of the YP and on the lack of the population recovery, after the application of the measures to reduce the fishing effort, culminating with the establishment of a moratorium on both recreational and commercial fishing, applied in 2012. Our main results are that the YP abundance (evaluated at different life stages), as well as the distribution of fish species within the community, are related to the progressive degradation of the water quality (especially turbidity) and to the loss of submerged aquatic vegetation (SAV).

In Chapter I, we calculated the discharge in nutrients and sediments coming from the watershed draining the LSP, quantifying the magnitude of these inputs since 1980. Nitrogen and turbidity inputs in the LSP showed an increasing trend, while phosphorous concentrations decreased. These two opposite trends in nutrients discharge mirrored a different use of fertilizers after the Québec law on environmental quality was adopted in 1972. We also reconstructed the evolution of SAV since 1960, showing that its abundance increased till the 1980s, up to a plateau and then markedly decrease till nowadays, showing a dome-shape curve. For the period 1990-2007, for which we had complete time series, we developed a system of structural equations with the objective of building a network based on *a priori* knowledge of the system, to evaluate statistical causality between variables, and quantify the strength of these relationships. SAV biomass decreased because of the progressive water quality degradation. As suspended solids and phosphorous are counteracting forces, one inhibiting SAV growth because of the light limitation for photosynthesis, and the other boosting SAV growth because of fertilization, the interplay between these two variables results nevertheless in a net decrease in SAV biomass. Both nutrients and sediments origin from agricultural lands enter the LSP thanks to water runoff. We found that commercial yield was positively influenced by SAV abundance suggesting that this latter represent a quality habitat for YP, probably providing food resources and shelter from predation (Paradis et al., 2014). Surprisingly, in the best model, SAV was found not to affect juveniles' growth (despite the fact that we cannot dismiss this relationship because it was retained in competing, non-rejected models). Interestingly, YP growth was a function of turbidity and water level. The negative relationship between juveniles' growth and turbidity confirms that water quality degradation is a major driver for many biotic compartments in LSP. Turbidity and suspended solids are probably two major causes of decline for both SAV and the YP. High water levels are usually positively associated with juvenile fish growth, probably because of a higher proportion of flooded grounds which are highly productive in terms of invertebrates. However, when water levels are very high, laboured soils are flooded, releasing high sediment concentrations which might be flushed to the lake. Albeit higher floods imply an increased availability of invertebrates for early YP ontogenetic stages (Farly et al., 2019), on the other hand, the turbidity generated by water receding might be flushed along the littoral zone, presumably negatively affecting late juveniles feeding activity and therefore their growth. Moreover, juveniles' growth was positively related to commercial landings (both decreasing trends), again supporting the idea that the decline of YP abundance is, at least partially, indirectly associated with water quality degradation.

In Chapter II, we evaluated YP larvae distribution in relationship with the water column light environment. YP larvae display positive phototropism during their first weeks (Sandström, 1999) but are also very sensitive to UV radiation given their low pigmentation. Therefore, a behavioural response to cope with solar radiation (which might eventually reduce larvae mortality), is expected. We evaluated YP distribution both at the scale of the water column (proxy of a behavioural choice) and between isobaths (different UV risk in function of the depth, likely to affect larvae mortality). By means of a remote sensing approach, we calculated surface solar irradiance and coefficients of light attenuation in the water (i.e., $K_d$), to calculate the solar irradiance at the depth of the sampling nets, following the law of Lambert-Beer. Larvae abundance correlated positively with aquatic vegetation (especially for bottom nets), confirming the importance of aquatic vegetation (both submerged and emerged) as a habitat of choice for YP.

At the scale of the water column, we found that YP larvae were always more abundant at the bottom, probably because of a form of behavioural habitat choice (e.g., to match with food resources/avoid predation). A positive relationship was found between larvae abundance and photosynthetically active radiation (PAR), meaning that larvae still look for well illuminated layers despite the preference for bottom water layers. No effect of UV radiation was found, probably because larvae are released from UV risk by simply lowering down in the water column (UVs damaging potential is low at depths higher than c.a. 0.5 m, results of the Chapter II). The comparison between larvae abundance at two isobaths revealed that they were more abundant at the deep isobath, confirming the larvae preference from bottom water layers. Moreover, our analyses revealed a positive effect of turbidity on larvae abundance at the shallow isobath, probably because turbid waters protect larvae from the UV risk. In this chapter, we showed that larvae can perform a habitat choice being strictly associated to SAV, and that the underwater light environment (i.e., visible light and turbidity) might potentially affect both behaviour and survival, presumably as a function of UV risk.

In the Chapter III, we evaluated the association between fish species and a gradient of SAV abundance and turbidity, to predict relative abundances, species richness and diversity change in a scenario of turbidity augmentation and further SAV decrease. We found that the species richness and fish abundance (especially for phytophile species) were positively related to SAV. These results confirmed the importance of SAV as a key variable for fish, driving the community structure. Turbidity was positively related to Shannon diversity and species richness, but negatively to fish abundance. These findings might be the result of a different predation rate between clear and turbid waters. In LSP, predation was found to be higher in turbid waters (Laplante-Albert et al., 2010), which might explain the lower fish abundances at turbid sampling stations. On the other hand, predation might release interspecific competition, allowing for higher species richness and diversity (Paine 1966; Parrish and Saila, 1970; Menge and Sutherland, 1976).

In a nutshell, the research presented in this dissertation provides evidence that SAV abundance and water quality are two major compartments determining the 'ecological functioning' of the LSP. Water quality (especially its clarity) was found to be causally linked with SAV abundance, in turn driving YP abundance. SAV is a pivotal habitat for all ontogenetic stages of the YP, affecting the abundance of young larvae, juveniles' growth, as well as the abundance of the adults. SAV and turbidity are key variables structuring the fish community, affecting fish abundance, species richness and diversity at the scale of the sampling station. Therefore, we might summarize the main results presented in this thesis as: the degradation of the water column light environment caused by sedimentary turbidity, induced a reduction in SAV abundance, and both these phenomena negatively affected the YP population. These environmental variables also play a key role in determining the fish species distribution across the LSP.

The results reported in this dissertation shed light on the ecology of the LSP, especially regarding the interactions between fish species and their habitat. The approaches used in the three chapters, allowed to quantify the mechanisms behind habitat degradation and the YP decline at multiple scales, providing a broader understanding of the functioning of this ecosystem at the broad scale as well as at the microhabitat level (i.e., at the scale of the water column). By explicitly testing potential causal pathways linking inputs from the watershed to the LSP, SAV abundance change and fisheries, our study represents a novel contribution to scientific literature. This dissertation highlights the key role of fish habitat degradation (e.g., decrease in SAV beds, impaired optical properties of the water column) as a link between anthropogenic activity in the watershed and the long-term viability of the fisheries. Our results show how these changes at the watershed level can affect fish populations -either directly or indirectly- by driving SAV dynamics. In particular, submerged aquatic vegetation beds can experience an extensive abundance loss even in non-eutrophic waters, when the light environment is not favorable for their growth. Inputs of nutrients and sediments from the watershed can be a major cause of habitat degradation and fish populations decline, especially regarding commercially exploited fish species.

The observation that SAV was decreasing in abundance, was already suggested by previous studies (e.g., de la Chenelière et al., 2014), but a quantitative characterization at the scale of the whole lake was still missing. By reconstructing SAV abundance over more than 50 years, we put the bases for a better understanding of SAV dynamic and its drivers (at least partially). Simoneau (2017) provided a categorization of the water quality of LSP tributaries, measuring turbidity, as well as nitrogen, phosphorous, and sediments concentration. We used these data to calculate the total discharge to the LSP, providing knew knowledge on the magnitude of the amount of such compounds discharged yearly into the LSP. Noteworthy, we showed a negative relationship between sediments concentration and SAV abundance, suggesting that important SAV abundance losses can occur also in non-eutrophic waters. Indeed, most of the case studies of SAV loss reported in literature are associated to high nutrients concentrations (e.g., Scheffer et al., 1993; Scheffer and van Nes, 2007; Capon et al., 2015; Hilt et al., 2018). Our findings suggest that in LSP, SAV decrease can be mostly driven by sedimentary turbidity rather than by the trophic state. However, other factors might have contributed to the SAV decline, like the effect of periphyton overgrowth and grazing on SAV which should deserve a further exploration.

Even though we showed the pivotal role of SAV driving YP population decline, we are aware that other unmeasured variables were probably involved. Moreover, some of the relationships we showed deserve further investigation. For instance, Farly et al. (2019) found that higher water levels were positively related to zooplankton subsidies from the floodplain to the lake, suggesting that the littoral fish community largely benefits from zooplankton production from the floodplain. This floodplain contribution to the lake is deemed to increase juvenile fish growth. In the Chapter I we found the opposite, with higher water levels being associated to a lower YP juvenile growth. Even if these two studies are not comparable because of different sampling methods and the temporal window analyzed, this apparent contradiction is worth mentioning.

The aim of this thesis specifically focuses on the causes impeding the YP population recovery rather than the decline itself. In the section '*From ecology to management*' (see below) we provide recommendations to re-establish the YP population and stabilize the fish community, specially focusing on water quality and the sustain of SAV beds.

## Research perspectives

### *Is Lake Saint-Pierre undergoing a regime shift?*

Increase in turbidity and nitrogen concentrations together with SAV loss, are concerning signals for the stability of an aquatic ecosystem. The relevant question is: will LSP change towards a turbid, phytoplankton/periphyton-dominated state? It is very difficult to predict the future trophic state of an aquatic ecosystem, especially because nutrient thresholds triggering a regime shift can be system specific. Regarding the LSP, the risk seems not to be imminent. Most of the cases of regime shift reported in the literature occurred in eutrophic waters (e.g., Blindow et al., 1992; Scheffer and van Nes, 2007). The trophic state of the LSP varies from oligotrophic to mesotrophic (Hudon et al., 2012), depending on the water mass and on the proximity to shores and tributaries (Frenette et al., 2003). Therefore, LSP is still in a clear water stage (despite the increase in turbidity) dominated by macrophytes. Given the relative low nutrient concentrations, periphyton and phytoplankton are not supposed to be competitively advantaged over macrophytes (Hudon et al., 2012). Nevertheless, SAV is decreasing because of turbidity. However, turbidity in LSP is mostly sedimentary, deriving from agricultural soils runoff (Hébert and Blais, 2017), rather than to phytoplankton growth and therefore, this type of turbidity is not associated to a trophic change.

Nevertheless, we warn to be cautious for the future about the state of the LSP. In the last 30 years phosphorous discharge to the LSP decreased, contrarily to nitrogen which is still increasing (Chapter I) and might represent an important driver towards eutrophication. Agricultural lands surrounding LSP have been enriched to the point that the soil's buffer capacity to retain nutrients has been exceeded, with an estimate of centuries to millennia to return to below-threshold values (Goyette et al., 2018). This means that nitrogen and phosphorous stocked in agricultural soils are likely to be exported to LSP for centuries, interfering with efforts to reduce nutrient inputs from other sources (Goyette et al., 2018). Moreover, nutrients release from lake sediments might keep concentrations elevated in the water (Hilt et al., 2006). Although absolute nutrient concentrations are often key for regime shifts, it has also been suggested that variations in the nitrogen/phosphorous ratio are better predictors of this phenomenon, or at least for SAV decline (Lacoul and Freedman, 2006). In LSP, phenomena of SAV loss in favour of filamentous cyanobacteria along a gradient of nitrate depletion (i.e., impaired nitrogen/phosphorous ratio) have been reported (Vis et al., 2008; Hudon et al., 2012). For these reasons, caution in nutrients discharge to the LSP is recommended.

### ***Turbid water with the eyes of a perch: better to swim in coffee or in dangerously clear waters?***

In this dissertation, turbidity has been presented as one of the most important factors inducing habitat degradation, especially regarding its negative effect on SAV abundance, which in turn negatively affects the YP population. Therefore, one could think that turbidity is consistently deleterious throughout all ontogenetic stages of the YP. However, things are not so clear-cut. The YP in LSP is exposed to a panoply of different anthropogenic (e.g., pesticides and contaminants loads) and natural (e.g., predation, UV risk) stressors, and turbidity can eventually mitigate the strength of some of these pressures. Figure 1 represents a schematic synthesis of the results from the three chapters on the relationships between the YP and turbidity.

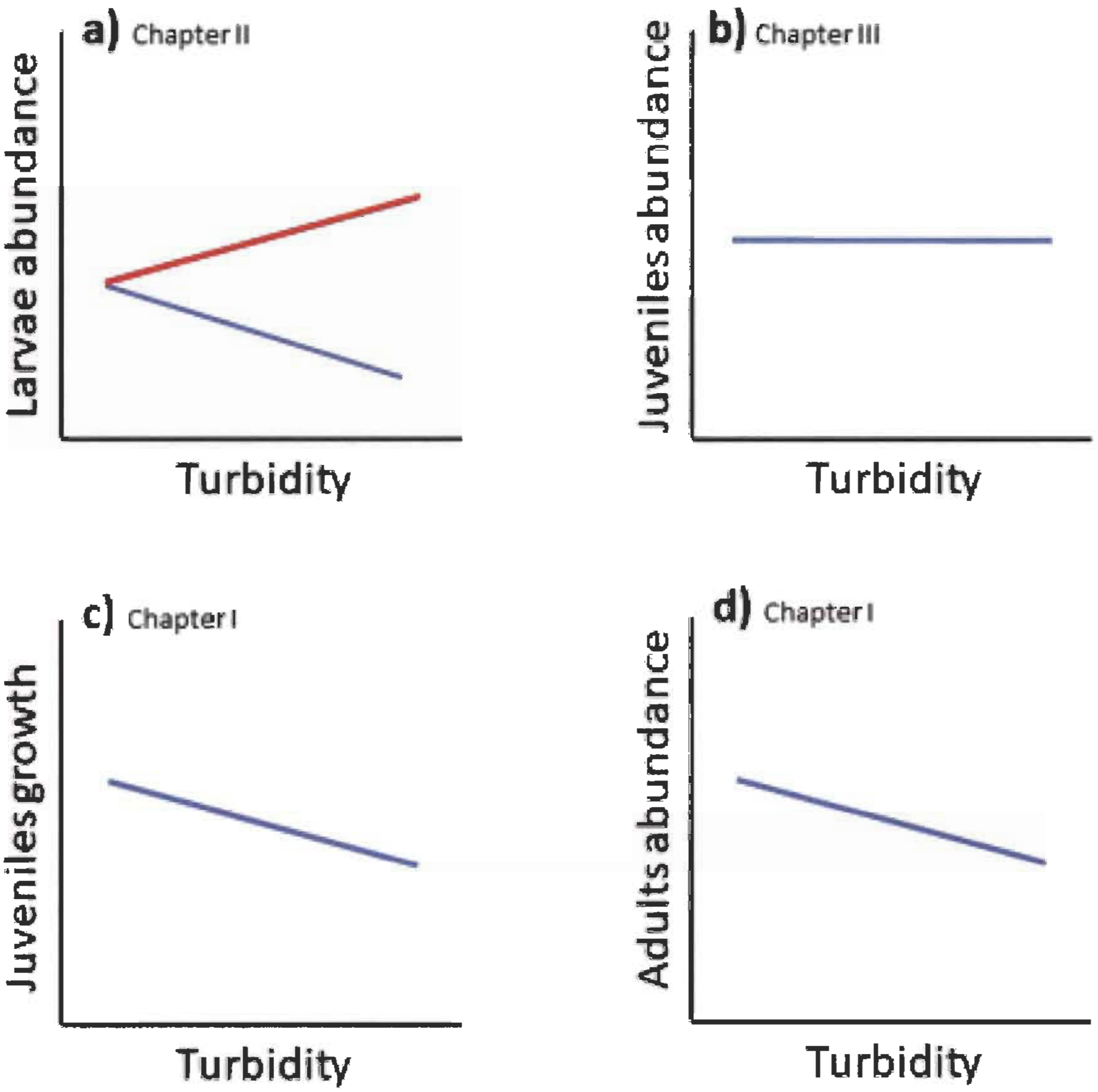

**Fig. 1.** Effect of turbidity in relation with the yellow perch ontogenetic stage. This figure represents a general framework summarising the results from the three chapters of this thesis. Blue lines represent the overall effect of turbidity, the red line, the partial effect of turbidity depending on the isobath (see the text below).

The relationship between turbidity and YP is dependent on the ecological context and on the YP ontogenetic stage. However, larvae were systematically more abundant in deeper waters and negatively related to turbidity (Fig. 1a, blue line), but were proportionally more abundant in shallow turbid waters compared to shallow clear waters (Fig. 1a, red line). In the context of the Chapter II, we interpreted the higher YP larvae abundance in deeper waters as a form of UV risk avoidance, with larvae using shallower areas only in presence of turbid waters, which might protect them from the UV risk. In this context, turbidity seems to have a positive effect on larvae abundance (Fig. 1a), or at least allowing them to use a favourable habitat that they could not exploit if waters were ‘dangerously clear’.

Juvenile YP abundance did not correlate with turbidity (Fig. 1b, results from Chapter III), with this life stage occupying habitats along the whole gradient of this variable. Whether juveniles’ abundance seems not to be affected by turbidity, results from Chapter I showed that growth was negatively related to turbidity (Fig. 1c). Based on SEM, turbidity affects juveniles’ growth directly (probably because of impaired foraging, Radke and Gaupisch, 2005), and indirectly via SAV habitat degradation. For instance, Figueiredo and collaborators performed a series of experiments on tropical fish, measuring invertebrate consumption in relationship with different turbidity levels finding that i) predators reduced feeding activity at high turbidity levels (both at organic at sedimentary turbidity, Figueiredo et al., 2019; Figueiredo et al., 2020), ii) in turbid waters, fish feeding activity was not related to macrophytes cover (Figueiredo et al., 2013), and iii) turbidity reduced feeding independently from the prey type (Figueiredo et al., 2013). These results pinpoint the fact that overall, turbidity disrupt fish food intake, mostly because of impaired visual cues. Nevertheless, the distribution of the YP showed that turbid waters were not avoided. Further investigation is needed to assess the relationship between survival and juveniles’ abundance and growth, especially at the first winter, which might be an important bottleneck for the YP population recruitment (Post 1990; Farmer et al., 2015).

In the Chapter I, we provided information on the indirect links between turbidity and the YP, with suspended solids (which is a component affecting the optical measure of turbidity), negatively affecting SAV abundance, and in turn leading to a reduced YP commercial yield. This is to be interpreted as a proxy of the adult population size, namely individuals that can be collected by the commercial fishery. Therefore, we can conclude that turbidity plays a negative role on commercial fishery and on the abundance of adults (Fig. 1d), via a reduction of SAV abundance. Nevertheless, despite a probable protecting effect of turbidity on larvae exposed to UV risk, the overall contribution of turbidity on the YP seems deleterious.

### *Remote sensing and indirect proxies: integrative tools to fill the gaps*

In the three chapters presented in this dissertation, we used different approaches to calculate variables that were not measured during the sampling campaigns or did not fully match with the time series we were analyzing. We used remote sensing and satellite imagery analyses to calculate proxies of SAV abundance, water optical properties and solar irradiance.

For instance, satellite pictures analyses allowed us to calculate the enhanced vegetation index (EVI), a proxy of aquatic vegetation abundance (Gao et al., 2000; Huete et al., 2002). Even if we had semi-quantitative measurements of aquatic vegetation abundance, such values were taken at the small scale (i.e., at the station) and were available only for certain years of sampling. To reconstruct the aquatic vegetation on the long-term (Chapter I), we needed more temporal data points and a more complete characterization of the study system. In these circumstances, remote sensing represents a very interesting tool, allowing to "go back to the past". Thanks to such an approach, we could extract EVI values at hundreds of sites in the LSP for the years 1985 to 2012. However, our goal was to describe the SAV change on the long term, going back as much as possible. Therefore, we calculated the difference in water levels between the lake inlet and outlet as a proxy of aquatic vegetation biomass. The underlying assumption is that SAV abundance influences water retention time by exerting attrition, such that the difference in water levels increases as a function of water flow reduction (Morin, 2001). By validating the goodness of the correlation between EVI and the difference in water levels, we put the bases for the back-calculation of aquatic vegetation over the past 60 years, allowing us to reconstruct a long-term dynamic, which would not have been possible with the only data measured in the field.

In Chapter II, we also used indirect proxies to calculate variables that were not directly measured in the field. We calculated UV and visible light irradiance (at 340 and 443 nm) at the water surface (i.e., incident radiation) based on the position of the sun and corrected in function of the cloud coverage. Coefficients of light extinction (i.e., $K_d$, a proxy of the colour of the water) were also calculated from satellite imagery, to predict $K_d$ at each sampling station, based on reflectance from Landsat 7 and 8. Values obtained from satellite imagery were validated with *in-situ* measurements. Then, we calculated the UV and visible light irradiance at the depth of the sampling nets based on the Lambert-Beer law of light attenuation. The irradiance at depth was used to assess the relationship between YP larvae distribution and the underwater light environment.

The examples provided above, show how remote sensing represents a precious tool for the modern ecologist, providing access to data that were not directly measured in the field, broadening the spectrum of explanatory variables for ecological studies.

### ***Broad and small scales: benefits and limitations***

The perception of the environment and its interacting components depends on the scale considered, both for spatial and temporal phenomena (Wiens 1989; Levin 1992; Wheatley and Johnson 2009). The evaluation of ecological phenomena is therefore contextual to the spatio-temporal scale accounted for. The objective of this section is to review the approaches used in the three chapters in relation with the choice of the spatial, and to a lesser extent, the temporal scales. Figure 2 reports on the spatio-temporal resolution considered in each chapter of the thesis.

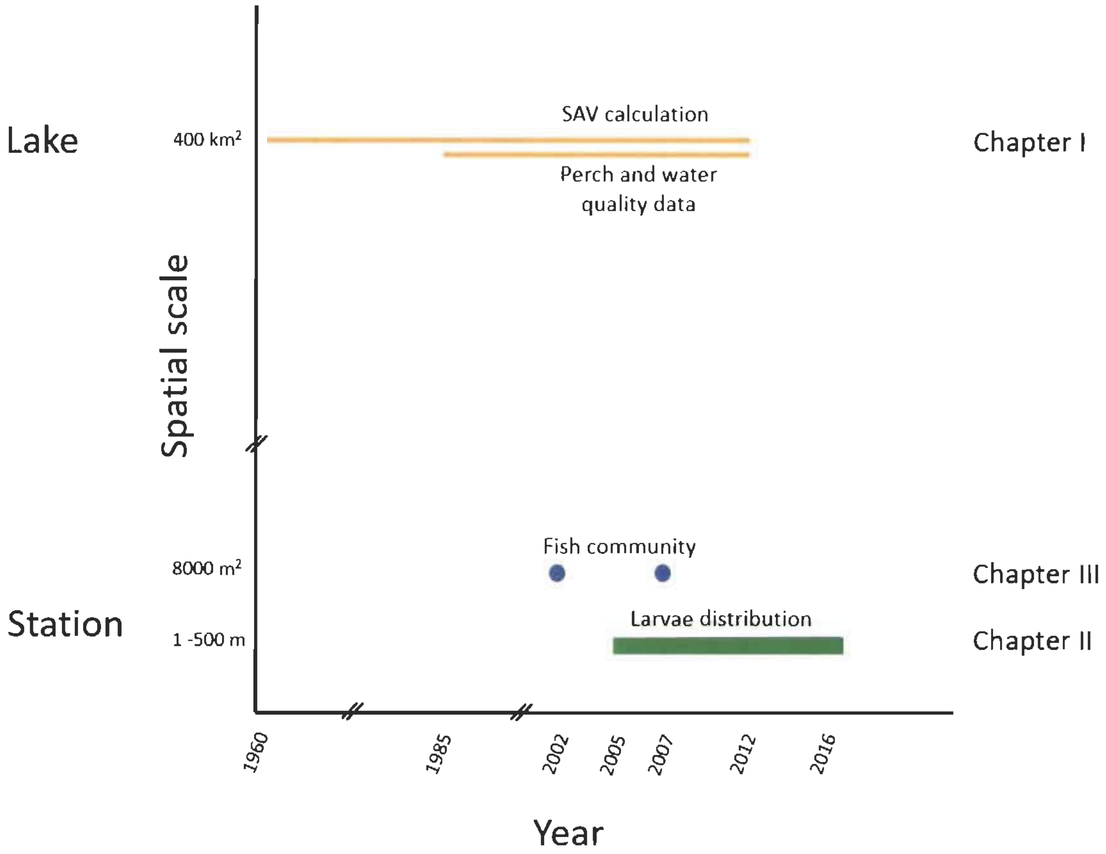

**Fig. 2.** Spatio-temporal resolution of the data considered in the three chapters of this thesis.

In the Chapter I, the goal was to depict the general picture of the LSP environmental changes, bridging the land-water gap by putting in relation the lake dynamics to the ones of the watershed. To match different time series and build the structural equation modelling network, spatio-temporal data were aggregated to obtain one value per variable and per year. On one side, we were constrained by variables measured only at the scale of the lake (i.e., low spatial resolution, e.g., temperature, water levels), and on the other we had variables with higher spatial resolution but measured only once a year (e.g., YP growth and abundance). Therefore, beside the operational need to aggregate the data to allow for a time series match, our approach was deliberately broad scale, to reconstruct patterns on the long term. This approach allowed us to include more variables in the structural equation modelling network, but on the other hand, we sacrificed the understanding of phenomena ongoing at the small scale. Therefore, despite the study scale was relevant to describe large scale phenomena, we are aware that some of the relationships evaluated would have been better described at a finer scale.

The Chapter II was intrinsically structured to match two spatial scales, corresponding to different hypotheses stated a priori. We analyzed YP larvae vertical aggregation patterns at the water column scale (less than one m deep), and between two isobaths spaced at least 500 m. This approach allowed us to show that certain variables affected YP larvae aggregation no matter the scale (e.g., SAV was significant for both vertical and horizontal axes), whether other variables affected YP abundance depending on the scale accounted for (e.g., PAR). These differences probably underlie distinct YP behaviours (e.g., stress avoidance and habitat choice for the vertical axis and mortality avoidance and dispersal for the horizontal axis), which influence YP larvae distribution depending on the scale at which the stressor operates.

In the Chapter III, we investigated the environmental factors driving fish species distribution in LSP. Despite the fact that we had data from almost 140 stations, we could not exploit the temporal component in our analyses. Unfortunately, all the samples were nested into only two years of sampling, and each station was sampled only once per year. Therefore, we are aware that the associations we found between environmental variables and fish species are to be interpreted more as an instant snapshot, rather than a description of the variables structuring the community on the long term. Nevertheless, the sampling stations were situated across the lake, providing a good spatial gradient along different water masses, shorelines, and tributaries. The scientific contribution of this chapter is not meant as a description of the fish community response to global change, rather as an evaluation of fish species habitat *preferendum*, which in a changing world, might help us to infer about an eventual future community rearrangement.

### *Accounting for space and time in ecological analyses*

Space and time are two key components in ecological processes. An ecosystem might be considered as the result of processes acting at multiple spatial and temporal scales.

While assessing species dynamics, community variations (e.g., relative abundance and/or species composition), or environmental changes, it is fundamental to account for space and time. LSP is highly spatially-heterogenous: SAV is very patchy, community species composition and the water quality differ considerably from a portion of the lake to another, depending for instance on the water masses and tributary inputs. Temporally, LSP has been submitted to a multitude of environmental changes (and which represents the core of this thesis).

In the three chapters of in this dissertation, we specifically modelled time and space. While working in numerical ecology (and especially with time series), data non-independence (e.g., spatio-temporal autocorrelation) may be problematic because most of the statistics assume data independence. Depending on whether this assumption is respected or not, it might affect the quality of statistical analyses and the interpretation of the results. For instance, time series data are intrinsically non-independent, given that each data point depends on the previous one and it is likely to be similar (i.e., autocorrelated) to the next one. Therefore, it is important to specify the data dependency structure by making explicit the degree of proximity (and therefore higher chances of similarity) between data points. A misspecification in the analysis of such structured data might result in an increased possibility of errors of type I, due for example to autocorrelation.

In the Chapter I, we accounted for non-independence among years by including an autocorrelation term in our analyses. We screened for the autocorrelation structure in our data and applied a first-order autoregressive model (AR1). First-order autocorrelation derives from the correlation between the error terms of two adjacent time points. AR1 specifies that the response variable at a given time, depends linearly on its own previous value and on a stochastic term (which is an imperfectly predictable term). Once such model is applied, each temporal data point is not anymore (or very low) autocorrelated with the previous/following data point.

In the Chapter II, space has been modelled with an exponential term of autocorrelation on sampling sites coordinates. This means that the degree of autocorrelation between sites follows an inverse exponential curve, with the degree of autocorrelation being high for close sites but decaying abruptly as a function of the Euclidean distance between sites. Time has been accounted for by using nested random effects, namely, the year as simple random effect or the station nested into the year, and the day of the year nested into the year depending on the analysis.

In Chapter III, no significant spatial autocorrelation was detected among sites. Moreover, given that we had only two temporal data points, there was no need to account for temporal autocorrelation either.

### *Three chapters: insights on a more holistic conceptual framework*

The main axis of this thesis is represented by the causal relationship between water quality, SAV abundance and fish. Two environmental variables, namely turbidity and SAV abundance, were consistently found to affect the YP throughout all ontogenetic stages analyzed, driving the abundance of larvae and adults, and to a lesser extent the growth of juveniles. These variables were also involved in determining the fish distribution within the community, influencing species richness and diversity, as well as the fish abundance.

The Figure 3 shows a conceptual framework linking the three chapters of this thesis, illustrating the relationships between the studied variables. In this figure, I reported some links (dotted lines) that were not explicitly analyzed by our research but that would deserve a further exploration, allowing for an explicit link among the three chapters. For instance, it would be interesting to model the YP population dynamics (e.g., with a Leslie matrix), evaluating the relative contribution of each ontogenetic stage to the overall population size. With data at hand, it would be possible to estimate which are the most sensitive life stages, and how they contribute to the overall population dynamics of the YP.

In the context of this dissertation, we explained the distribution of fish in function of environmental variables, but biotic interaction among species (e.g., competition, predation) has not been specifically accounted for. We are aware that environmental variables can explain only partly the species community structure. Therefore, to describe mechanisms behind the YP distribution and the community structure in the LSP, there is a need to assess the importance of phenomena like species co-occurrence, competition, and predation. Joint species distribution modelling represents a tool allowing to move from species-level to community analyses, integrating phylogeny, species traits and environmental variables to model species occurrence in the community (Ovaskainen et al., 2017).

Despite not trivial, I would be interested in evaluating the feedback processes between water quality and SAV. Water quality affects SAV biomass, but this latter also helps water depuration which in turn would favour SAV growth. Shedding light on this circular phenomenon would contribute to the understanding of the complex links structuring the macrophytes (and fish) communities.

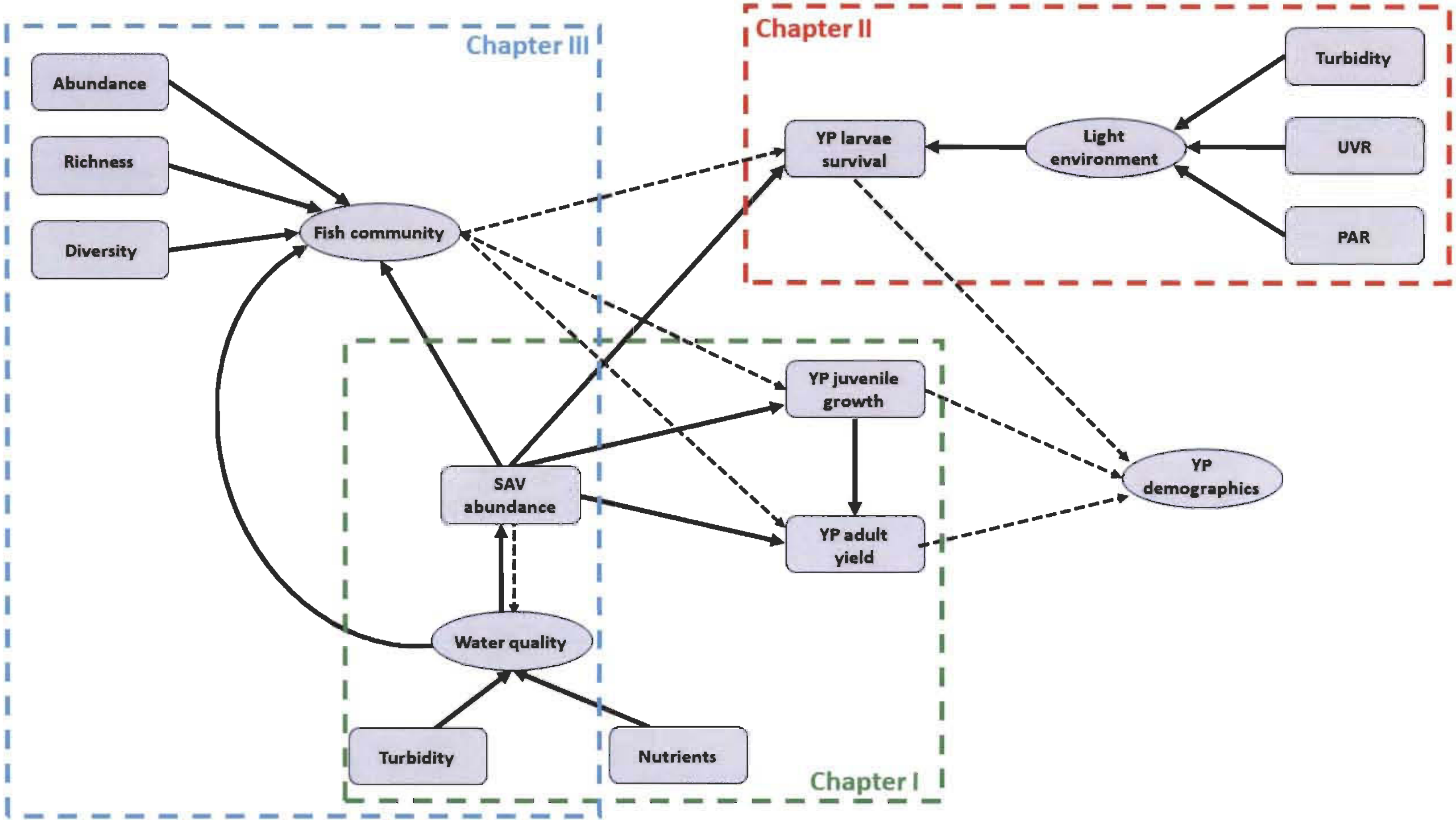

**Fig. 3.** Conceptual framework linking the three chapters of this thesis, illustrating the relationships between the studied variables. The black arrows represent the links tested in the context of this thesis (not all the links were tested in a connected causal network), while dotted arrows represent links of interest that would be interesting to analyze. Square boxes represent variables that were measured or calculated, round boxes represent latent variables which cannot be measured but can be explained by measurable predictors.

### *From ecology to management*

The scientific research reported in this dissertation was meant not only to shed light on the ecological processes structuring fish populations, communities, and their relationships with pivotal environmental variables. A fundamental objective of this thesis was also to provide information that the practitioner can use to rehabilitate the ecosystem quality and potentially restore SAV and the YP population.

To this goal, the Chapter I was deliberately focused to depict the general portrait of the YP in relationship with the environmental changes in water quality and SAV abundance of the LSP. Our major findings were: i) water quality in the LSP deteriorated during the last decades and this is mainly due to inputs from the watershed that come from an intensively cultivated region. Nitrogen and sedimentary turbidity represent the most concerning issues for water quality in this system; ii) SAV markedly decreased since the late 1980s probably due to increased sedimentary turbidity; iii) YP abundance is intimately connected with the water quality degradation and with the SAV abundance decrease. The link between fish and SAV is at the core of this dissertation. In Chapter II, we showed that YP larvae are positively associated to aquatic vegetation (mostly submerged but also emerged), both on the vertical and horizontal axes. In Chapter III, we found evidence that SAV and turbidity are counteracting variables, driving fish distribution and the community assemblage.

Therefore, these three chapters provide relevant information that the practitioner can use to attempt a restoration. Given the importance of SAV in shaping the ecology of the LSP, it is straightforward that a decline in biomass and coverage should determine important changes in fish communities, affecting both species relative abundance and the community composition. We strongly believe that management efforts should focus on SAV restoration. However, this is more difficult than it might appear. One could think that a rapid SAV recovery could be helped by transplanting macrophytes in the LSP. This has been shown to be time- and money-consuming, often leading to poor results. Whether the issue is the trophic state of the system and/or the optical water environment, plant transplantation is proven to be poorly effective (Hilt et al., 2006). Transplantation is almost useless when water quality attained a non-favourable state for vegetation (e.g., degraded light environment). An emblematic example is provided by macrophytes restoration efforts operated in the Chesapeake Bay, the largest estuary in the USA. SAV reduction has been recognized to be caused by an increase in turbidity related to eutrophication (Shafer and Bergstrom, 2010; Lefcheck et al., 2017). To allow SAV recovery and to improve water clarity, a restoration effort started in 1978 involving the large-scale planting of whole plants, cuttings, seeds, and tubers of several seagrass species (i.e., *Zostera marina*, *Vallisneria americana*, and *Ruppia maritima*), followed by an environmental program established in 1987 that aimed to reduce nutrient inputs by 40% by the year 2000 (Hennessey 1994; Boesch 2006; Shafer and Bergstrom, 2010). Aquatic vegetation is currently recovering in several areas of the estuary, but not at the scale of the whole bay, mostly because turbidity is still strongly limiting SAV development (Orth et al., 2010; Shafer and Bergstrom, 2010). Despite this example is to be considered as mostly successful, it took several decades, a huge human, logistic and financial resources, and still vegetation did not completely recovery, especially in areas with low quality water.

For these reasons, our recommendations to restore SAV beds in LSP would be to start from the distal cause (i.e., water quality), reducing sediments and nutrient discharge from the watershed to the lake, rather than focusing on SAV itself. Despite the Québec law on environmental quality was adopted in 1972 with the aim of reducing nutrients charges, these efforts allowed a slight reduction in P concentrations, while N continued to increase (Simoneau, 2017). A stricter management of these fertilizers to avoid eutrophication is required, both for regarding agricultural use (nitrogen) as well as waste water's treatment. To reduce sediment inputs, we believe that a reconversion of agricultural surfaces is needed. Perennial crops should be preferred to intensive annual crops, the latter poorly stabilizing soil and involving land labour, which are two major sources of soil erosion due to water runoff (Foley et al., 2005). These approaches are the most appropriate to improve water quality and to allow SAV recovery. Based on the literature, reduction of eutrophication and turbidity are the most effective measures, with transplantation efforts to be less efficient (Hilt et al., 2006).

To restore LSP water quality, a project joining many researchers from three universities of Québec (Pôle d'expertise multidisciplinaire en gestion durable du littoral du lac Saint-Pierre), has been implemented since 2018. The objective is to promote a type of agriculture respectful of the littoral zone of the LSP, reducing nutrients, pesticides, and sediment discharge. The goal of this project is to support less-impacting crops, adapted and durable in the context of the LSP floodplain, which would help to restore littoral and aquatic habitats. We hope that our research will help the development of this ambitious project.

## Conclusion

In this dissertation we traced the portrait of an increasingly endangered and degraded ecosystem and evaluated some of the causes impeding the YP population recovery after the 2012 moratorium on commercial and recreational fishing. This thesis provides relevant information to restore this ecosystem and the YP population. It also provides an original scientific contribution on the mechanisms structuring freshwater ecosystems, especially regarding freshwater shallow fluvial lakes. To assure a future sustainable fishery, a particular attention needs to be dedicated to fish habitat, especially to the recovery of submerged aquatic vegetation. A healthy habitat will increase species resilience to harvesting, thus augmenting the chances of a durable exploitation. To allow submerged aquatic vegetation recovery, inputs from the watershed must be reduced, especially concerning sediments, to improve water clarity, as well as regarding nutrients, to avoid a further eutrophication. Therefore, fisheries management practices should thus explicitly take into account land use in the watershed and not only the aquatic ecosystem.

# REFERENCES

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011). The value of estuarine and coastal ecosystem services. Ecological Monographs 81: 169-193.

Bertolo A, Blanchet FG, Magnan P, Brodeur P, Mingelbier M, Legendre P (2012). Inferring processes from spatial patterns: The role of directional and non-directional forces in shaping fish larvae distribution in a freshwater lake system. PLoS ONE 7(11): e50239.

Blindow I (1992). Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwater Biology 28: 15-27.

Boesch DF (2006). Scientific requirements for ecosystem-based management in the restoration of Chesapeake Bay and coastal Louisiana. Ecological Engineering 26: 6–26.

Brinson, MM, Malvárez AI (2002). Temperate freshwater wetlands: types, status, and threats. Environmental Conservation 29: 115-133.

Caires AM, Chandra S, Hayford BL, Wittmann ME (2013). Four decades of change: dramatic loss of zoobenthos in an oligotrophic lake exhibiting gradual eutrophication. Freshwater Science 32: 692-705.

Capon SJ, Lynch AJJ, Bond N, Chessman BC, Davis J, Davidson N, Finlayson M, Gell PA, Hohnberg D, Humphrey C, Kingsford RT, Nielsen D, Thomson JR, Ward K, Nally Mac R (2015). Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. Science of the Total Environment 534: 122–130.

Chow-Fraser P, Lougheed V, Le Thiec V, Crosbie1 B, Simser L, Lord J (1998). Long-term response of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. Wetlands Ecology and Management 6: 19-42.

de la Chenelière V, Brodeur P, Mingelbier M (2014). Restauration des habitats du lac Saint-Pierre : un prérequis au rétablissement de la perchaude. Le Naturaliste canadien, 138: 50-61.

Farly L, Hudon C, Cattaneo A, Cabana G (2019). Seasonality of a floodplain subsidy to the fish community of a large temperate river. Ecosystems 22: 1823-1837.

Farmer TM, Marschall EA, Dabrowski K, Ludsin SA (2015). Short winters threaten temperate fish populations. Nature Communications 6: 1-10.

Fausch KD, Torgersen CE, Baxter CV, Li HW (2002). Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52: 483-498.

Figueiredo BRS, Mormul RP, Benedito E (2013). Non-additive effects of macrophyte cover and turbidity on predator–prey interactions involving an invertivorous fish and different prey types. Hydrobiologia 716: 21-28.

Figueiredo BRS, Calvo C, López-Rodríguez A, Mormul RP, Teixeira-de Mello F, Benedito E, Meerhoff M (2019). Short-term interactive effects of experimental heat waves and turbidity pulses on the foraging success of a subtropical invertivorous fish. Water 11,2109.

Figueiredo BRS, Granzotti RV, Fiori L, Nieman CL, Benedito E (2020). Cascading effects of predation risk under high organic and inorganic turbidity: impacts on individuals and shoals of a mesopredator fish. Aquatic Ecology 54: 855-868.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Helkowski JH (2005). Global consequences of land use. Science 309, 570–574. Francis, R.I.C.C., 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36: 883-902.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004). Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35: 557-81.

Frenette JJ, Arts MY, Morin J (2003). Spectral gradients of downwelling light in a fluvial lake (Lake Saint-Pierre, St-Lawrence River). Aquatic Ecology 37: 77-85.

Frenette JJ, Massicotte P, Lapierre JF (2012). Colorful Niches of Phytoplankton Shaped by the Spatial Connectivity in a Large River Ecosystem: A Riverscape Perspective. PLoS ONE 7(4): e35891.

Gao X, Huete AR, Ni W, Miura T (2000). Optical-biophysical relationships of vegetation spectra without background contamination. Remote Sensing of Environment 74: 609-620.

García-Ruiz JM, Beguería S, Nadal-Romero E, González-Hidalgo JC, Lana-Renault N, Sanjuán Y (2015). A meta-analysis of soil erosion rates across the world. Geomorphology 239: 160-173.

Gleick PH (2003). Water use. Annual Review of Environment and Resources. 28: 275-314.

Goyette JO, Bennett EM, Maranger R, 2018. Low buffering capacity and slow recovery of anthropogenic phosphorus pollution in watersheds. Nature Geoscience 11: 921-925.

Hébert S, Blais D (2017). Territoire et qualité de l'eau : développement de modèles prédictifs. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques, Direction générale du suivi de l'état de l'environnement et Direction de l'expertise en biodiversité, ISBN 978-2-550-77770-0 (PDF), 30 pp.

Hennessey TM (1994). Governance and adaptive management for estuarine ecosystems: the case of Chesapeake Bay. Coastal Management 22: 119-145.

Hidding, B, Bakker ES, Hootsmans MJM, Hilt S (2016). Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. Oikos 125: 1489-1495.

Hilt S, Alirangues Nuñez MM, Bakker ES, Blindow I, Davidson TA, Gillefalk M, Hansson LA, Janse JH, Janssen ABG, Jeppesen E, Kabus T, Kelly A, Köhler J, Lauridsen TL, Mooij WM, Noordhuis R, Phillips G, Rücker J, Schuster HH, Søndergaard M, Teurlincx S, van de Weyer K, van Donk E, Waterstraat A, Willby N, Sayer CD (2018). Response of submerged macrophyte communities to external and internal restoration measures in north temperate shallow lakes. Frontiers in Plant Science 9: 194.

Hilt S, Gross EM, Hupfer M, Morscheid H, Mählmann J, Melzer A, Poltz J, Sandrock S, Scharf EV, Schneider S, van de Weyer K (2006). Restoration of submerged vegetation in shallow eutrophic lakes – A guideline and state of the art in Germany. Limnologica 36: 155-171.

Hilt S, Köhler J, Kozerski HP, van Nes EH, Scheffer M (2011). Abrupt regime shifts in space and time along rivers and connected lake systems. Oikos 120: 766-775.

Hudon C (1997). Impact of water level fluctuations on St. Lawrence River aquatic vegetation. Canadian Journal of Fisheries and Aquatic Sciences 54: 2853-2865.

Hudon C, Cattaneo A, Tourville Poirier AM, Brodeur P, Dumont P, Mailhot Y, Amyot JP, Despatie SP, de Lafontaine Y (2012). Oligotrophication from wetland epuration alters the riverine trophic network and carrying capacity for fish. Aquatic Sciences 74: 495-511.

Hudon C, Jean M, Létourneau G (2018). Temporal (1970–2016) changes in human pressures and wetland response in the St. Lawrence River (Québec, Canada). Science of the Total Environment 643: 1137-1151.

Hudon, C, Carignan R (2008). Cumulative impacts of hydrology and human activities on water quality in the St. Lawrence River (Lake Saint-Pierre, Quebec, Canada). Canadian Journal of Fisheries and Aquatic Sciences 65: 1165-1180.

Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83: 195-213.

Jackson LJ (2003). Macrophyte-Dominated and Turbid States of Shallow Lakes: Evidence from Alberta Lakes. Ecosystems 6: 213-223.

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T (1999). Trophic dynamics in turbid and clearwater lakes with special emphasis on the role of zooplankton for water clarity. Hydrobiologia 408/409: 217-231.

Kelly DJ, Schallenberg M (2019). Assessing food web structure in relation to nutrient enrichment, macrophyte collapse and lake resilience in shallow lowland lakes. New Zealand Journal of Marine and Freshwater Research 53: 603-619.

Körner S, Schreiber ESG, Walz N (2002). Herbivory on submerged macrophytes – who's to blame? Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 28: 967-970.

La Violette N, Fournier D, Dumont P, Mailhot Y (2003). Caractérisation des communautés de poissons et développement d'un indice d'intégrité biotique pour le fleuve Saint-Laurent, 1995–1997. Faune et Parcs Québec, Direction de la recherche sur la faune, Québec.

Lacoul P, Freedman B (2006). Environmental influences on aquatic plants in freshwater ecosystems. Environmental Reviews 14: 89-136.

Laplante-Albert KA, Rodríguez MA, Magnan P (2010). Quantifying habitat-dependent mortality risk in lacustrine fishes by means of tethering trials and survival analyses. Environmental Biology of Fishes 87: 263-273.

Lefcheck JS, Orth RJ, Dennison WC, Wilcox DJ, Murphy RR, Keisman J, Gurbisz C, Hannam M, Brooke Landry J, Moore KA, Patrick CJ, Testa J, Weller DE, Batiuk RA (2018). Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. Proceedings of the National Academy of Sciences of the United States of America 115: 3658-3662.

Lefcheck JS, Wilcox DJ, Murphy RR, Marion SR, Orth RJ (2017). Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. Global Change Biology 23: 3474-3483.

Levin SA (1992). The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Magnan P, Dumont P, Mailhot Y, Coulombe F, Therrien L (2004). État du stock de perchaude du lac Saint-Pierre en 2003 et recommandations sur le niveau d'exploitation soutenable en 2004. Comité aviseur sur la gestion de la perchaude du lac Saint-Pierre.

Magnin E (1966). La pêche commerciale sur le fleuve Saint-Laurent et sa place dans l'ensemble des pêches commerciales de la province de Québec. Université de Montréal, Département des Sciences biologiques, Québec.

Mailhot Y, Dumont P, Paradis Y, Brodeur P, Vachon N, Mingelbier M, Lecomte F, Magnan P (2015). Yellow perch (*Perca flavescens*) in the St. Lawrence River (Québec, Canada): Population dynamics and management in a river with contrasting pressures. Biology of Perch, eds Couture P, Pyle G (CRC Press), pp. 101-147.

Massicotte P, Bertolo A, Brodeur P, Hudon C, Mingelbier M, Magnan P (2015). Influence of the aquatic vegetation landscape on larval fish abundance. Journal of Great Lakes Research 41: 873-880.

Menge BA, Sutherland JP (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. The American Naturalist 110: 351-369.

Morin J (2001). Modélisation des facteurs abiotiques de l'écosystème fluvial du lac Saint-François, fleuve Saint-Laurent. Université du Québec, Institut national de la recherche scientifique, INRS-Eau. PhD thesis.

Orth RJ, Williams MR, Marion SR, Wilcox DJ, Carruthers TJB, Moore KA, Kemp WM, Dennison WC, Rybicki N, Bergstrom P, Batiuk RA (2010). Longterm trends in submersed aquatic vegetation (SAV) in Chesapeake Bay, USA, related to water quality. Estuaries and Coasts 33: 1144-1163.

Ovaskainen O, Tikhonov G, Norberg A, Blanchet FG, Duan L, Dunson D, Roslin T, Abrego N (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20: 561-576.

Paine RT (1966). Food web complexity and species diversity. The American Naturalist 100: 65-75.

Paradis Y, Bertolo A, Mingelbier M, Brodeur P, Magnan P (2014). What controls distribution of larval and juvenile yellow perch? The role of habitat characteristics and spatial processes in a large, shallow lake. Journal of Great Lakes Research 40: 172-178.

Parrish JD, Saila SB (1970). Interspecific competition, predation and species diversity. Journal of Theoretical Biology 27: 207-220.

Phillips G, Willby N, Moss B (2016). Submerged macrophyte decline in shallow lakes: what have we learnt in the last forty years? Aquatic Botany 135: 37-45.

Post JR (1990). Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): *in situ* estimates and bioenergetic models. Canadian Journal of Fisheries and Aquatic Sciences 47: 554-560.

Radke RJ, Gaupisch A (2005). Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): Possible implications for fish community structure in lakes. Naturwissenschaften 92: 91-94.

Sand-Jensen K, Borum J (1991). Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. Aquatic Botany 41: 137-175.

Sandström A (1999). Visual ecology of fish – a review with special reference to percids. Fiskeriverket Rapport 2: 45-80.

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993). Alternative equilibria in shallow lakes. Ecology and Evolution 8: 275-279.

Scheffer M, van Nes EH (2007). Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia 584: 455-466.

Shafer D, Bergstrom P (2010). An introduction to a special issue on large-scale submerged aquatic vegetation restoration research in the Chesapeake Bay: 2003-2008. Restoration Ecology 18: 481-489.

Sheppard JN, James NC, Whitfield AK, Cowley PD (2011). What role do beds of submerged macrophytes play in structuring estuarine fish assemblages? Lessons from a warm-temperate South African estuary. Estuarine, Coastal and Shelf Science 95, 145-155.

Simoneau M (2017). Qualité de l'eau des tributaires du lac Saint-Pierre : évolution temporelle 1979-2014 et portrait récent 2012-2014. Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques. Direction générale du suivi de l'état de l'environnement, ISBN 978-2-550-76229-4 (PDF), 54 p. + 13 ann. (http://www.mddelcc.gouv.qc.ca/eau/lac-st-pierre/qualite-eau-tributaires.pdf). Bibliothèque et Archives nationales du Québec.

Vis C, Cattaneo A, Hudon C (2008). Shift from chlorophytes to cyanobacteria in benthic macroalgae along a gradient of nitrate depletion. Journal of Phycology 44: 38-44.

Whatley MH, van Loon EE, van Dam H, Vonk JA, van der Geest HG, Admiraal W, 2014. Macrophyte loss drives decadal change in benthic invertebrates in peatland drainage ditches. Freshwater Biology 59: 114-126.

Wheatley M, Johnson C (2009). Factors limiting our understanding of ecological scale. Ecological Complexity 6: 150-159.

Wiens JA (1989). Spatial scaling in ecology. Functional Ecology 3: 385-397.