UNIVERSITÉ DU QUÉBEC

FACTEURS DÉTERMINANT LA DIVERSITÉ FONCTIONNELLE DU ZOOPLANCTON DANS LES HERBIERS SUBMERGÉS DU LAC SAINT-PIERRE (FLEUVE SAINT-LAURENT)

THÈSE PRÉSENTÉ(E)

COMME EXIGENCE PARTIELLE DU

DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

OFFERT PAR L'UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EN ASSOCIATION AVEC

L'UNIVERSITÉ DU QUÉBEC À TROIS-RIVIÈRES

PAR

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AOÛT 2023

UNIVERSITÉ DU QUÉBEC

DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT (PH. D.)

Programme offert par l'Université du Québec à Montréal (UQAM)

en association avec

l'Université du Québec à Chicoutimi (UQAC)

l'Université du Québec à Rimouski (UQAR)

l'Université du Québec en Abitibi-Témiscamingue (UQAT)

et l'Université du Québec à Trois-Rivières (UQTR)

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Thèse soutenue le 15 juin 2023

REMERCIEMENTS

Tout d'abord, je voudrais remercier mes codirecteurs de thèse, M. Andrea Bertolo (UQTR) et Mme Bernadette Pinel-Alloul (UdeM) pour m'avoir donné l'opportunité de travailler avec eux. Votre confiance m'aura permis de faire un passage au doctorat et de pousser plus loin ce projet de recherche. Au début du projet, je voyais le zooplancton comme étant un maillon de la chaîne alimentaire, des petites « bébites » vivant dans l'eau. Pourtant, plus je travaillais sur ce projet, plus je connaissais les espèces présentes dans mon aire d'étude, et plus je trouvais ce monde microscopique et leurs interactions avec leur environnement fascinant. Bernadette m'a dit un jour qu'elle prendrait du temps pour peindre un tableau de zooplancton. Ce tableau, j'en suis certaine, sera un chef-d'œuvre illustrant bien sa passion et le dévouement qu'elle leur a porté tout au long de sa carrière. Pour Andrea, les communautés zooplanctoniques sont surtout des organismes permettant de tester de nouvelles approches, de comprendre les mécanismes derrière les relations entre les communautés et leur environnement. Chacun à votre manière, vous avez influencé ma vision de la recherche scientifique et contribué au développement de la personne que je suis aujourd'hui. Ensemble, vous m'avez appris à regarder plus loin tout en gardant le message scientifique simple et clair, à développer mon esprit critique, mais surtout, à être persévérante et résiliente. Vos accomplissements en tant que chercheurs, mais aussi en tant que personnes, sont une grande inspiration pour moi. Votre passion pour l'écologie, votre ouverture d'esprit, votre travail acharné et constant me serviront de modèle toute ma vie. Vous côtoyer tout au long de cette aventure aura été un privilège pour moi. Merci d'avoir été là et de m'avoir soutenu tout au long de ces années.

Je voudrais également remercier les membres de mon comité d'encadrement, soit M. Raphaël Proulx (UQTR) et Mme Christiane Hudon (Environnement Canada) pour les discussions que nous avons eus et qui m'ont permis d'améliorer grandement cette thèse. Merci à Raphaël de m'avoir toujours rappelé que la recherche devait « être le fun! ». Cette vision positive m'a grandement aidé à accepter les rejets de notre article du cours de « Méta-analyses » sans trop d'amertume! Comme quoi, plus un travail de recherche reçoit de commentaires, plus l'article qui en découle ne peut que s'améliorer! Merci particulièrement à Christiane qui aura fourni tout au long des campagnes d'échantillonnage une ressource spécialisée permettant de monter la base de données sur la végétation aquatique submergée. Je veux également te remercier pour m'avoir donné l'opportunité d'aller travailler au bureau d'Environnement Canada avec Morgan et toi. Tu m'as offert un encadrement exceptionnel qui a mené à la publication du chapitre 3 de cette thèse. Cette période de ma vie aura été intense, mais ô combien enrichissante! Je tiens également à remercier du fond du cœur Zofia Taranu, avec qui nous avons collaboré étroitement pour la réalisation du premier chapitre de cette thèse. Ton arrivée dans mon parcours aura insufflé une nouvelle énergie et m'aura redonné la motivation de poursuivre jusqu'à la toute fin.

Je voudrais également remercier les membres du jury, M. Gilbert Cabana (UQTR), Mme Alison Derry (UQAM) et Mme Gesche Winkler (UQAR), pour le temps qu'ils ont accordé à la lecture et l'évaluation de ma thèse.

Cette thèse n'aurait pas été la même sans l'aide des assistants de rechercher qui m'ont aidé dans l'identification du zooplancton et qui ont permis à mon projet d'avancer même lorsque les cours du doctorat prenaient beaucoup de mon temps. Merci à Myriam Boisvert, qui a été ma toute première assistante et qui est montée avec moi à l'UdeM apprendre l'identification du zooplancton de la meilleure, Mme Ginette Méthot. Merci à Lucas Deschamps, Annie Picard, Angela Paquet-Walsh, Joëlle Guitard qui m'ont aidé pour mes analyses de zooplancton, mais qui ont aussi mis de la vie dans le laboratoire. Merci également aux membres de mon laboratoire ainsi qu'aux membres du département, qui sont devenus des amis chers. Nos discussion, pauses-café, soirées ont tous été des moments qui ont rendu mon passage au doctorat mémorable. Merci à Angela, Vincent et Audréanne, Matteo, Simon, Luc, Charles, Lucas, Louis, Ian, Irene, Zaccaria, Philippe, Marc et tous les gens qui ont, un jour ou l'autre, croisé et influencé mon chemin.

Je tiens à remercier les membres du département des sciences de l'environnement qui travaillent dans l'ombre, mais qui ont un rôle extrêmement important à jouer dans notre parcours. Merci Catarina Leote Franco Pio, Marie-Andrée Fallu et Chantal Fournier pour avoir toujours su nous donner l'heure juste ou nous orienter vers la bonne ressource/formulaire/information. Sans vous, il aurait été facile de se perdre dans les dédales administratifs que peut représenter un doctorat! Merci spécialement à Marie-Andrée de m'avoir encouragé à faire partie du comité étudiant du GRIL. Cette expérience a été extrêmement enrichissante et m'aura permis de faire de belles rencontres au cours de mon passage aux cycles supérieurs.

Je tiens à remercier ma famille qui a toujours été présente et qui m'a soutenu tout au long de mon (long!) parcours. À mes parents, qui m'ont appris à saisir les opportunités qui se présentent et à toujours terminer ce que je commence, à Annik qui a toujours fourni une oreille attentive lorsque j'avais besoin de parler, à Pierre-Luc et à Tommy qui sont toujours là pour rire et dédramatiser les situations. Merci à mon beau-frère Renald et à mes belles-sœurs Catherine et Jessica-Marie d'être présents pour nous. Merci également à ma belle-famille de nous avoir supportés Guillaume et moi durant tout ce temps et d'avoir toujours été présents lorsque nous en avions besoin. Jean-Guy, Suzie, Benjamin, Evelyne, Élianne et Alexis, merci beaucoup!

Finalement, je voudrais spécialement remercier Guillaume. Merci de faire partie de ma vie. Nous en avons partagé des choses depuis le début de notre aventure commune! De la vie insouciante du baccalauréat aux études graduées qui ont, avouons-le, apporté son lot de stress, mais également beaucoup de belles discussions. Je suis heureuse de t'avoir eu à mes côtés pour partager ces moments. Depuis le tout début, tu es mon co-équipier, autant dans ma vie étudiante, amoureuse que familiale. Je n'aurais pas pu choisir meilleur partenaire pour m'aider et me soutenir dans mes projets et mes décisions. Bien d'autres aventures nous attendent et je suis fière de pouvoir les partager avec toi et nos deux enfants, Abigaëlle et Émile. Je t'aime! Abi et Émile, je vous remercie pour la motivation supplémentaire que vous m'avez apportée. Être votre mère m'apporte une joie et une fierté indescriptible!

Cette thèse n'aurait pu être réalisée sans le support financier provenant du Fond Québécois de la Recherche Nature et Technologie (ISI-FRQNT), du Conseil de Recherches en Sciences Naturelles et Génie du Canada (CRSNG), du Centre de Recherche sur les Interactions Bassins versants – Écosystèmes Aquatiques (RIVE- UQTR), du Groupe de Recherche Interuniversitaire en Limnologie et en environnement aquatique (GRIL) et d'Environnement Canada (Centre Saint-Laurent). Le support logistique et technique fourni par le GRIL a permis une bonne coordination des membres du GRIL non seulement sur le terrain, mais également pour le partage des données par la suite.

DÉDICACE

Je dédie cette thèse à Guillaume Rheault et à mes deux enfants, qui m'ont donné la motivation de terminer. Je dédie aussi cette thèse à mes parents, qui m'ont toujours appris qu'on devait terminer ce qu'on commence.

AVANT-PROPOS

Les chapitres 1, 2 et 3 sont présentés sous forme d'articles scientifiques. Les données qui ont été analysées dans cette thèse proviennent d'un travail effectué en collaboration avec différents chercheurs membres du GRIL (Groupe de recherche en limnologie et en environnement aquatique) provenant de plusieurs universités et partenaires affiliés (UQTR, UdeM, UQAM, Université Concordia, Environnement Canada). Plus précisément, ma participation à ce grand projet s'est concentrée sur les communautés zooplanctoniques du lac Saint-Pierre (LSP) qui ont été échantillonnées durant les étés 2012, 2013 et 2014. La logistique du terrain relevait du professionnel de recherche du GRIL. Toutefois, la réalisation du volet zooplanctonique était entièrement à ma charge, avec l'aide de mes directeurs de recherche, Andrea Bertolo et Bernadette Pinel-Alloul. J'ai activement participé à la collecte des échantillons sur le terrain, à l'identification du zooplancton en laboratoire et à l'analyse des données. Je confirme avoir écrit chacun des articles présentés dans cette thèse, avec la collaboration de mes directeurs et coauteurs qui ont grandement contribué à les améliorer. Les versions finales présentées dans cette thèse sont le résultat de la contribution active de l'ensemble des coauteurs. Le premier article associé au chapitre 1 de cette thèse est en préparation pour soumission à la revue *Ecology and Evolution*. Le second article associé au chapitre 2 a été publié dans la revue *Hydrobiologia*. Finalement, le troisième article associé au chapitre 3 a été publié dans la revue *Journal of Great Lakes Research*.

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

CS : Complexité structurelle

GRIL: Groupe de recherche interuniversitaire en limnologie et en environnement aquatique

HMSC: Hierarchical Modeling of Species Community

JSDM: Joint Species Distribution Modeling

LSP : Lac Saint-Pierre

SAV : Submerged aquatic vegetation

VAS : Végétation aquatique submergée

RÉSUMÉ

Comprendre comment sont structurées les communautés est toujours une question d'intérêt en écologie. Dans les milieux aquatiques, le zooplancton est un modèle clé pour comprendre le fonctionnement des écosystèmes lacustres. Dans les lacs peu profonds, la végétation aquatique submergée constitue des habitats structurellement complexes qui favoriseraient une plus grande diversité de niches écologiques disponibles pour le zooplancton.

L'objectif général de ce projet est de comprendre comment les communautés de zooplancton sont organisées dans l'espace dans un herbier de végétation aquatique submergé (VAS) hétérogène afin de comprendre les impacts potentiels d'une diminution de la VAS sur la diversité taxonomique et fonctionnelle des communautés zooplanctoniques.

Dans un premier temps, nous avons utilisé une approche à l'échelle du paysage afin de déterminer l'importance relative des filtres biotiques et abiotiques dans l'assemblage des communautés de zooplancton en utilisant trois années consécutives de suivi (2012-2014; chapitre 1). La grande variabilité interannuelle observée dans les conditions environnementales a eu un impact important sur la force et la direction des relations observées entre les espèces zooplanctoniques et les variables environnementales. Malgré une grande variabilité dans la composition en espèces et dans la réponse des espèces face aux conditions environnementales, les traits fonctionnels présents dans les communautés ont répondu de manière similaire chaque année, suggérant une redondance fonctionnelle dans les traits du zooplancton. Ces résultats sont un bel exemple de la façon dont la redondance fonctionnelle pourrait agir comme une police d'assurance en favorisant la résilience des fonctions écosystémiques.

Dans le but de comprendre l'impact d'une diminution de l'abondance de la VAS, nous avons analysé la relation entre la VAS et la biomasse du zooplancton le long d'un gradient d'abondance de VAS durant l'été 2012 (chapitre 2). Nous avons utilisé quatre indices de diversité fonctionnelle, soit la richesse, l'équitabilité, la divergence et la dispersion. Nos résultats montrent que la VAS explique 9% de la variation totale de la biomasse de zooplancton. De même, la VAS explique 13% de la diversité fonctionnelle du zooplancton. Les résultats obtenus montrent que la dispersion des traits des espèces de zooplancton est reliée à la biomasse de VAS tandis que la régularité des traits dans l'espace de trait est inversement reliée à cette variable. La réduction de la VAS pourrait donc avoir un impact négatif sur la biomasse et la diversité fonctionnelle du zooplancton et par conséquent, sur les fonctions écosystémiques en raison du rôle clé joué par le zooplancton.

Plusieurs études ont montré que la structure des plantes en elle-même pouvait engendrer des changements dans la biodiversité du zooplancton. L'objectif du troisième chapitre était de comprendre comment la complexité structurelle de la VAS influençait la structure des communautés zooplanctoniques et la diversité fonctionnelle. Nous avons testé une méthode non destructrice pour évaluer les caractéristiques de l'habitat, notamment le couvert de VAS et sa complexité à partir de photos subaquatiques. Nous avons montré que l'utilisation de la photographie était un outil prometteur pour l'évaluation rapide du couvert et de la complexité de l'habitat en milieu aquatique. L'abondance de zooplancton était positivement reliée aux indices de couvert et de complexité de la VAS. La variation dans les traits du zooplancton crustacé était plus faible dans les habitats plus complexes. Une augmentation de la complexité de l'habitat n'aurait donc pas favorisé un trait fonctionnel en particulier dans la communauté. Bien que les indices de couvert et de complexité utilisés aient eu une influence sur les indices de diversité du zooplancton, il reste difficile de départager complètement les effets de la complexité de la VAS de l'effet du couvert offert par la VAS.

Dans un contexte où la VAS connaît une diminution importante dans le lac Saint-Pierre, la perte d'une dimension importante de la niche écologique du zooplancton que représente la VAS pourrait résulter en une perte de biodiversité taxonomique, mais aussi un risque de perte de redondance fonctionnelle au sein des communautés de zooplancton.

Mots clés : zooplancton, végétation aquatique submergée, lac peu profond, diversité fonctionnelle

ABSTRACT

Understanding the factors governing the dynamic of communities structure is crucial to ecological science and conservation of ecosystems. In aquatic environments, zooplankton are important elements in the aquatic food chain and are key to improve our understanding of the functioning of lake ecosystems as they respond quickly to changes in environmental conditions. In shallow lakes, submerged aquatic vegetation (SAV) constitutes structurally complex habitats that would favor a greater diversity of ecological niche available to zooplankton.

The general objective of this project was to understand how zooplankton communities are spatially organized in a heterogeneous submerged aquatic vegetation bed. Our goal was to understand the potential impacts of a decrease in SAV on taxonomic and functional diversity of zooplankton communities.

First, we used a landscape-scale approach to determine the relative importance of biotic and abiotic filters in the assembly of zooplankton communities using three consecutive years of monitoring (2012-2014; Chapter 1). The great interannual variability observed in environmental conditions had a significant impact on the strength and direction of the observed relationship between zooplankton species and environmental variables. However, functional traits present in the community responded similarly each year, suggesting functional redundancy in zooplankton traits. This chapter provides one of the first clue of how functional redundancy could act as an insurance policy in natural aquatic ecosystems by promoting the resilience of ecosystem functions.

In order to understand the impact of a decrease in SAV abundance, we focused on the relationship between SAV and zooplankton biomass along a SAV gradient during the summer of 2012 (Chapter 2). We used four functional diversity indices: richness, equitability, divergence and dispersion. Our results show that SAV explains 9% of the total variation in zooplankton biomass. Similarly, SAV explains 13% of the functional diversity of zooplankton. The results obtained showed that the dispersion of zooplankton species traits was related to the biomass of SAV while traits equitability was inversely related. Reducing the SAV abundance could therefore have a negative impact on the biomass and functional diversity of zooplankton, and on ecosystem functions due to the key role played by zooplankton in aquatic ecosystems.

Several studies have shown that plant structure itself can lead to changes in zooplankton biodiversity. The objective of the third chapter was to understand how the structural complexity of SAV influences the structure of zooplankton communities and functional diversity. We tested a non-destructive method to assess habitat characteristics, including SAV cover and complexity using digital imagery. Zooplankton abundance was positively related to SAV cover and complexity indices. Variation in crustacean zooplankton traits was lower in more complex habitats. Therefore, an increase in habitat complexity would not have favored a particular functional trait in the community. Although the cover and complexity indices had an influence on the zooplankton diversity indices, it remains difficult to completely separate the effects of SAV complexity to the effect of SAV cover. Nevertheless, the results of this chapter suggest that digital imagery could be a promising tool for the rapid assessment of SAV cover and complexity.

In a context where SAV is experiencing a significant decrease in Lake St. Pierre, the loss of an important dimension of the zooplankton niche represented by the SAV could result in taxonomic and functional diversity loss and decreasing functional redundancy within zooplankton communities.

Keywords : zooplankton, submerged aquatic vegetation, shallow lakes, functional diversity

INTRODUCTION

1.1 Théorie des communautés écologiques

Comprendre pourquoi certaines espèces sont trouvées ensemble à un moment et à un endroit donné fait partie d'une des plus vieilles questions en écologie. Pour répondre à cette question, Vellend (2016) a proposé la théorie des communautés écologiques (angl. : *theory of ecological communities*). Cette théorie intègre la dynamique d'assemblage d'espèces dans une communauté sous quatre processus généraux, soit la sélection, la dispersion, la dérive écologique et la spéciation. La composition d'une communauté dépend de différences de performance (angl. : *fitness*) entre les individus d'une espèce le long d'un gradient environnemental (sélection) ainsi que de leur capacité à se propager à partir des communautés voisines (dispersion). La dérive écologique fait référence aux paramètres démographiques qui entraînent le maintien ou l'extinction des populations locales, quelles que soient les différences de fitness ou les capacités de dispersion des espèces. Dans un contexte écologique où la dispersion n'est pas sévèrement limitée et où la spéciation est un processus relativement lent, la sélection et la dérive sont les deux principaux processus qui déterminent la composition des communautés.

Les processus de sélection sont associés à des filtres environnementaux qui agissent à différentes échelles spatiales et sont le résultat de pressions biotiques et abiotiques entraînant une variation du succès de reproduction entre les espèces et les individus (Zobel, 1997; Vellend, 2016). Alors que la théorie des métacommunautés s'est concentrée sur l'importance relative des processus spatiaux et environnementaux dans le contrôle des structures des communautés (Leibold et al. 2004; Cottenie, 2005), il est maintenant reconnu que les traits fonctionnels et les liens phylogénétiques doivent également être pris en compte pour fournir une compréhension plus complète des réponses des communautés face aux gradients environnementaux (Perez-Neto et al. 2012; Spasojevic et al. 2014; Gianuca et al. 2017).

Les liens phylogénétiques représentent les liens de parenté entre les espèces, mis en évidence par la présence de caractères dérivants d'un ancêtre commun. Ces liens sont représentés par des arbres phylogénétiques qui peuvent être construits de plusieurs manières, soit à partir de séquences génomiques (Nascimento et al., 2017) ou encore à partir de l'identité taxonomique des espèces.

Les relations phylogénétiques incorporent les caractéristiques à l'échelle des espèces avec lesquelles on peut calculer le degré de parenté entre celles-ci et utiliser cette information comme un indice de diversité phylogénétique (Vellend, 2011). La phylogénie et les traits des espèces ne sont pas indépendants puisque les traits sont le résultat de l'évolution. Il est donc attendu que les espèces reliées phylogénétiquement soient similaires en termes de traits et d'occurrence (Harvey et Pagel, 1991). Lorsque les traits des espèces ne sont pas bien définis, la phylogénie peut être utilisée comme substitut pour les traits contrôlant les niches trophiques (Vincent et al. 2020). Cependant, il arrive que les traits fonctionnels présents dans une communauté soient de meilleurs prédicteurs des fonctions écosystémiques que la phylogénie (Gianuca et al. 2017). Comprendre le contexte environnemental qui maximise ou minimise la diversité fonctionnelle de la communauté permet de mieux évaluer quelles conditions dans les milieux naturels pourraient exercer la plus forte influence sur la distribution des traits dans la communauté en agissant comme filtres.

Les traits fonctionnels sont des caractéristiques d'un organisme qui décrivent ses fonctions écologiques ainsi que ses réponses aux facteurs environnementaux (Diaz et Cabido, 2001). Ils peuvent être des traits morphologiques qui représentent des adaptations à différentes diètes ou différents habitats, des traits physiologiques (p. ex. la tolérance à la température), des traits reproductifs (p. ex. le nombre d'œufs et le diamètre des œufs) ou des traits comportementaux (p. ex. le comportement de migration ou les soins parentaux) (Bremner et al. 2003; Dumay et al. 2004). Ces traits fonctionnels peuvent caractériser la performance et les interactions des espèces et constituer des traits de réponse (angl. : *response traits*). Ils peuvent être utilisés pour expliquer l'assemblage des communautés le long de larges gradients environnementaux (Vogt et al. 2013). En revanche, les traits d'effet (angl . : *effect trait*) sont utilisés pour suivre les processus et les fonctions de l'écosystème. Par exemple, en utilisant la physiologie et la composition corporelle de l'organisme, il est possible d'extrapoler d'un individu à une évaluation du stock et du flux d'énergie à l'échelle de l'écosystème (Hébert et al. 2017). La valeur moyenne ou la variation des traits fonctionnels des organismes présents dans un écosystème donné permet de mesurer la diversité fonctionnelle.

Des données empiriques (Tilman et al. 1997) et théoriques (Loreau 2000) supportent l'idée que la diversité fonctionnelle peut affecter la dynamique de disponibilité des ressources dans les écosystèmes à court terme et la stabilité de l'écosystème à long terme. Deux mécanismes pourraient expliquer l’influence de la diversité fonctionnelle sur la dynamique de disponibilité des ressources, soit l’effet d'échantillonnage (angl.: *sampling effect*) et l’effet de complémentarité des niches. L'hypothèse de l’effet d'échantillonnage (Loreau, 1998; Diaz et Cabido, 2001) prédit que plus la richesse en espèces est élevée à un site donné, plus la probabilité d’avoir des espèces avec un trait particulier important pour le fonctionnement des écosystèmes est élevée. La théorie de la complémentarité des niches (Tilman et al. 1997; Loreau et Hector, 2001), quant à elle, stipule qu’une plus grande diversité taxonomique serait associée à un plus grand nombre de traits fonctionnels, ce qui permettrait une utilisation plus efficace des ressources dans un environnement spatialement et temporellement variable. Donc, plus le chevauchement entre les niches est réduit (c.-à-d. plus les traits sont complémentaires), plus fort devraient être les effets de la diversité sur le fonctionnement de l’écosystème (Diaz et Cabido, 2001). Il arrive que plusieurs espèces occupent la même fonction (redondance fonctionnelle), ce qui aurait aussi un impact sur la stabilité des écosystèmes à long terme. Par exemple, l’écosystème serait protégé contre une perte de fonction dans le cas où une espèce disparaîtrait. C’est ce qu’on appelle l’hypothèse de l’assurance fonctionnelle (angl. : *insurance hypothesis*) (Yachi et Loreau, 1999). La diversité fonctionnelle peut donc être utilisée comme indicateur des facteurs gouvernant l’assemblage des communautés et de l’impact des perturbations et/ou des gradients environnementaux sur la structure des communautés. De plus, elle peut servir d’indicateur des fonctions écosystémiques telles que la productivité, la résilience et le recyclage des nutriments (Villeger et al. 2008).

La complexité structurelle (CS) de l’habitat, qui se définit comme étant l’hétérogénéité dans l’arrangement des structures physiques, de leur diversité, abondance et densité dans l’habitat (Tokeshi et Arakaki, 2012), est reconnue pour avoir des effets sur tous les niveaux d’organisation, de l’individu aux communautés (Soukup et al., 2022). La CS de l’habitat joue un rôle dans l’écologie, la physiologie et le comportement des espèces animales qui y vivent (Shumway et al. 2007). Les organismes étant sensibles aux structures physiques des habitats, la disponibilité de ces structures a tendance à se refléter sur la fonctionnalité et l’organisation des communautés. Depuis MacArthur et MacArthur (1961), de nombreuses études ont montré que les habitats structurellement complexes peuvent supporter une diversité et une abondance plus importante que les habitats homogènes (Lapointe et Bourget, 1999; Bracewell et al. 2018; Soukup et al. 2022). Par exemple, l’étude de MacArthur et MacArthur (1961) met en évidence que la structure physique des communautés de plantes (c.-à.-d. comment le feuillage est distribué verticalement) est plus importante que la composition en espèces de plantes pour expliquer la diversité des espèces d'oiseaux. Des effets de la CS de l'habitat sur la diversité des espèces ont été trouvés notamment sur des arthropodes (Brose, 2003; Lassau et Hochuli, 2004), des mammifères (Williams et al. 2002), des amphibiens et des reptiles (Atauri et de Lucio, 2001). Une étude de Mellin et al. (2012) sur les poissons dans les récifs coralliens montre que la complexité de l'habitat explique en grande partie la richesse en espèce, l'abondance et la structure des communautés à plusieurs échelles dans les milieux marins. L'hypothèse prédisant une relation positive entre la CS de l'habitat et la biodiversité repose sur le concept de niche écologique, où la complexité de l'habitat contribue à la disponibilité des niches écologiques, soutenant une diversité d'organismes qui peuvent coexister dans un habitat donné (Pennak, 1957). Ainsi, une relation similaire est à prévoir entre la complexité de l'habitat et la diversité fonctionnelle, mais elle n'a encore jamais été montrée en milieu d'eau douce.

Plusieurs études ont montré des effets locaux de la CS, comme l'augmentation de la richesse et de l'abondance des espèces dans les habitats plus complexes (Kelaher et Castilla, 2005; Matias et al. 2010; Kovalenko et al. 2012). Cependant, la majeure partie de ces auteurs ont focalisé sur les effets au niveau des individus (p. ex. efficacité des prédateurs dans un gradient de complexité) plutôt qu'au niveau des communautés (Kovalenko et al. 2012). La taxonomie des organismes est communément utilisée, mais peu d'études ont analysé explicitement la relation entre la complexité structurelle et la diversité fonctionnelle. De plus, la majorité des études se sont intéressées à la complexité en milieu terrestre (Proulx et Parrott, 2008, 2009; Thebault et Fontaine, 2010), et beaucoup reste à faire en milieu aquatique.

1.2 Les communautés zooplanctoniques dans les lacs peu profonds

Les communautés de zooplancton d'eau douce sont reconnues pour être spatialement structurées et dynamiques dans le temps, étant influencées par de nombreux processus abiotiques (par ex. : acidification, eutrophisation et brunissement, Pinel-Alloul et al. 1990; Yan, 1986; Haberman et Haldna, 2014; Wissel et al. 2003) et biotiques (par ex. : prédation and compétition, Brook et Dodson, 1965; DeMott, 1989; Hu et Tessier, 1995) prenant place à différentes échelles spatiales (Pinel-Alloul, 1995; Pinel-Alloul et Ghadouani, 2007; Pinel-Alloul et al. 2021). Le zooplancton étant un maillon trophique important dans les réseaux trophiques aquatiques (Taranu et al. 2021), ils sont des organismes modèles clés pour comprendre comment les processus naturels et anthropiques influencent les patrons de diversité, la distribution des espèces ainsi que leurs fonctions.

Dans les dernières années, l'approche basée sur les traits a été de plus en plus utilisée pour déterminer la diversité fonctionnelle du zooplancton dans les écosystèmes lacustres (Barnett et al. 2007; Barnett et Beisner, 2007). Le zooplancton étant des consommateurs primaires et secondaires dans les écosystèmes aquatiques, ils montrent une grande diversité de traits et de stratégies alimentaires qui impactent les autres niveaux trophiques et les flux de matériel et d'énergie (Litchman et al. 2013). Une récente compilation des traits du zooplancton révèle cependant qu'il y a encore beaucoup à faire pour avoir une base de traits complète (Hébert et al. 2016). L'approche basée sur les traits a été utilisée soit de manière théorique (Hébert et al. 2017), ou encore pour comparer les communautés zooplanctoniques de plusieurs lacs différents, et donc sur une échelle régionale (Litchman et al. 2013; Vogt et al. 2013). À notre connaissance, aucune étude ne s'est penchée sur la variabilité spatiale et temporelle de la diversité fonctionnelle du zooplancton au sein d'un écosystème lacustre.

Dans les lacs peu profonds, la végétation aquatique submergée (VAS) jouerait également un rôle très important dans la structuration des communautés zooplanctoniques en leur offrant entre autres un refuge contre la prédation par les poissons planctivores et en leur fournissant des niches écologiques diversifiées. Le zooplancton y effectue des migrations horizontales journalières entre les eaux libres et la VAS afin de trouver refuge contre la prédation par les poissons zooplanctivores (Timms et Moss, 1984, Schriver et al. 1995). La VAS aurait un effet structurant sur les communautés zooplanctoniques car la pression de prédation sur les gros individus y serait réduite (Brooks et Dodson, 1965). L'explication la plus retenue pour expliquer ce phénomène est que la densité de la VAS agirait en diminuant le champ visuel des poissons, réduisant ainsi le pourcentage de rencontre entre le zooplancton et les poissons (Manatunge et al. 2000).

La CS de l'habitat aurait des impacts potentiels importants sur les interactions prédateurs-proies (Schriver et al. 1995, Kovalenko et al. 2012). En augmentant la CS de l'habitat, la VAS diminuerait la capacité de nage des poissons et la probabilité de détection des proies (Heck et

Crowder, 1991, Manatunge et al. 2000). Cet effet serait indépendant de l'augmentation de la densité des tiges associée à une abondance accrue de la VAS, comme l'ont démontré Warfe et Barmuta (2004) à l'aide de macrophytes artificiels. Une augmentation de la CS de l'habitat aura donc pour effet de réduire la pression de prédation sur le zooplancton de grande taille, entraînant une augmentation générale de la taille des individus au sein de la communauté (Bonecker et al. 2011).

La présence de VAS favorise le zooplancton non seulement en réduisant l'efficacité de prédation des poissons zooplanctivores, mais aussi en favorisant la présence de poissons piscivores de grande taille dans la zone littorale, avec des conséquences sur l'abondance et l'activité des poissons zooplanctivores (Burks et al. 2002). Bien que l'efficacité du refuge pour le zooplancton diminue avec l'augmentation de la densité des poissons zooplanctivores (Schriver et al. 1995, Manatunge et al. 2000, Burks et al. 2001) et des prédateurs benthiques tels que les macroinvertébrés (Vetti Kvam et Kleiven, 1995, Sagrario et al. 2009), la VAS n'en demeure pas moins un élément clé dans le maintien des communautés zooplanctoniques, notamment dans les systèmes fluviaux où elles empêchent le courant d'entraîner le zooplancton (Basu et al. 2000).

La réduction du risque de prédation pourrait donc expliquer en partie la très grande diversité taxonomique et fonctionnelle de zooplancton qu'on observe dans la VAS comparativement à la zone pélagique (Walseng et al. 2006). Deux autres facteurs clés pourraient expliquer cet effet sur la biodiversité, soit une plus grande hétérogénéité de l'habitat (c.-à-d. la composition spatiale et la configuration des conditions environnementales) ainsi qu'une plus grande CS dans la zone littorale que dans la zone pélagique. La présence de niches écologiques différentes serait en fait favorisée par l'hétérogénéité de l'habitat, en permettant de maintenir un plus grand nombre d'espèces que dans l'habitat pélagique. Cette plus grande diversité du zooplancton devrait être associée à une plus grande diversité de traits fonctionnels, favorisant en retour une plus grande efficacité dans l'utilisation des ressources (Willis et al. 2005, Mellin et al. 2012). Dans le cas du zooplancton, cela pourrait se traduire par un meilleur contrôle du phytoplancton car une gamme plus large de spectres de tailles pourrait être broutée (Ye et al. 2013).

1.3 Contexte et objectif de la thèse

Les herbiers de VAS en milieu d'eau douce sont en déclin partout dans le monde, dû aux stress naturels (changement climatique) et anthropiques (par ex. : un enrichissement important en nutriment) auxquels ils sont soumis (Zhang et al. 2017; Hudon et al. 2018). Notre étude a été réalisée au Lac Saint-Pierre (LSP), un grand lac fluvial peu profond qui supporte le cinquième des marais et marécages du fleuve Saint-Laurent (Québec, Canada). Étant bordée par des zones d'agriculture intensive, sa zone littorale n'échappe pas aux perturbations causées par les activités anthropiques en plus d'être vulnérables aux variations des niveaux d'eau (Hudon, 1997). Sur la rive sud du LSP, l'enrichissement organique provenant des bassins versants des rivières Yamaska et Saint-François (deux des principaux tributaires du LSP) ainsi qu'un apport important en nutriments favoriserait le développement d'une cyanobactérie diazotrophique, *Lyngbya wollei* (Levesque et al. 2012), coïncidant avec une faible biomasse de VAS (Hudon et al. 2018). Selon les données sur la distribution de la VAS dans ce système, les tapis de VAS couvraient une grande partie de sa superficie il y a seulement une décennie. En effet, une étude récente montre que la probabilité de rencontrer de la VAS dans le LSP est passée de 60% en 2007 à seulement 20% en 2021 (Laporte et al. en prép). Par conséquent, cet écosystème subit une diminution de la CS de l'habitat (Levesque et al. 2012) et une homogénéisation de l'habitat. On peut donc se questionner sur l'influence de la CS de l'habitat et de son homogénéisation sur la structure des communautés zooplanctoniques du LSP. À notre connaissance, aucune étude ne s'est penchée précisément sur l'impact de l'homogénéisation de la CS sur la structure et la diversité fonctionnelle des communautés de zooplancton au sein des écosystèmes lacustres.

L'objectif général de ce projet est i) de comprendre comment les communautés de zooplancton sont organisées dans l'espace et dans le temps dans un herbier de végétation aquatique submergée hétérogène et ii) de comprendre les impacts d'une diminution de l'abondance de la VAS et d'une homogénéisation de l'habitat sur la diversité taxonomique et fonctionnelle des communautés zooplanctoniques.

Dans le cadre de cette thèse, nous avons utilisé deux échelles différentes afin de tester nos hypothèses. Dans un premier temps, nous avons analysé dans les chapitres 1 et 2 la structure des communautés avec une approche à l'échelle du paysage (26 km^2). Nous avons appliqué un modèle conjoint de distribution des espèces (angl. : *joint species modeling approach*) afin d'explorer comment les communautés zooplanctoniques sont organisées dans le temps et dans l'espace à travers des herbiers de VAS (Chapitre 1). Cette approche nous a permis de modéliser la co-occurrence des espèces sur 3 années de suivi (2012 à 2014), tout en intégrant la phylogénie et les traits fonctionnels des espèces.

Deuxièmement, nous avons examiné plus spécifiquement la relation entre l'abondance de la VAS et les caractéristiques clés des communautés zooplanctoniques (abondance, diversité taxonomique et fonctionnelle) pendant l'été 2012 (Chapitre 2). Un partitionnement de la variation nous a permis d'estimer l'importance relative de différentes variables dans la structuration des communautés zooplanctoniques.

Finalement, afin d'isoler l'impact de la structure physique de la VAS sur la structuration des communautés zooplanctoniques, nous avons analysé l'effet du couvert végétal et de la complexité structurelle (CS) de la VAS sur la diversité taxonomique et fonctionnelle du zooplancton à une échelle fine (150 m^2) en appliquant une approche *in situ* de photographie subaquatique (Chapitre 3). Ceci nous a permis de contrôler l'effet confondant que pourraient avoir les variables spatiales et environnementales qui covarient avec la VAS à de plus grandes échelles (p. ex.: profondeur, variables physico-chimiques, etc.) sur les communautés zooplanctoniques.

Cette thèse, en faisant le lien entre la diversité taxonomique et fonctionnelle du zooplancton et la VAS, contribue à mieux comprendre les processus écologiques qui se déroulent dans les lacs peu profonds tout en intégrant les variations extrêmes des conditions environnementales qui peuvent survenir dans les zones littorales des grands lacs fluviaux. En raison du rôle clé du zooplancton dans les écosystèmes aquatiques, la réduction de la VAS pourrait avoir un impact négatif important sur les fonctions écosystémiques et les niveaux trophiques supérieurs.

CHAPITRE 1

TAXONOMIC, FUNCTIONAL AND PHYLOGENETIC TRAITS EXPLAIN NICHE RESPONSES OF CRUSTACEAN ZOOPLANKTON COMMUNITIES IN SUBMERGED AQUATIC VEGETATION BEDS

Cet article sera soumis pour publication à la revue *Ecology and Evolution* en janvier 2023

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1.1 Abstract

In this study, we used information on zooplankton functional traits and phylogeny within a joint species distribution modeling (JSDMs) framework to explore how crustacean zooplankton communities are organized across a heterogeneous submerged aquatic vegetation (SAV) bed of a large, shallow fluvial lake (Lake Saint-Pierre, Québec, Canada). We also evaluated whether spatial patterns changed over time, by sampling the zooplankton communities over the span of three summers (2012-2014) at approximately 30 sites along the south shore of the lake. We investigated how biotic and abiotic processes shaped species co-responses and determined metacommunity dynamics characterized by among-year variation in hydrological conditions. Across the entire dataset, we noted a total zooplankton richness of 72 taxa, where the cladocerans were largely represented by macrophyte-associated taxa – *Bosmina*, Chydoridae (*Chydorus*, *Pleuroxus*, *Camptocercus*, *Eurycercus*), and Sididae (*Diaphanosoma brachyurum*, *Sida crystallina*). Copepods were represented by one calanoid (*Eurytemora carolleeae*) and three cyclopoids (*Acanthocyclops robustus, Eucyclops agilis*, *Mesocyclops edax)*. Both abiotic (water conditions) and biotic (SAV habitat and filamentous algae) factors were found to be important drivers of the variation in zooplankton communities. Albeit their relative importance changed over the years, environmental gradients in trophic status (calcium, nutrients, and chlorophyll *a*) and dystrophy (DOC, water color) had a major influence on zooplankton niche dimensionality. SAV was another key environmental factor explaining the environmental niche of the Chydoridae and Sididae. An important proportion of the variance in species niches was explained by functional traits and, even though the identity of the most abundant species changed over years, species traits responded similarly to environmental gradients, suggesting a functional redundancy across time. Our application of state-of-the-art modeling framework helped highlight the extent to which traits can explain the variation among species in their responses to both abiotic and biotic factors.

Keywords:

JSDM, littoral zooplankton, ecological niches, functional traits, phylogeny, macrophytes, shallow lakes, abiotic and biotic drivers.

1.2 Introduction

A key objective in ecology is to obtain an integrative understanding of how abiotic and biotic factors are linked to community structure, including taxonomic, functional and phylogenetic attributes, over space and time (Gianuca et al. 2017; Ovaskainen et al. 2017; Vincent et al. 2020). Whereas the metacommunity approach has focused on the relative importance of spatial and environmental processes in controlling community structure based on species assemblages (Liebold et al. 2004; Cottenie, 2005), it is now recognized that functional traits and phylogeny should also be considered to provide a more complete understanding of community responses to environmental gradients (Spasojevic et al. 2014; Gianuca et al. 2018; Peres-Neto et al. 2012).

Patterns in biodiversity and species coexistence are the results of multiple interacting processes such as evolutionary history, trait variation, species interactions, dispersal limitations, environmental variation and landscape heterogeneity (Peres-Neto et al. 2012). The scale at which these processes act upon organisms and communities, however, varies among ecosystem types (e.g., terrestrial and aquatic) and trophic levels. In aquatic ecosystems, though broad-scale processes such as evolutionary history and dispersion tend to impact higher trophic levels, primary producers are most likely limited by environmental filtering (Beisner et al. 2006). Zooplankton, which find themselves as a trophic link embedded in the middle of aquatic food webs, respond to both abiotic (e.g., acidification, eutrophication, and browning, Pinel-Alloul et al. 1990; Yan 1986; Haberman and Haldna 2014; Wissel et al. 2003) and biotic (e.g., predation and competition, Brook and Dodson 1965; DeMott 1989; Hu and Tessier 1995; Bolduc et al. 2016; 2020) factors taking place at different scales (Pinel-Alloul et al. 1995). They thus represent key model organisms to track the effect of both abiotic and biotic processes on the co-occurrence of taxonomic and functional groups across the limnoscape (Taranu et al. 2021).

Functional diversity can be measured from the functional traits of species, linking these attributes to ecosystem function (e.g., anti-predator defense, habitat type, and trophic group; Barnett et al. 2007). These functional traits can characterize species performance and interactions and constitute “response traits” used to explain how communities assemble along broad environmental gradients (Vogt et al. 2013). In contrast, “effect traits” are used to track ecosystem processes and functions, that is, using organismal physiology (e.g., excretion, egestion, respiration, growth) and body composition (size and elemental requirements) they allow one to extrapolate from an individual to an ecosystem-wide assessment of energy stock and flux (Hébert et al. 2017). Indeed, zooplankton are important primary and secondary consumers in aquatic ecosystems, exhibiting a high diversity of traits and feeding strategies which impacts other trophic levels and the cycling of materials and energy (Litchman et al. 2013). A recent compilation of zooplankton traits revealed a knowledge gap in currently available and studied traits (Hébert et al. 2016). Consequently, many traits are derived from knowledge on the closest taxa (e.g., Bolduc et al. 2016). When traits are not well defined, phylogeny can be used as a surrogate for traits controlling trophic niches (Vincent et al. 2020). Integrating traits and phylogeny in community metrics may thus provide deeper insight in species assembly processes across large spatial scales (Gianuca et al. 2016).

In this study, we applied a Joint Species Distribution Modeling (JSDMs) approach, making use of the Hierarchical Modeling of Species Communities (HMSC) framework outlined in Ovaskainen et al. (2017), to explore how zooplankton communities are organized in space and time across a heterogeneous submerged aquatic vegetation (SAV) bed. Our conceptual framework (Figure 1) aimed to investigate how abiotic and biotic processes shape species co-responses (based on abundance data) and determine metacommunity dynamics over the span of three summers (2012-2014) that vary in hydrological conditions. Whereas we did not analyze explicitly interannual differences here, we used this multi-year sampling as an occasion to test the consistency of the zooplankton responses over time. To account for the functional structure, we used a set of response and effect traits measured directly on zooplankton species or derived from the literature. Finally, we used zooplankton taxonomy to create a phylogenetic tree that accounted for phylogenetic dependencies among species. The ultimate study goal was to determine how much variation in zooplankton community structure is determined by abiotic (water conditions) and biotic (aquatic vegetation) factors and to understand the relative importance of functional traits and phylogeny in determining the observed environmental niche space. In particular, we examined the role of aquatic vegetation (SAV and filamentous algae) as a driver of zooplankton taxonomy and function, relative to the effect of water quality (nutrients, chlorophyll *a* and transparency), hydrology and lake morphometry (water flow and depth).

1.3 Methods

1.3.1 Study system and sampling design

We sampled crustacean zooplankton communities across the same set of stations over three consecutive summers (24, 32 and 34 stations in 2012, 2013 and 2014, respectively) on the south shore of LSP. This system is a large (≈ 300 km^2), shallow (mean depth = 3 m) fluvial lake of the St. Lawrence River, Quebec, Canada (Figure 2). It is characterized by two extensive shallow littoral zones, separated by a deep (> 11 m) navigation channel. The water flow along this channel limits zooplankton dispersal between the northern and southern shores (Basu et al. 2000). Zones of emergent and submerged aquatic vegetation (SAV) cover approximately 70% of the lake area (Jean and Létourneau, 2014). SAV is mainly dominated by *Vallisneria americana* Michx. and *Potamogeton richardsonii* (A. Benn) Rydb (Bolduc et al. 2016). Since the late 1980s, SAV abundance has declined in LSP (Giacomazzo et al. 2020). In the last decade, the study area was found in some occasions to be largely colonized by benthic cyanobacteria, which coincided with reduced SAV biomass, a phenomenon considered as a symptom of ecosystem degradation (Lévesque et al. 2012; Hudon et al. 2014). This led to a pronounced heterogeneity in the SAV beds, where some areas are composed of dense vegetation while others have sparse to none.

We selected sampling stations placed on a regular grid (500 m ca.) in an area covering roughly 26 km^2 (Figure 2). Sampling was carried out during the daytime (between 7 a.m. and 5 p.m.) over a single week at approximately the same period each year, i.e., at the beginning of August, which corresponds to the maximum abundance and growth of SAV beds.

1.3.2 Environmental variables

The *a priori* selection of environmental variables was based on the literature and their importance as environmental drivers of zooplankton (Table 1). These variables have been shown to govern the growth and productivity of zooplankton (total dissolved nitrogen, TDN; total dissolved phosphorus, TDP; and calcium concentrations, Ca), the risk of predation (water color, A440nm; suspended particulate matter, SPM; and SAV), their preferred habitat (water depth and water flow) and availability of food and shelter resources (chlorophyll-*a*, Chl*a;* dissolved organic carbon, DOC; SAV and filamentous algae).

At each station and on each year, water depth, water flow and physico-chemical water conditions were measured *in situ* as described in Bolduc et al. (2016). Filtration and analysis methods used for nutrients (TDN and TDP) are described in D'Arcy and Carignan (1997). The calcium ions (Ca2+; hereafter Ca) were measured by ion chromatography (Dionex DX-500). Water color was measured at 440 nm absorbance following methods used by Cuthbert and Del Giorgio (1992). To determine DOC concentrations, water was filtered using a 0.45 µm syringe filter (Nalgen SFCA). Filters were then stored in acid-washed vials at 4°C prior to analysis and placed in a wet persulfate oxidation solution. DOC analysis was performed using an Aurora 1030 TOC Analyzer equipped with an auto sampler (model 1088, IO Analytical Instruments). SPM was determined by water filtration on pre-burned 25 mm diameter Whatman GF/F filters (nominal pore size 0.7 mm) until saturation (< 15 PSI). Filters were weighted before and after filtration on a balance (± 0.0001g) and results were reported in mg/L. To determine Chl*a* concentrations, water was filtered with a 25 mm diameter Whatman GF/F filters (nominal pore size 0.7 mm). Filters were kept frozen until analysis. Chl*a* extraction was done overnight and in the dark with 95% ethanol. Spectrophotometric analyses of the solution were performed as in Bergmann and Peters (1980). We used Lorenzen equations (Lorenzen, 1967) to calculate Chl*a* concentration. At each station, SAV was harvested with a double-head rake (35 cm wide) (Yin et al. 2000) dragged over approximately 1 m (sampling area of 0.35 m^2). Vascular macrophytes were identified at the species level and reported in g m^{-2} of dry weight. Dry weight of filamentous chlorophytes and benthic cyanobacterium *Lyngbya wollei* were also measured. To visualize environmental heterogeneity and to discriminate the most important factors, we ran a principal component analysis (PCA) of the environmental matrix for each year.

1.3.3 Crustacean zooplankton community sampling and analyses

Crustacean zooplankton community was sampled using a submersible pump (Rule^{TM}, model 1500) (Masson et al. 2004) to integrate water both vertically and horizontally by gently oscillating the pump up and down the water column while moving it from one side to the other of the boat. The pump was connected to a digital water flow meter (Gardena^{TM}, model 9188) to obtain a precise estimation of the volume of water collected, which was subsequently filtered with a zooplankton net (153 µm mesh size). This method allowed us to collect all crustaceans from a large volume of water (approx. 200 L per station) to offset the relatively low density of crustacean zooplankton found in LSP (Bolduc et al. 2016; Bolduc et al. 2020). The use of a large mesh-size net may have resulted in loss of small organisms such as nauplii, but it was necessary to prevent the net from clogging due to plant detritus. Zooplankton organisms were narcotized in water saturated with carbon dioxide and fixed in a 4% sugar-formaldehyde solution prior to identification (Prepas, 1978). Crustacean zooplankton identification was conducted at the species level when possible, using the identification keys of Edmondson (1959), Haney et al. (2010), and Thorp and Covich (2009) for the cladocerans, and Edmondson (1959), Smith and Fernando (1978), and Hudson et al. (2003) for the copepods. Within each sample, the length of the first 30 individuals of each crustacean species was measured to determine the mean biomass of each species based on length-weight specific relationships (Malley et al. 1989). Species assemblages and community composition, frequencies of occurrence and mean abundance and biomass of each species were likewise quantified (Table S1).

1.3.4 Zooplankton functional traits

To build the zooplankton species traits matrix, each species was classified according to six functional traits based either on direct measurements (mean dry weight and maximum length) or data retrieved from the literature (swimming capacity, habitat preference, feeding type and trophic level) (Barnett et al. 2007; Massicotte et al. 2014)

(Table S2). Since functional traits of zooplankton are rather scarce in the literature, we selected these traits to obtain the most complete database possible. Given the lack of precise information at the species/genus level for most taxa, the broad taxonomic group (i.e., cladocerans, calanoids, cyclopoids and harpacticoids) of each individual was used as a proxy for the trait *swimming capacity* (Drenner, 1980). This trait was classified into three levels, namely “poor”, “intermediate” and “good” swimmers. The trait *habitat* refers to the preferred habitat of the species (“littoral”, “generalist” or “pelagic”). The trait *feeding type* was classified into five levels, namely “filtration”, “stationary suspension”, “surface feeding”, “grasping” and “current-cruiser”. Finally, the trait *trophic guild* was separated in four levels, either “detritivore”, “herbivore”, “omnivore” and “carnivore”. Nauplii and copepodite stages were considered as distinct “functional species” from adults because of their smaller size and trophic habits (Reid and Williamson, 2010).

1.3.5 Zooplankton phylogeny

To account for the phylogenetic dependencies among species, we included a fourth matrix consisting of the taxonomic tree (as a proxy for the phylogenetic tree) among zooplankton species, as recommended by Ovaskainen and Abrego (2020). The taxonomic tree was calculated under the Brownian motion model of evolution (Paradis and Shliep, 2019) and represents the shared phylogenetic path length among species. In the calculated matrix, the diagonals represent the total distance of each species from the root of the tree while the off-diagonals elements are the total branch lengths shared by particular pairs of taxa (Harmon, 2019). We expected that if phylogeny had a strong relationship with species niches, species taxonomically close to one other would have similar traits compared to taxonomically distant species. Thus, if functional traits included in the model were relevant, then the parameter ρ measuring the importance of the phylogenetic signal in explaining model residuals would be zero (non-significant). In contrast, if these traits were irrelevant, then the phylogenetic signal would account for a significant proportion of the structure remaining in the residuals (i.e., parameter ρ would be greater than zero and the relevant traits influencing species niches would be assumed to be missing from the model; Ovaskainen and Abrego, 2020).

1.3.6 Joint Species Distribution Modeling (JSDM) via Hierarchical Modeling of Species Community (HMSC)

We applied the Hierarchical Modeling of Species Community framework (HMSC; Ovaskainen et al. 2017; Ovaskainen and Abrego, 2020) to identify the drivers of zooplankton community structure in LSP. HMSC is a JSDM (Warton et al. 2015; García-Girón et al. 2021) allowing to model community data based on species traits and environmental covariates by considering phylogenetic relationship among species (Ovaskainen and Abrego, 2020) together with the spatio-temporal context of the study.

Separate HMSCs were run for each year to highlight year-to-year variability in zooplankton communities and environmental gradients (i.e., water flow, SAV cover, etc.). To avoid convergence problems and develop more robust models, in each annual model we withdrew species present in less than three sampling sites. We used the individual sites visited as the unit of sampling in each model (thus 24, 32 and 34 sites in 2012, 2013 and 2014, respectively). The abundance of each species, reported as number of individuals per liter, present in the sampling sites was used as the response variable in our models (Y matrix; Figure 1). To reduce asymmetry in the zooplankton species biomass data and meet the model assumptions (i.e., residuals normally distributed), we log-transformed the response matrix.

Selected environmental variables (X matrix; Figure 1 and Table 1) were considered as fixed effects in the models. To improve model fit, we reduced the asymmetry in heavily skewed environmental variables (SPM, Chl*a*, water flow, SAV and filamentous algae) using a log transformation. The same explanatory variables were log-transformed in all three years to ease interannual comparisons of the results. To test for spatial non-independence among sampling units, we included sampling site coordinates as a random effect. Here, we utilize spatially structured latent variables as proposed by Ovaskainen et al. (2016).

Finally, species functional traits and phylogeny were used to aid the estimation of species niches (Ovaskainen and Abrego, 2020). For each year, we built a taxonomic tree from the function *as.phylo.formula()* in the "ape" package (Paradis and Schliep, 2019) from a set of nested taxonomic variables. Based on the taxonomical tree produced, a correlation matrix was obtained with the function *vcv()* of the same package. We relied on the classification of the Integrated Taxonomic Information System (ITIS, 2022) when different resources had a disagreement regarding taxonomy. Nauplii and copepodites were classified as distinct functional species among the copepod families, assigning cyclopoid nauplii and copepodites to the *Cyclopidae* family and calanoid nauplii and copepodites to the *Temoridae* family. Zooplankton species traits and phylogenetic relationship were considered as a fixed effect in the HMSC models.

Using all above-listed variables, we fit the HMSC models using the function *Hmsc()* in the HMSC R-package (Tikhonov et al. 2020 and 2021) assuming the default prior distribution as described in Ovaskainen and Abrego (2020). We sampled the posterior distributions with two Markov Monte Carlo chains (MCMC), for a total of 7 500 iterations. We selected 1 000 posterior samples per chain (n = 2000) and recorded every 5th step (thin = 5) of the iterations. We evaluated MCMC convergence by examining the potential scale reduction factors of the model parameters (Gelman and Rubin, 1992a,b). The scale reduction factors should be close to 1, indicating that the two chains gave consistent results. The explanatory power of each model (coefficient of determination or R^2) was obtained by comparing the observed to predictive values.

To quantify the drivers of community structure, we partitioned the variation explained among the fixed and random effects of the models. We examined the positive or negative response of each species to each environmental variable with at least 95% posterior probability, as well as the influence of traits on species niches. To further examine the interaction among niche dimensionality and traits, we investigated how the community-weighted mean (CWM) trait values behaved over the environmental gradients. All statistical analyses were performed within the R computing environment (R Core Team, 2021, version 4.1.1).

1.4 Results

1.4.1 Environmental conditions in a highly variable system

Inter-annual variability in environmental conditions at our study sites was highly variable and strongly influenced by spring floods coming from the Great Lakes and the Yamaska and St.-François Rivers (Figure 2). The summer of 2012 was characterized by historically low water levels compared to 2013 and 2014, which explains why water depths were two-fold lower in 2012 relative to 2013 and 2014 (Table 1; historical data available at: meds-sdmm.dfo-mpo.gc.ca). However, given to the presence of dense SAV beds in the area, the water flow was generally low during the three years (Table 1). Nutrients concentrations were high, with the highest concentration found in 2013 while TDP was significatively lower in 2013 compared to 2012 and 2014 (Table 1). Calcium concentrations were also high, with a significantly higher concentration in 2014. In contrast, water color was significantly lower in 2014 (Table 1). Despite a similar water level in 2013 and 2014, SPM was significantly higher in 2014 compared to 2013. Chl*a*, used as a proxy for algal resources, did not vary significantly during the three-year survey, whereas DOC, used as proxy for the microbial loop, was significantly lower in 2014. SAV abundance tended to be higher in 2013 compared to 2012 and 2014 while the filamentous algae tended to be less abundant in 2014 relative to 2012 and 2013 values (Table 1). However, annual variation in SAV and filamentous algae was not significant due to a large proportion of stations without vegetation and extreme values in some years (SAV in 2013, filamentous algae in 2012 and 2013) (see Figure S1 for the distribution maps of SAV and filamentous algae in each year).

The first two axes of the environmental PCA accounted for ~50% of the variation among study sites across years (70% in 2012, 53% in 2013, and 47% in 2014) and suggested important environmental interannual heterogeneity (Figure 3; see Figure S1 for spatial distribution of water variables in each year). For example, in 2012, Chl*a*, SPM, SAV and Ca concentrations contributed the most to PCA axes 1 and 2. Shallow waters were related to an increase in nutrients concentration (TDN and TDP) and in water color (A440nm and DOC; PCA1). However, as the water depth did not exceed 1.5 meters in

2012 (Table 1), SAV distribution was poorly related to the physical characteristics of the study area (water depth and water flow). Higher algal biomass (Chl*a*) and SAV biomass were rather positively related to suspended particulate matter (SPM) and TDN (PCA2). Filamentous algae biomass was negatively related to water flow and Ca concentration but tended to correlate with nutrients (TDP), water color and DOC (PCA1). In 2013, the gradients of water depth, water color (A440nm), DOC, TDN, Chl*a* and Ca concentration were the best contributors to environmental heterogeneity among sites. Water flow was positively related to Ca and SPM while TDP was negatively related to water color (A440nm) and DOC (PCA1). As in 2012, Chl*a* and SAV was positively related to TDN, but they were negatively related to water depth (PCA2). In 2014, the environmental variables showing the greatest variation were those associated with productivity (TDN and TDP), Ca concentration, DOC and water color (Figure 3). The biomass of SAV was higher in shallow, stagnant waters with low concentrations of nutrients (TDN, TDP) and SPM (PCA1), while Chl*a* was positively related to Ca but negatively related to water color and DOC (PCA2). In summary, the year 2012 was characterized by shallow and colored waters, with a negative gradient of SAV and nutrients from upstream to downstream. The years 2013 and 2014 were characterized by a higher water level, with a large gradient in SAV biomass in 2013 but a much lower SAV biomass in 2014 despite higher water transparency (Figure S1).

1.4.2 Crustacean zooplankton community structure and heterogeneity among years

We identified 72 zooplankton taxa (species and genera) over the three-year study period, including 40 cladocerans, 2 calanoid copepods, 23 cyclopoid copepods, and 7 harpacticoid copepods, not accounting for nauplii and copepodite stages (see Table S1 for details). The observed diversity was 62 species in 2012 (35 cladocerans, 2 calanoids, 18 cyclopoids, 7 harpacticoids), 40 species in 2013 (28 cladocerans, 1 calanoid, 8 cyclopoids and 3 harpacticoids) and 39 species in 2014 (22 cladocerans, 1 calanoid, 12 cyclopoids and 4 harpacticoids) (Table 2). After removing rare species (three or less occurrences in each year), 36, 17 and 21 species in 2012, 2013 and 2014 were respectively considered in our models.

Total zooplankton abundance was twice as high in 2012 relative to 2013 and 2014, with respectively 1894, 846 and 861 ind.L^{-1}. Total biomass was also greater in 2012 than in 2013 and 2014, with respectively 1432, 612 and 191 µg.L^{-1} (Table 2, Table S1). The total biomass observed in 2014 was lower than in 2013 despite a similar abundance of individuals, suggesting that the species and stages present in 2014 were smaller. Indeed, the abundance of the large Daphnidae, Chydoridae and Sididae was greatly reduced in 2014 (Table S1). Cladocerans and cyclopoid copepods were dominant in 2012 accounting for 45% and 52% of the total crustacean abundance and 68% and 28% of the total crustacean biomass, respectively (Table 2). The dominance of the cyclopoid copepods increased in 2013 and 2014, both in abundance (82-95%) and biomass (49-68%) while the cladocerans declined (2-13% in abundance, 23-49% in biomass). Calanoids were found in low abundance and biomass over the three-year survey and harpacticoids were very scarce (Table 2). The nauplii stage of cyclopoid and calanoid has increased over the years, representing respectively 36%, 63% and 90% of total zooplankton abundance in 2012, 2013 and 2014.

A few taxa of zooplankton were widely distributed across the study sites (Table S1). Among the cladocerans, *Bosmina* sp. (99% of sites), *Diaphanosoma brachyurum* (94%), *Sida crystallina* (79%), *Ceriodaphnia* (55%), and the Chydoridae (*Chydorus* sp., *Eurycercus lamellatus*, *Alona* sp. *Camptocercus* sp. and *Pleuroxus* sp. in 2012) were the most common. Copepods were widely represented by one species of calanoids (*E. affinis,* 79% of sites), and three species of cyclopoids (*A. robustus,* 90%; *E. agilis*, 42%; and *M. edax*, 37%). Calanoid and cyclopoid nauplii (68 and 99%, respectively) and copepodites (87 and 98%, respectively) were also commonly found. Over all the years studied herein, these widely distributed taxa contributed the most to the spatial variation in zooplankton community and showed important variation in abundance and biomass among years (Table S1, Figure S2). Considering abundance estimates, some cladocerans (*Bosmina*, *S. crystallina*, *Chydorus*), copepodite and nauplii stages of cyclopoids and calanoids (mainly *A. robustus* and *E. affinis*) explained most of the spatial variation in zooplankton communities. Considering biomass estimates, the contribution of large Chydoridae (*E. lamellatus, Camptocercus rectirostris, Acroperus* sp.) was particularly important in

2012, while that of other cladocerans (*Bosmina*, *S. crystallina*) and cyclopoid copepods (mainly *A. robustus*) was more important in 2013 and 2014.

1.4.3 Examining the environmental niche dimensions of the zooplankton community

The three yearly models showed that the abundance and composition of zooplankton taxa were well explained by the environmental variables, with R^2 of 0.67, 0.63 and 0.59 for 2012, 2013 and 2014, respectively (Figure 4). The potential scale reduction factors for the β-parameters (i.e., slopes of environmental variables) was close to one for the three models (1.01, 1.01 and 1.00 for 2012, 2013 and 2014, respectively), suggesting that the degree of consistency among the two MCMC chains was high and the models converged well.

Variance partitioning showed that sampling site coordinates, included in the model as a random effect, accounted for less than 15% of the variation in zooplankton abundance on average, and explained little of the variance for most species every year (Figure 4). However, it did explain 50% or more of the variation of a few species in 2012 (*Chydoridae* sp., *Nitokra hibernica*) (Figure 4A). This situation also occurred in 2013, where two species (*E. lamellatus*, *E. agilis*) were poorly explained by the environmental covariates (Figure 4B). However, these species did not represent a large percentage of the zooplankton abundance (Table S1). Overall, the models indicated that there was no spatial collinearity between sites as the spatial scale parameters of the first two leading latent factors showed that the variation occurred at a scale of 0 km (i.e., the leading factors are non-spatial, and the variation is independent among sampling sites).

The relative importance of the environmental variables shaping zooplankton communities were clearly different from year to year (Figure 4). In 2012, calcium concentration was the most important driver, followed by water colour (A440) (Figure 4A). These two variables accounted respectively for 13.9 % and 13.0% of the variance in zooplankton abundance on average. SPM and DOC both explained on average 8.8 % of the zooplankton variation. Algal biomass (Chl*a*) and the physical descriptors of the environment (water flow and water depth) had a similar contribution (7%) across species.

SAV and filamentous algae biomass were less important (< 5%) in shaping the zooplankton community structure during the summer of 2012. For the most abundant taxa (*Bosmina*, *Chydorus*, cyclopoid copepodites and nauplii, in bold in Figure 4A), abiotic environmental factors associated to water quality (TDN, TDP, Ca), color and turbidity (DOC, A440nm, SPM) and water depth and flow were the most discriminant compared to biotic factors related to vegetation (SAV) and filamentous algae in 2012.

Calcium concentration was also the most important variable shaping the zooplankton community in 2013, explaining more than 15% of the total variation on average (Figure 4B). Compared to 2012, SAV biomass and Chl*a* concentration were more important variables, each representing 9% of the variation in zooplankton abundance on average. Submerged aquatic vegetation (SAV) and filamentous algae appeared to be the most influential for the large cladoceran *Sida crystallina*. Nutrients (TDN, TDP), water depth and the variables related to water color (DOC, SPM and A440) each accounted for approximately 7% of the variation. In 2013, variation in zooplankton community composition was least explained by water flow and filamentous algae (<5%). For the most abundant taxa (*Bosmina*, *A. robustus*, calanoid nauplii, cyclopoid nauplii and copepodites, in bold in Figure 4B), abiotic factors related to water quality, color and depth remained the most important in 2013.

In 2014, zooplankton community was structured by DOC and SPM concentrations (10-11%), followed by water flow and depth (9%) (Figure 4C). TDN and TDP accounted respectively for 9.3 % and 7.5 % of the zooplankton variation, on average. The relative contribution of algal biomass (Chl*a*) and vegetation (SAV) was approximately 7%. SAV contribution was more important for small cladocerans (*Bosmina*), especially chydorids (*Rynchotalona falcata*, *Monospilus dispar*, *Camptocercus* sp.). Water color and turbidity (DOC, A440nm, SPM) were more discriminant for the large cladocerans *Daphnia* while algal biomass (Chl*a*) was important for the calanoid and cyclopoid copepods. Unlike previous years, Ca concentration and water color were the least important variables (6%) in shaping zooplankton community structure.

In general, there were relatively strong signals of environmental niche filtering by both abiotic (water quality, depth and flow) and biotic (SAV, filamentous algae) factors, especially in 2012 and 2014 (Figure 5). Zooplankton relative abundance and responses to environmental gradient varied greatly interannually (Table S1). While all significant relationships between zooplankton species and Ca concentrations were positive in 2012 (Figure 5A), nearly half of the relationships were negative in 2013 and 2014 (Figures 5B and 5C). Moreover, the same species was found to respond inconsistently to increased Ca concentrations throughout the years. For example, *Bosmina* sp., a widespread genus, had a positive relationship with Ca concentration in 2012, no relationship in 2013 and a negative relationship in 2014. As TDN increased over the three-year period, the response of zooplankton community structure changed from a largely positive relationship in 2012 to negative in 2013 and 2014. Conversely, TDP showed a trend from a negative relationship in 2012 toward a positive one for the following years. Water color (A440nm), which was significantly clearer in 2014, showed a positive relationship with zooplankton species in 2012 and 2013, while this relationship was negative in 2014. This was the case for an abundant species, *A. robustus*, which showed a positive relationship in 2012, no significant relationship in 2013 and finally a negative relationship to the water color in 2014. While the relationship between zooplankton communities and water color changed over time, the relationship with DOC and SPM was more consistent. Indeed, zooplankton community responded positively to DOC concentrations and negatively to SPM for both 2012 and 2014. There were no significant relationships between these variables and zooplankton species in 2013. Chl*a* concentration generally showed a positive relationship with zooplankton over the three years, except for *Ceriodaphnia* sp. in 2012 and *Camptocercus* sp. in 2014.

The relationship between SAV abundance and zooplankton species is another example of the variability of the LSP system and the responses of zooplankton community (Figure 5). While SAV abundance was positively related to the zooplankton species in 2012, except for *Ilyocryptus* sp., two significant relationships were positive in 2013 and one in 2014. In 2013, *S. crystallina* and *E. affinis* were positively related to the SAV while only *Camptocercus* sp. responded positively to SAV in 2014. Negative relationships with

SAV were recorded for *Ilyocryptus* sp. in 2012, *Moina micrura* in 2013, and *Bosmina*, *R. falcata*, *M. dispar*, *Alona*, and the harpacticoid copepodites in 2014. Filamentous algae showed positive relationships with zooplankton species in 2012, while one in two relationships were positive in 2013 and finally all the significant relationships were negative in 2014. Considering the variables related to the physical habitat, water depth was negatively related to several species for the three years, except for calanoids nauplii in 2012 and *Camptocercus* sp. in 2014. Water flow was negatively related to 19 zooplankton species in 2012, was positively correlated to only one species in 2013, namely *E. affinis*, and nearly all relationships were positive in 2014, except for calanoid nauplii (Figure 5).

1.4.4 Do species traits explain the variance in species niches?

We found significant relationships between zooplankton species traits based on community weighted means (CWM; Figure 6) and environmental attributes. We also found a strong phylogenetic signal in our HMSC analyses (ρ parameter > 0).

In 2012, filter-feeding zooplankton species (mainly Cladoceran Chydoridae species, Table S2) showed a significant positive relationship to DOC concentrations (Figure 6A). A similar pattern, albeit not significant, was found in 2013 and 2014. Filter-feeding zooplankton decreased with increasing water depth and flow, with a significant relationship in 2014 ans 2012 respectively (Figure B-C). Overall, for the three years, grasping feeders (cyclopoid copepods; Table S2) tended to decrease with higher DOC concentration and to increase with water depth and flow (Figure 6A-C). In contrast, surface feeders (harpacticoids) and suspension feeders (calanoids) did not show any relationships either for DOC concentration and water flow and depth.

Changes in traits related to habitat selection were associated with water color (A440nm) and algal biomass (Chl*a*) in 2014 (Figure 6D-E). Littoral species (mainly Chydoridae) were positively related to darker water color and generalist taxa (mainly composed of *Bosmina* and Cyclopoids copepodites) were related to increasing Chl*a*. However, most pelagic taxa (e.g., *Daphnia* spp., calanoids) were not significantly related to water color and Chl*a*.

In 2013, the proportion of large zooplankton species was positively related to SAV biomass. (Figure 6F). This relationship, albeit non-significant, was also present in 2014, but not in 2012 when SAV was more evenly distributed throughout the study area. The relative abundance of the large-body *S. crystallina* was more important in 2013 (3.39%) compared to 2012 (0.58%) and 2014 (0.31%, Figure 5). Zooplankton CWM biomass decreased with TDN and Chl*a* concentration, but this relationship was only significant in 2014 (Figure 6G-H), when the relative abundance of cyclopoida and calanoida nauplii was the highest, accounting for 90% of the total abundance (Figure 5).

1.5 Discussion

1.5.1 Environmental conditions in a highly variable system

Our results show clearly that environmental conditions were highly variable among years and sites, principally controlled by the climatic variations and the movement of water masses of tributary inputs at the confluence of the Great Lakes and the Yamaska and St.-François Rivers (Figure 2). The summer of 2012 was characterized by historically low water levels and warmer water temperatures compared to 2013 and 2014. In turn, water level and temperature fluctuations have been shown to greatly impact SAV growth and biomass in our study area, and therefore have an impact on nutrient levels in water (nitrate uptake and sequestration; Botrel et al. 2022). According to Botrel et al. (2022), the contribution of nitrate input from the Saint-François River varied from 100%, 63% and 40% for 2012, 2013 and 2014, respectively, in our study area. Water flow was generally low during all three years due to the drag imposed by SAV abundance (Bulat et al. 2019). Taken together, we noted three main abiotic gradients over space and time that reflect the contrasting characteristics of water masses originating from Lake Ontario (high conductivity, clear waters) and from tributaries (low conductivity, brown waters) on the south shore of LSP (Levesque et al. 2012): i) a gradient associated with increasing water depth, ii) a trophic gradient associated with decreasing nutrients (TDN, TDP), algal resources (Chl*a*), particulate matter (SPM) and Ca concentrations, and iii) a dystrophy gradient associated with increasing water color and DOC (Figure S1). The water depth gradient was negatively related to the SAV in some years (2013 and 2014) and sites (the upstream shallow sites at the confluence of south shore tributaries being the most vegetated; Figure S1). The filamentous algae and nutrient gradient were most pronounced in 2012 and to a lesser extent in 2013 (Figure S1) when high DOC and SPM from tributaries inputs likely increased algal heterotrophic growth that relies on organic carbon (Levesque et al. 2012). This interannual variation within environmental variables could have played an important role by driving changes in the environmental filters thus shaping zooplankton community structure dynamics.

1.5.2 Environmental niche dimensions of the zooplankton community

Our results show how a powerful state-of-the-art approach such as HMSC analysis can be applied successfully to highlight the drivers of environmental niches of crustacean zooplankton after considering both phylogeny and spatial factors, but also how they can vary dramatically over time. As predicted, both abiotic (water conditions) and biotic (SAV and filamentous algae) factors *a priori* selected were important drivers, as they explained more than 60% of the variation in zooplankton communities (Figure 4).

Overall, the dominant cladocerans and copepods found in vegetated littoral sites of LSP are typical of lotic environments. All copepods reported in this study were previously found across the fluvial-estuary continuum of the St. Lawrence River (Pinel-Alloul et al. 2011; Taranu et al. 2023). They have diverse biological reproductive and behavioral traits resulting in a great variety of life strategies that enable them to survive in stressed environments (Dole-Olivier et al., 2000; Barnett et al. 2007; Hebert et al. 2016). For example, the high occurrence of cyclopoid species in our study sites is likely due to their ability to survive as dormant stages in river backwaters where they emerge at spring (Selgeby, 1975; Wahl et al., 2008).

Zooplankton species abundance responded to the main environmental gradients, namely i) the trophic gradient associated to nutrients, Ca, SPM and Chl*a*, and ii) the dystrophy gradient associated to DOC and water color (Figure 3). Trophic factors had a stronger influence in 2012 and 2013 when the SAV biomass was higher, while the dystrophic factors were more influential in 2014 when DOC and water color were low. In system subject to spring flooding, the mass effect (i.e., arrival of species that are not necessarily adapted to the environmental conditions) can interfere with our ability to detect the effect of environmental filters on zooplankton communities (e.g., Xiong et al. 2017; Rizo et al. 2020). However, our results showed different responses of zooplankton taxa among years, highlighting that habitat filtering as an important process in shaping zooplankton community structure. Most studies are conducted over a one-year period, making it difficult to assess interannual differences of zooplankton community structure in a changing environment. Our study shows clearly that huge variations in the strength and even in the direction of the relationship among environmental gradients and zooplankton are possible. The magnitude of the interannual variability of environmental conditions and zooplankton community structure outlines the importance of multi-year monitoring in a highly dynamic system such as LSP.

The relationship with biotic components (SAV) is another example of the variability of the responses of zooplankton communities, being the most steeply positive in 2012 (most of species) and 2013 (mainly *S. crystallina* and *E. affinis*) (Figure 5). SAV provides a physically complex refuge for zooplankton. Zooplankton species distribution in macrophyte-dominated lakes is usually a compromise between costs and benefits, both through the interactions between predator and prey and by searching for the optimal feeding conditions (Schriver et al. 1995; Jeppessen et al. 1997; Meerhoff et al. 2007; Declerk et al. 2007). In previous studies within the same system, zooplankton community biomass was shown to be strongly related to SAV biomass (Bolduc et al. 2016) and complexity (Bolduc et al. 2020). In our study, we considered a taxonomic and phylogenetic-based approach to show again that SAV was an important driver of zooplankton taxonomic and functional community structure, especially due to the responses of cladocerans Chydoridae and Sididae. The Chydoridae are especially adapted to SAV due to their mode of locomotion and feeding behaviors (Dole-Olivier et al. 2000). They move as scrapers, crawlers and scramblers within the complex structure of aquatic plants while feeding on detritus, organic matter and associated algae (Beklioglu and Jeppensen, 1999; Adamczuk, 2014). In the SAV beds, *V. americana* and *P. richardsonii* were the dominant macrophytes, offering a good refuge for the chydorids (Bolduc et al. 2016, 2020). The refuge effect provided by SAV, combined with the water color, is also important for the Sididae family, composed of the widely distributed phytophilous-benthic species *Diaphanosoma brachyurum* and *S. crystallina* (Gonzàlez Sagrario and Balseiro, 2010). Small-bodied *Diaphanosoma* are also known to prefer SAV habitats colonized by complex plants such as *Myriophyllum* (Kuczynska-Kippen, 2009), while *S. crystallina* is specially adapted to live attached to the plant leaves (Fairchild, 1981).

Filamentous algae also showed positive relationships with most of the zooplankton species in 2012 and 2014. Most of these species are intermediate swimmers and may prefer to hide in beds of macrophytes and associated filamentous algae as suggested by Fairchild (1981). A negative relationship between filamentous algae and poor swimmer *S. crystallina* was found in 2013, probably because enough SAV habitat without filamentous algae was available (Figure S1).

Heatplots (Figure 5) allowed to better understand the details of the environmental filtering model detected by variance partitioning (Figure 4). In general, there were significant signals of environmental niche filtering by both abiotic (water quality, depth and flow) and biotic (SAV, filamentous algae) factors, especially in 2012 and 2014 (Figure 5). Zooplankton responses to environmental gradient varied greatly interannually as the same species could react differently to these gradients among years (Figure 5). For example, *A. robustus* was positively related to water color in 2012, not related in 2013 and negatively related in 2014. According to the literature, water color could reduce the predation risk by planktivorous fishes and therefore the need for zooplankton to seek refuge in macrophytes (Estlander et al. 2009). The different responses of *A. robustus* observed in our study could be explained by the existence of a threshold in water color, reducing predation risk over a given value of water color (Figure S1). These variations suggest that the environmental niche is very variable through space and time and conditioned by limiting measured factors and other unmeasured ones as fish predation effects. This highlights the importance of considering several dimensions of the environmental niches to better understand the effects of abiotic and biotic components on aquatic communities (Martin et al. 2018) but also the importance of multi-year monitoring.

1.5.3 Do species traits explain the variation in species niches?

As zooplankton species vary in body size, habitat preference, feeding type and swimming capacity (Table S2), we assessed how these functional traits influenced the responses of zooplankton communities to environment heterogeneity in water conditions and SAV abundance. A previous study by Bolduc et al. (2016) showed that SAV was associated with a higher functional diversity in zooplankton, suggesting an increased number of ecological niches in SAV habitats.

Here, calculating the community weighted mean (CWM) of each functional trait allowed us to describe the functional responses of zooplankton communities (Figure 6). This analysis provided a complementary perspective of how communities responded to the environment compared to the analysis based solely on individual responses of zooplankton species (see Figure 5 vs Figure 6). For example, the filter-feeders (mainly Cladoceran) showed positive relationships with DOC (2012) and a negative relationship with water depth and flow (2014; Figure 6). The positive relationship between filter-feeders and DOC was related to the great abundance of *Chydorus* sp and *Bosmina* sp. which are genera composed of small species (Figure 5). An increase in DOC, especially from terrestrial source, would affect both resource quality and availability for large zooplankton (Tonin et al. 2022). Nearly all species were negatively related to water depth, reflecting the negative relationship in the CWM. As water depth increased, SAV declined and water flow increased (Bulat et al. 2019), thus providing less protection against predators and against being exported by the water flow (Masson et al. 2004). This was particularly important in 2012, where the filter-feeders, who are generally known to be poor swimmers, were negatively related to the water flow.

Zooplankton habitat types were related to changes in water color (A440nm) and algal biomass (Chl*a*). Littoral species, mostly Chydoridae, were positively related to water color, which is in concordance with the findings of Estlander et al. (2008), who found that when transparency is high, cladoceran abundance and growth followed SAV development in the littoral zone. However, few species are strictly littoral (Walseng et al. 2006). In shallow lakes, zooplankton species are likely to perform diel horizontal migration, especially when the abundance of SAV is high, which reduces planktivory and promotes the abundance of piscivorous fish (Burks et al. 2002). During the day, zooplankton species can therefore migrate toward SAV beds, complicating the interpretation of the relationship between the trait of habitat type and environmental variables. The generalist taxa, and more specifically cyclopoids nauplii, were positively related to Chl*a* (Figure 6), which could be due to the high demand for food during this stage of life to allow their development and survival. However, some species, such as *A. robustus*, are generally less affected by the availability of food (Hopp and Maier, 2005).

Finally, body size (max length) increased with SAV biomass in 2013 while species mean biomass (CWM) decreased with TDN and Chl*a* in 2014 (Figure 6). This is mainly explained by the large gradient in Sididae body size in SAV in 2013, and the inverse relationship between SAV and TDN in 2014 (Figure 3). By living attached to SAV, *S. crystallina* are directly impacted by the abundance and complexity of SAV beds (Fairchild, 1981). Moreover, SAV competes for the same resources used by phytoplankton. Therefore, it is expected that *S. crystallina* biomass will decrease with increasing Chl*a*.

As expected, given the scarce availability of functional traits in the literature, the strong phylogenetic signal in our models suggests that functional traits are probably more important than suggested by the results presented above (Ovaskainen and Abrego, 2020). However, even if the identity of the most abundant species changed according to the abiotic and biotic gradient, the traits in the community responded in a similar way to these gradients from year to year, suggesting a functional redundancy in the zooplankton traits. These results are an example of how functional redundancy, due to asynchronic response of species to environmental conditions, could act as an insurance policy by promoting the resilience of ecosystem functions (Yachi and Loreau, 1999). In the actual era of anthropogenic pressure, climate change and habitat homogenization, the importance of functional redundancy in natural systems will need to be described in further detail to better understand the drivers of functional redundancy and the consequences of species loss (Burgess et al. 2019).

1.6 Caveats

Despite the clear advances allowed by this powerful approach, several caveats may limit the interpretation of the HMSC modeling output in our study (Garcia-Girón et al. 2021). First, missing environmental covariates related to fish predation might have confounded the interactions between zooplankton communities and SAV habitat. Another difficulty for disentangling the effects of water conditions and SAV is that both influenced each other. A previous study assessing their joint effects on zooplankton community structure based on functional groups (Bolduc et al. 2020) showed that water color (or transparency) and water depth explained a larger fraction of zooplankton variation when combined with SAV cover and complexity indices (14%) than alone (9%). Finally, the extreme variability of the littoral SAV habitats in large fluvial lakes as observed during our three-year study could make it more difficult to detect strong and consistent interactions between the environment and aquatic community. However, even in this extremely variable ecosystem, we found significant relationship between zooplankton taxa and traits and the environment, showing that they are a good model to study species traits-environment relationship in a highly dynamic system since they respond rapidly to a changing environment.

1.7 Conclusions and implications for future research

Using a joint species distribution modeling allowed us to understand how abiotic and biotic processes shaped species co-responses and to determine how species traits, based on community weighted means, explained variation in species niches in a highly dynamic system. The huge variation among years in the strength and in the direction of the relationship among environmental gradients and zooplankton taxa outlines the importance of multi-year monitoring in order to have a better understanding of the underlying processes shaping zooplankton community assemblage. We found that both abiotic (water conditions) and biotic variables (SAV habitats and filamentous algae) were important drivers of the variation in zooplankton communities. SAV has been found to decrease worldwide, likely due to multiple stressors such as anthropic activity and global climate change (Zhang et al., 2017). Lake St. Pierre is no exception to this reality, where Laporte et al. (submitted paper) showed a decrease in probability to observe SAV from approximately 60% in 2007 to 20% in 2021. The loss of this niche dimension can result in zooplankton taxonomic diversity loss, but also a risk for losing functional redundancy. Even though our results using multi-year analysis showed that event if different species are present in the community, traits based on community weighted mean responds similarly to environmental conditions. Therefore, a loss of diversity should be taken seriously. These results are the first step towards a better understanding of functional redundancy in a dynamic system where species composition change from year to year, but we need to pursue the effort to understand the role of diversity in the functioning of these key ecosystems.

1.8 Acknowledgments

This study is a contribution of the Groupe de Recherche Interuniversitaire en Limnologie (GRIL) and the Canada-Québec St. Lawrence Action Plan. Financial support was provided by the NSERC (Discovery grant to BPA: RGPIN-2015-04875), the Fond Québécois de la Recherche Nature et Technologie (ISI-FQRNT 186430), the RIVE-UQTR Research centre, and the GRIL, which supported P. Bolduc doctoral studies. We would like to thank Myriam Boisvert, Lucas Deschamps, Annie Picard and Joëlle Guitard for their technical assistance for zooplankton identification. We also thank Guillaume Rheault for the discussions about the sampling design and the statistical analysis and the technical staff of Environment and Climate Change Canada for SAV data collection. Thanks to Morgan Botrel and Stéphanie Massé for the coordination during sampling and laboratory analysis. The authors declare that there is no conflict of interest.

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1.10 Tables

Table 1. Environmental variables included in the models (2012, 2013 and 2014). For each year, mean value and standard deviation are reported as well as the dimension of the niche represented.

	2012	2013	2014	Units	Niche dimension
Variable	Mean (sd)	Mean (sd)	Mean (sd)		
ABIOTIC FACTORS					
Calcium (Ca)	583.54 (70.74)	618.94 (48.41)	721.24 (74.14)*$^{+}$	µmol/l	Use in zooplankton carapace construction (Hessen, 2000)
Total dissolved nitrogen (TDN)	408.33 (100.12)	548.25 (110.77)*	530.91 (87.38)*	µg/l	Proxies of aquatic ecosystem productivity (Johnson et Luecke, 2012)
Total dissolved phosphorus (TDP)	16.64 (6.15)$^{+}$	11.52 (2.48)*	17.76 (5.48)$^{+}$	µg/l	
Chlorophyll *a* (Chla)	3.64 (2.98)	2.87 (1.22)	2.94 (1.01)	µg/l	Proxy of algal biomass
Water colour	0.10 (0.05)	0.12 (0.03)	0.01 (0.00)*$^{+}$	cm^{-1}	Predation risk (Estlander et al. 2009), UV-induced damage (Kirk, 1994)
Suspended particulate matter (SPM)	12.75 (14.65)	5.75 (4.18)	19.95 (21.78)$^{+}$	mg/l	
Dissolved organic carbon (DOC)	6.41 (1.66)	6.37 (0.82)	3.11 (0.81) *$^{+}$	mg/l	Proxy of microbial loop
Water depth	77.29 (33.17)	149.81 (42.76)*	161.50 (44.96)*	cm	Habitat: littoral vs pelagic zooplankton (Walseng, 2006)
Water flow	0.04 (0.04)	0.07 (0.11)	0.06 (0.07)	m/s	Risk of flushing (Masson. 2004)
BIOTIC FACTORS					
Submerged aquatic vegetation (SAV) (all species pooled)	13.98 (17.60)	23.86 (38.60)	5.55 (9.99)	dry weight (g/m2)	Habitat heterogeneity and complexity mediating fish-zooplankton interactions (Schriver et al., 1995)
Filamentous algae (all species pooled)	11.70 (37.05)	8.24 (29.01)	0.67 (1.68)	fresh weight (g/m2)	

*Significantly different from year 2012; $^{+}$ Significantly different from year 2013

Table 2. Total taxa richness, abundance (Ind.L-1) and biomass (µg.L-1) of crustacean zooplankton (Cladocera, Copepoda Calanoida, Cyclopoida and Harpacticoida) in the study sites in 2012, 2013 and 2014. See Table S1 for details.

Year	2012			2013			2014		
Groups	Taxa richness	Mean abundance	Mean biomass	Taxa richness	Mean abundance	Mean biomass	Taxa richness	Mean abundance	Mean biomass
Cladocera	35	862	971	28	106	302	22	19	43
Calanoida	2	47	54	1	42	36	1	13	19
Cyclopoida	18	984	406	8	696	274	12	819	129
Harpacticoida	7	1.25	0.9	3	1.3	0.3	4	0.2	0.15
Total	62	1894	1432	40	846	612	39	861	191

1.11 Figures

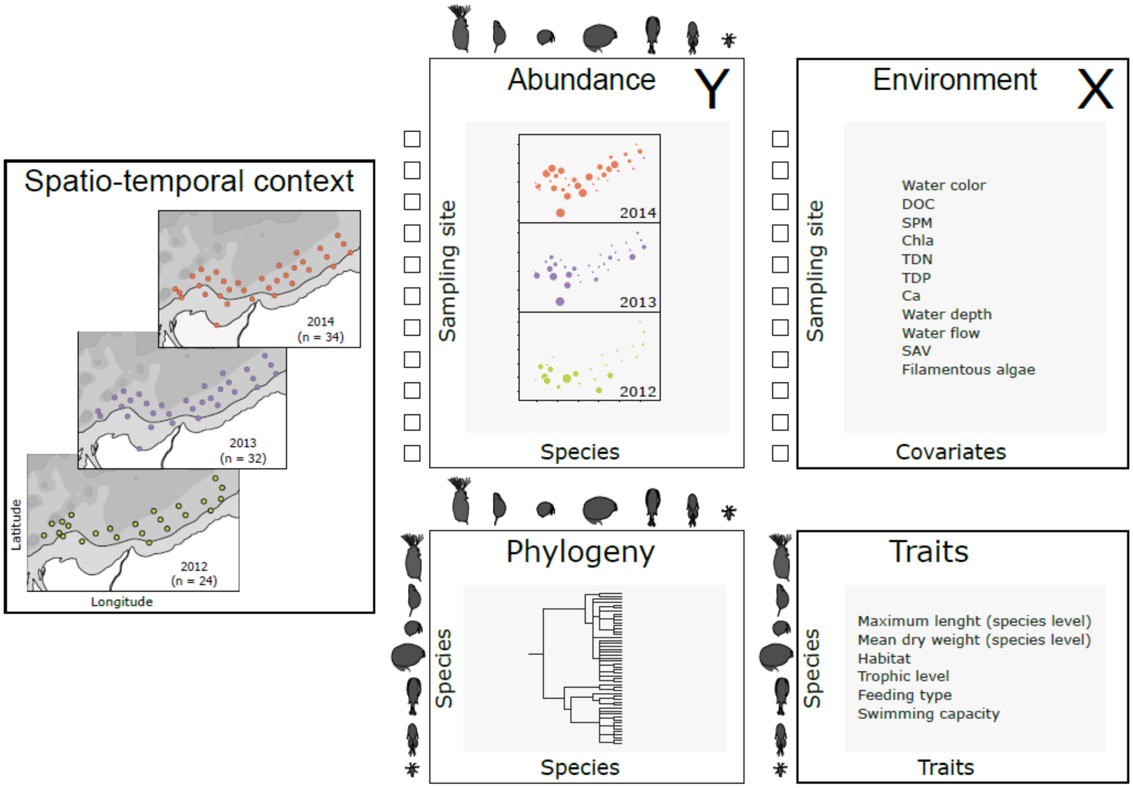

Figure 1. Conceptual framework of the study. Zooplankton species abundance data collected in August 2012, 2013 and 2014 were used as response variables (Y matrix). The environmental data matrix (X) was used as the covariate. The trait matrix consisted of a set of two traits measured directly on zooplankton species (maximum length and mean dry weight) and four traits derived from the literature (habitat, trophic level, feeding type, swimming capacity). To account for phylogenetic dependencies among species, we used zooplankton taxonomy. Environmental, trait variables and phylogeny were included as fixed effects while sampling site coordinates were used as random effects. Each year was analyzed separately.

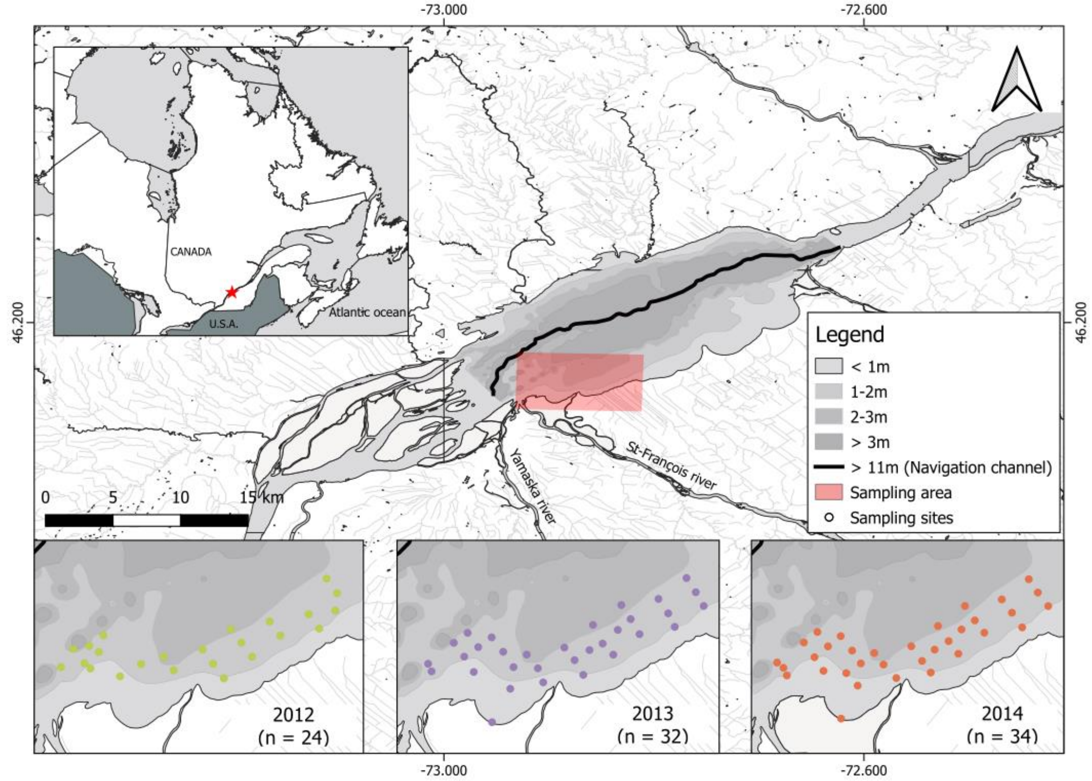

Figure 2. Map of the study area showing the bathymetry of the Lake Saint-Pierre and the location of the navigation channel. The sites sampled in 2012 (green dots), 2013 (purple dots) and 2014 (orange dots) are in the plume of the Yamaska and Saint-François rivers.

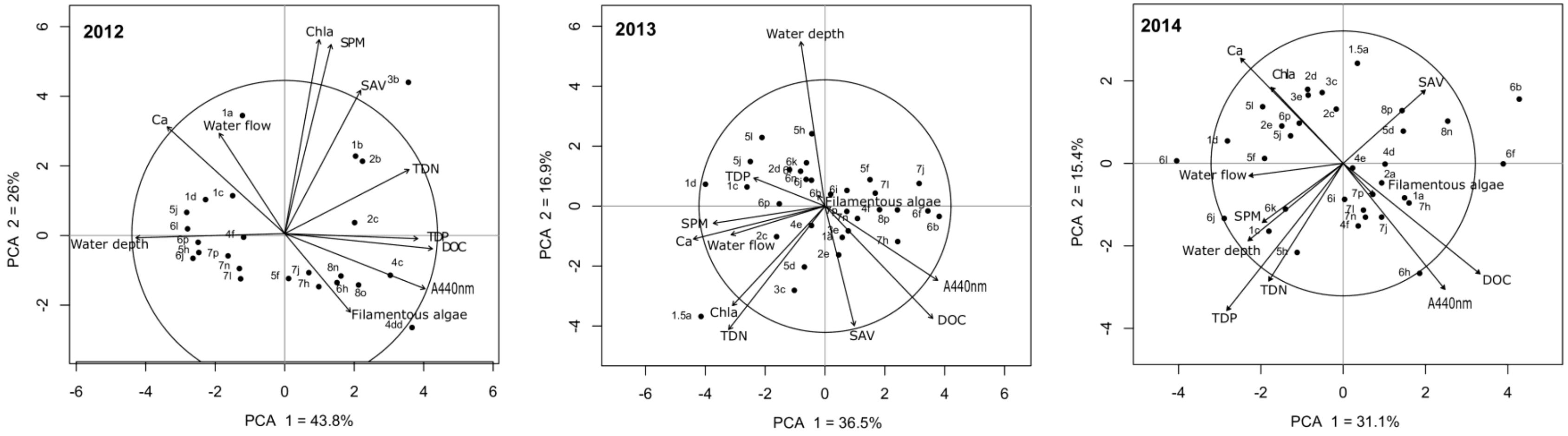

Figure 3. PCA based on environmental variables for the three years of analysis. Variables outside the circle are those contributing the most to the two PCA axes.

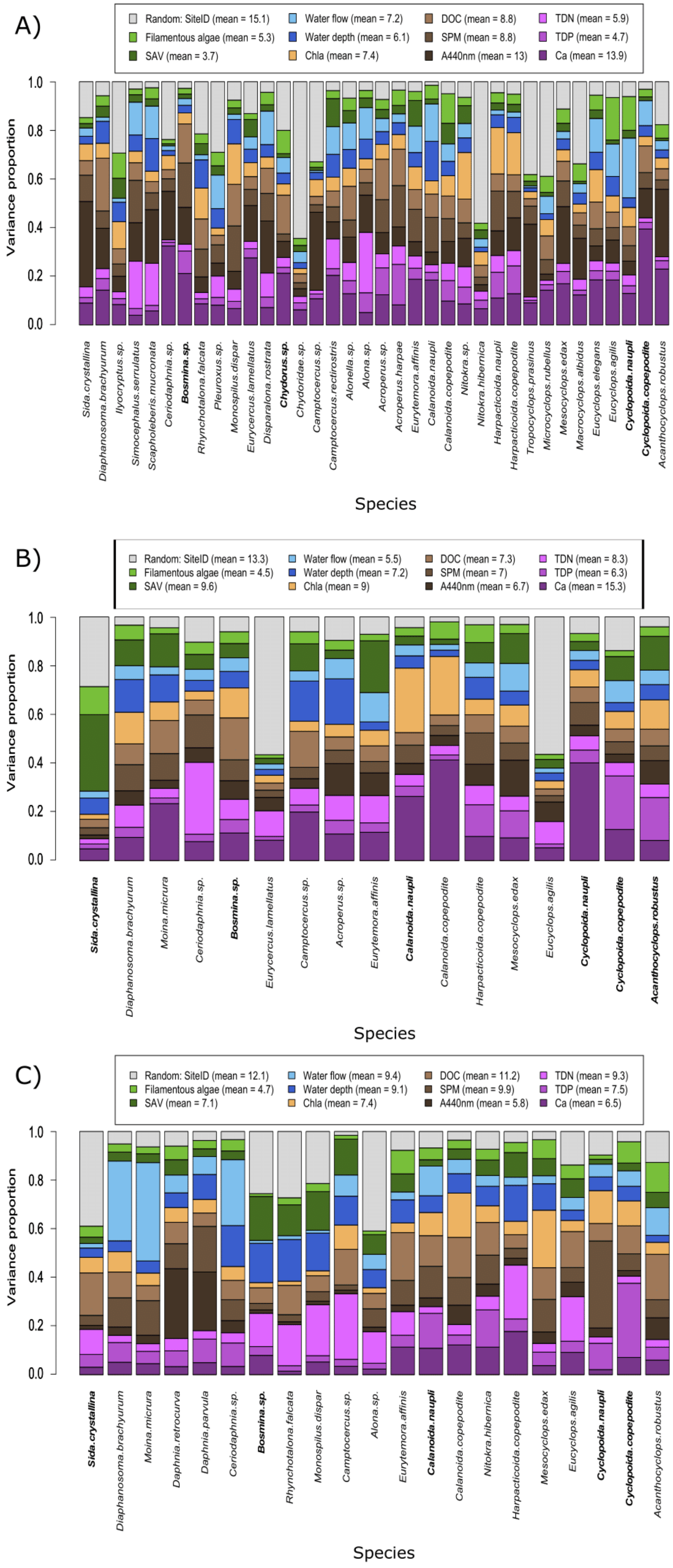

Figure 4. Variation partitioning among the explanatory variables explaining zooplankton species abundance. Panels A, B and C shows the variation partitioning of the 2012, 2013 and 2014 models respectively. The heights of the bars correspond to the explanatory power for each species. The species have been ordered according to their phylogenetic rank. The legends provide the mean proportion of variation (i.e., averaged over all species). Species in bold are those with the greater variance as shown in Fig. S2 (supplementary material). Overall, the three models explained respectively 67%, 63% and 59% of the species abundance.

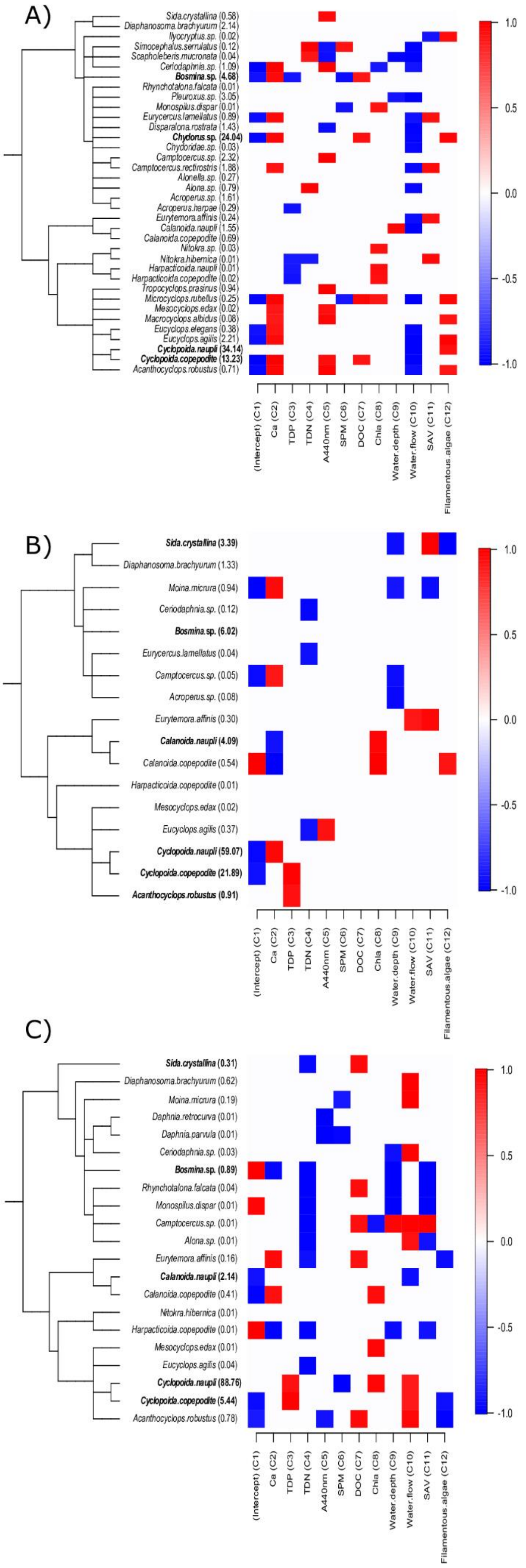

Figure 5. Heatplot of the importance of the explanatory variable included in the models. Panels A, B and C shows heatplots of the 2012, 2013 and 2014 models, respectively. The clusters represent the phylogenetic tree of selected species (excluding rare). The colors identify either significant positive (red) or negative (bleu) relationship between species and environmental variables, with a support level of 0.95. The number next to the species name represents their percent abundance. The species in bold are those showing the highest variability (Fig. S2, supplementary material).

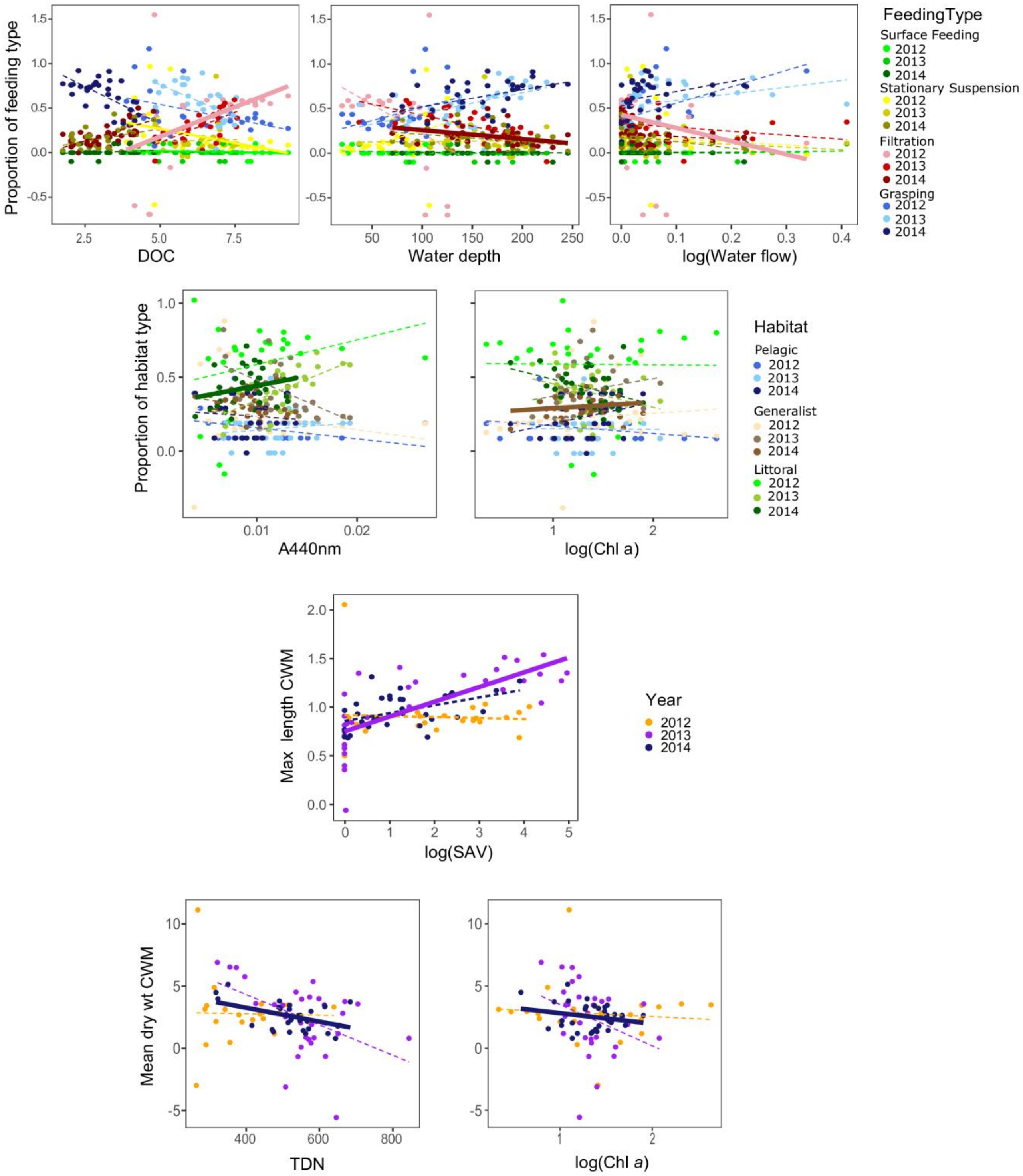

Figure 6. The responses of zooplankton species traits to environmental covariates based on the proportion of trait type (categorical traits) and community weighted means (CWM; quantitative traits). In all panels, solid lines represent significant relationship with at least 95% posterior probability. Dashed lines represent non-significant relationships.

1.12 Supplementary material

Table S1. Zooplankton species occurrence, mean abundance and mean biomass from 2012 to 2014. Total abundance and biomass are reported for each group.

		2012			2013			2014		
Group	**Species[1]**	Occurrence (/24)	Mean abundance (ind/l) (sd)	Mean biomass (µg/l) (sd)	Occurrence (/32)	Mean abundance (ind/l) (sd)	Mean biomass (µg/l) (sd)	Occurrence (/34)	Mean abundance (ind/l) (sd)	Mean biomass (µg/l) (sd)
Cladocera	*Acroperus harpae*	8	0.23 (0.69)	0.46 (1.36)	1	0.00 (0.01)	0.00 (0.02)	0		
	Acroperus sp.	6	1.27 (4.90)	3.21 (11.49)	8	0.02 (0.05)	0.15 (0.48)	3	<0.01	<0.01
	Alona sp.	15	0.62 (2.52)	0.45 (1.71)	3	0.00 (0.02)	0.02 (0.10)	5	0.00 (0.01)	0.00 (0.01)
	Alonella exigua	1	0.01 (0.04)	0.01 (004)	1	<0.01	<0.01	0		
	Alonella sp.	11	0.22 (0.59)	0.08 (0.16)	0			3	<0,01	<0,01
	Bosmina sp.	24	3.69 (11.37)	1.00 (2.60)	31	1.59 (2.30)	0.69 (0.99)	34	0.23 (0.40)	0.11 (0.19)
	Camptocercus rectirostris	13	1.49 (3.26)	7.38 (16.39)	3	0.09 (0.51)	0.42 (2.37)	1	<0.01	0.00 (0.01)
	Camptocercus sp.	7	1.83 (8.70)	5.87 (27.79)	5	0.01 (0.07)		6	0.00 (0.01)	0.02 (0.06)
	Ceriodaphnia dubia	2	0.00 (0.02)	0.00 (0.01)	1	<0.01	<0.01	0		
	Ceriodaphnia laticaudata	2	0.01 (0.03)	0.01 (0.03)	1	0.01 (0.07)	0.01 (0.05)	0		
	Ceriodaphnia reticulata	3	0.02 (0.07)	0.03 (0.15)	2	<0.01	<0.01	0		
	Ceriodaphnia sp.	19	0.86 (3.29)	0.61 (2.65)	13	0.03 (0.08)	0.02 (0.04)	18	0.01 (0.01)	0.01 (0.01)
	Chydoridae sp.	4	0.03 (0.11)	0.01 (0.03)	3	0.02 (0.12)	0.01 (0.05)	0		
	Chydorus brevilabris	1	0.02 (0.09)	0.01 (0.03)	0			0		
	Chydorus sp.	22	18.98 (82.54)	5.26 (21.87)	2	<0.01	<0.01	0		
	Chydorus sphaericus	0			1	0.02 (0.12)	0.01 (0.05)	0		
	Daphnia ambigua	1	0.00 (0.01)	<0.01	3	<0.01	<0.01	3	<0.01	<0.01
	Daphnia catawba	0			0			2	<0.01	0.00 (0.01)
	Daphnia longiremis	0			0			1	<0.01	<0.01
	Daphnia parvula	1	<0.01	<0.01	2	<0.01	<0.01	6	<0.01	<0.01
	Daphnia pulex	0			2	<0.01	<0.01	3	<0.01	0.00 (0.01)
	Daphnia retrocurva	1	<0.01	<0.01	2	<0.01	<0.01	10	0.00 (0.01)	0.01 (0.02)
	Daphnia sp.	1	<0.01	<0.01	1	<0.01	<0.01	2	<0.01	<0.01
	Diaphanosoma brachyurum	24	1.69 (4.21)	0.78 (1.84)	29	0.35 (0.85)	0.20 (0.35)	32	0.16 (0.28)	0.16 (0.30)
	Disparalona rostrata	10	1.13 (3.55)	1.52 (4.79)	0			0		

	Eurycercus lamellatus	17	0.71 (1.52)	8.14 (22.51)	6	0.01 (0.05)	0.37 (2.03)	3	0.01 (0.07)	0.36 (2.10)
	Ilyocryptus sp.	8	0.02 (0.06)	0.02 (0.07)	1	<0.01	<0.01	0		
	Latona glacialis	1	0.00 (0.01)	0.00 (0.02)	0			0		
	Leptodora kindti	0			3	<0.1	0.07 (0.35)	1	<0.01	0.00 (0.01)
	Macrothrix sp.	2	0.00 (0.01)	<0.01	0			0		
	Moina micrura	3	0.08 (0.32)	0.10 (0.36)	15	0.25 (0.79)	0.37 (1.10)	20	0.05 (0.10)	0.10 (0.23)
	Monospilus dispar	4	0.01 (0.02)	0.01 (0.03)	3	<0.01	0.00 (0.02)	5	0.00 (0.01)	0.01 (0.02)
	Oxyurella sp.	1	0.00 (0.01)	0.00 (0.01)	0			0		
	Pleuroxus sp.	14	2.41 (6.43)	3.65 (10.01)	0			1	<0.01	<0.01
	Pseudochydorus globosus	1	<0.01	<0.01	1	<0.01	0.00 (0.01)	0		
	Rhynchotalona falcata	4	0.01 (0.02)	0.00 (0.01)	1	<0.01	<0.01	6	0.01 (0.04)	0.01 (0.03)
	Scapholeberis mucronata	4	0.04 (0.10)	0.03 (0.10)	0			0		
	Sida crystallina	21	0.46 (1.18)	1.58 (3.16)	22	0.90 (2.43)	6.98 (19.73)	28	0.08 (0.22)	0.47 (1.21)
	Simocephalus serrulatus	8	0.10 (0.30)	0.23 (0.65)	0			0		
	Simocephalus sp.	3	0.00 (0.01)	0.00 (0.01)	0			0		
Total		**-**	**861.54**	**971.06**	**-**	**106.31**	**301.95**	**-**	**18.92**	**43.07**
Calanoida	*Calanoida* copepodites	21	0.54 (0.98)	0.73 (1.23)	25	0.14 (0.27)	0.33 (0.94)	32	0.11 (0.11)	0.20 (0.20)
	Calanoida nauplii	17	1.22 (1.34)	0.10 (0.10)	22	1.08 (1.40)	0.15 (0.27)	22	0.54 (0.88)	0.04 (0.07)
	Epischura lacustris	1	<0.01	<0.01	0			0		
	Eurytemora carolleeae	20	0.19 (0.29)	1.41 (2.24)	21	0.08 (0.13)	0.64 (1.03)	30	0.04 (0.07)	0.31 (0.51)
Total		**-**	**46.86**	**53.83**	**-**	**41.64**	**35.94**	**-**	**23.45**	**18.84**
Cyclopoida	*Acanthocyclops brevispinosus*	0			1	0.00 (0.01)	0.01 (0.03)	0		
	Acanthocyclops robustus	21	0.56 (1.80)	1.80 (5.71)	27	0.24 (0.75)	1.43 (4.76)	33	0.20 (0.29)	0.93 (1.29)
	Acanthocyclops sp.	1	<0.01	<0.01	0			0		
	Acanthocyclops venustoides	2	0.00 (0.02)	0.02 (0.11)	2	0.02 (0.11)	0.06 (0.32)	0		
	Cyclopoida copepodites	23	10.44 (21.74)	6.54 (9.37)	31	5.78 (6.23)	5.46 (5.90)	34	1.38 (1.32)	1.66 (1.58)
	Cyclopoida nauplii	24	26.94 (19.81)	2.24 (2.39)	32	15.61 (17.35)	1.32 (1.64)	33	22.49 (27.23)	1.15 (1.34)
	Cyclopoida sp.	2	<0.01	<0.01	0			1	<0.01	<0.01
	Cyclops scutifer	1	<0.01	<0.01	0			0		
	Diacyclops nanus	2	<0.01	0.00 (0.01)	0			0		
	Ergasilus sp.	1	<0.01	0.00 (0.01)	0			1	<0.01	<0.01

	Eucyclops agilis	14	1.74 (4.25)	4.13 (10.07)	14	0.10 (0.41)	0.27 (1.10)	11	0.01 (0.03)	0.04 (0.10)
	Eucyclops elegans	4	0.30 (1.13)	0.68 (2.70)	0			2	<0.01	<0.01
	Eucyclops prionophorus	2	<0.01	0.00 (0.01)	2	<0.01	<0.01	0		
	Eucyclops sp.	1	<0.01	0.00 (0.01)	0			0		
	Macrocyclops albidus	6	0.06 (0,22)	0.38 (1,10)	1	<0.01	0.01 (0.03)	1	<0.01	0.00 (0.01)
	Macrocyclops ater	3	0.00 (0.01)	0.05 (0.17)	0			1	<0.01	<0.01
	Macrocyclops fucus	0	<0.01	<0.01	0			1	<0.01	0.00 (0.02)
	Macrocyclops sp.	0			0			1	0.00 (0.01)	0.00 (0.02)
	Mesocyclops americanus	1	0.00 (0.02)	0.01 (0.03)	0			0		
	Mesocyclops edax	9	0.01 (0.03)	0.02 (0.04)	10	0.01 (0.01)	0.01 (0.03)	15	<0.01	0.01 (0.01)
	Microcyclops rubellus	11	0.20 (0.56)	0.23 (0.66)	3	<0,01	<0.01	3	<0.01	0.00 (0.01)
	Microcyclops varicans	0			0			2	0.00 (0.01)	0.00 (0.02)
	Orthocyclops modestus	1	<0.01	0.00 (0.01)	0			0		
	Paracyclops poppei	2	0.00 (0.01)	0.00 (0.02)	0			0		
	Tropocyclops prasinus	10	0.74 (3.59)	0.80 (3.89)	0			0		
Total		**-**	**984.43**	**406.10**	**-**	**696.29**	**273.91**	**-**	**818.85**	**129.14**
Harpacticoida	*Bryocamptus* sp.	1	<0.01	<0.01	0			0		
	Harpacticoida copepodites	14	0.02 (0.03)	0.01 (0.01)	6	<0.01	<0.01	10	<0.01	<0.01
	Harpacticoida nauplii	6	0.01 (0.02)	<0.01	1	0.04 (0.21)	0.01 (0.03)	0		
	Harpacticoida sp.	0			3	<0.01	<0.01	3	<0.01	<0.01
	Mesochra alaskana	1	<0,01	<0,01	0			0		
	Nitokra hibernica	4	0.01 (0.03)	0.01 (0.02)	2	<0.01	<0.01	11	0.00 (0.01)	<0.01
	Nitokra sp.	5	0.02 (0.09)	0.02 (0.09)	0			3	<0.01	<0.01
	Onychocamptus mohammed	2	<0.01	<0.01	0			1	<0.01	<0.01
	Schizopera borutzkyi	0			1	<0,01	<0,01	0		
Total		**-**	**1.25**	**0.87**	**-**	**1.30**	**0.27**	**-**	**0.20**	**0.15**
Arguloida	*Argulus* sp.	4	<0.01	0.00 (0.01)	0			0		
Total		**-**	**0.04**	**0.04**	**-**			**-**		
Yearly total			**1894.11**	**1431.91**		**845.54**	**612.07**		**861.41**	**191.20**

[1] In order to eliminate a convergence problem in the models, species present at three stations or less were withdrawn for the statistical analysis (underlined in gray). *Ergasilus* sp. and *Argulus* sp. were also removed as they are parasitic fish species.

Table S2. Zooplankton functional traits used in the models. Four traits were derived from the literature (swimming capacity, habitat, feeding type and trophic level) while two traits (maximum length and mean dry weight (MDW)) were measured directly on the zooplankton species present in the 2012, 2013 and 2014 samples.

						2012		2013		2014	
Group	Species	Swimming capacity	Habitat	Feeding type	Trophic level	Max length (mm)	MDW (µg)	Max length (mm)	MDW (µg)	Max length (mm)	MDW (µg)
Cladocera	*Acroperus harpae*	Bad	littoral	Filtration	Herbivore	0,70	2,57	0,70	3,89		
	Acroperus sp.	Bad	littoral	Filtration	Herbivore	0,78	2,77	1,00	6,53	0,53	1,03
	Alona sp.	Bad	littoral	Filtration	Herbivore	0,75	1,23	0,83	4,90	0,65	1,44
	Alonella exigua	Bad	littoral	Filtration	Herbivore	0,43	1,05	0,53	2,69		
	Alonella sp.	Bad	littoral	Filtration	Herbivore	0,70	0,56			0,48	1,12
	Bosmina sp.	Bad	generalist	Filtration	Herbivore	0,48	0,36	0,53	0,45	0,50	0,51
	Camptocercus rectirostris	Bad	littoral	Filtration	Herbivore	0,90	5,45	0,80	4,50	0,78	12,23
	Camptocercus sp.	Bad	littoral	Filtration	Herbivore	0,80	3,95	0,88	7,28	0,85	6,76
	Ceriodaphnia dubia	Bad	generalist	Filtration	Herbivore	0,63	1,49	0,68	3,49		
	Ceriodaphnia laticaudata	Bad	generalist	Filtration	Herbivore	0,65	1,05	0,63	0,79		
	Ceriodaphnia reticulata	Bad	generalist	Filtration	Herbivore	0,70	1,67	0,58	0,91		
	Ceriodaphnia sp.	Bad	generalist	Filtration	Herbivore	0,63	0,46	0,58	0,49	0,75	0,61
	Chydoridae sp.	Bad	littoral	Filtration	Herbivore	0,63	1,09	0,90	59,08		
	Chydorus sp.	Bad	littoral	Filtration	Herbivore	0,63	0,57	0,35	0,93		
	Daphnia ambigua	Bad	pelagic	Filtration	Herbivore	0,48	0,43	0,53	0,61	0,63	0,74
	Daphnia parvula	Bad	pelagic	Filtration	Herbivore	0,73	1,75	0,78	1,77	0,78	0,81
	Daphnia pulex	Bad	pelagic	Filtration	Herbivore			0,83	1,77	1,13	3,78
	Daphnia retrocurva	Bad	pelagic	Filtration	Herbivore	0,75	1,92	0,73	1,41	1,13	2,16
	Daphnia sp.	Bad	pelagic	Filtration	Herbivore	0,53	0,70	0,43	0,39	0,50	0,61
	Diaphanosoma brachyurum	Intermediate	littoral	Filtration	Herbivore	1,10	0,60	3,00	0,91	1,05	0,97
	Disparalona rostrata	Bad	littoral	Filtration	Herbivore	0,70	1,64				
	Eurycercus lamellatus	Bad	littoral	Filtration	Herbivore	1,50	9,91	1,85	30,31	1,88	26,61
	Ilyocryptus sp.	Bad	littoral	Surface Feeding	Detritivore	0,70	1,58	0,23	0,00		
	Leptodora kindti	Bad	pelagic	Current-cruiser	Carnivore			3,00	60,51	1,38	14,88

	Moina micrura	Bad	littoral	Filtration	Herbivore	0,83	1,63	0,80	1,62	0,90	2,10
	Monospilus dispar	Bad	littoral	Surface Feeding	Herbivore	0,45	1,66	0,60	4,03	0,55	1,83
	Pleuroxus sp.	Bad	littoral	Filtration	Herbivore	0,78	1,31			0,43	1,51
	Pseudochydorus globosus	Bad	littoral	Surface Feeding	Herbivore	0,43	3,10	0,60	12,01		
	Rhynchotalona falcata	Bad	littoral	Surface Feeding	Herbivore	0,43	0,55	0,28	0,29	0,43	1,51
	Scapholeberis mucronata	Bad	littoral	Filtration	Herbivore	0,60	1,04				
	Sida crystallina	Bad	littoral	Filtration	Herbivore	1,88	5,05	2,38	6,61	1,75	6,31
	Simocephalus serrulatus	Bad	littoral	Filtration	Herbivore	1,60	2,35				
	Simocephalus sp.	Bad	littoral	Filtration	Herbivore	0,55	0,47				
Calanoida	Calanoida copepodites	Good	pelagic	Stationary Suspension	Herbivore	1,00	1,69	1,08	1,82	1,08	1,91
	Calanoida nauplii	Bad	pelagic	Stationary Suspension	Herbivore	0,28	0,09	0,50	0,13	0,35	0,09
	Eurytemora carolleeae	Good	pelagic	Stationary Suspension	Herbivore	1,28	7,28	1,38	8,19	1,33	7,85
Cyclopoida	*Acanthocyclops robustus*	Intermediate	pelagic	Grasping	Omnivore	1,15	3,05	1,25	5,15	1,30	4,79
	Acanthocyclops venustoides	Intermediate	littoral	Grasping	Omnivore	1,00	4,66	0,80	3,09		
	Cyclopoida copepodites	Intermediate	generalist	Grasping	Omnivore	0,90	0,84	0,95	1,01	1,10	1,28
	Cyclopoida nauplii	Bad	littoral	Grasping	Omnivore	0,50	0,08	0,28	0,07	0,33	0,05
	Cyclopoida sp.	Intermediate	littoral	Grasping	Omnivore	0,50	1,34			0,58	1,87
	Eucyclops agilis	Intermediate	littoral	Grasping	Omnivore	0,98	2,37	0,83	2,82	0,98	3,15
	Eucyclops elegans	Intermediate	littoral	Grasping	Omnivore	0,85	2,28			0,80	3,69
	Eucyclops prionophorus	Intermediate	pelagic	Grasping	Omnivore	0,78	2,78	0,75	2,91		
	Macrocyclops albidus	Intermediate	littoral	Grasping	Omnivore	1,38	6,64	1,25	9,13	1,25	12,04
	Macrocyclops ater	Intermediate	littoral	Grasping	Omnivore	1,48	13,89			0,63	2,28
	Mesocyclops edax	Intermediate	pelagic	Grasping	Omnivore	0,83	2,19	0,83	2,39	0,90	2,51
	Microcyclops rubellus	Intermediate	littoral	Grasping	Omnivore	0,60	1,15	0,55	1,56	0,58	1,33
	Tropocyclops prasinus	Intermediate	pelagic	Grasping	Omnivore	0,60	1,16				

Harpacticoida	Harpacticoida copepodites	Bad	littoral	Surface Feeding	Detritivore	0,55	0,46	0,38	0,42	0,48	0,43
	Harpacticoida nauplii	Bad	littoral	Surface Feeding	Detritivore	0,33	0,11	0,28	0,15		
	Harpacticoida sp.	Bad	littoral	Surface Feeding	Detritivore			0,75	1,40	0,40	0,63
	Nitokra hibernica	Bad	littoral	Surface Feeding	Detritivore	0,55	0,99	0,50	0,98	0,68	0,91
	Nitokra sp.	Bad	littoral	Surface Feeding	Detritivore	0,63	0,98			0,50	0,99
	Onychocamptus mohammed	Bad	littoral	Surface Feeding	Detritivore	0,55	1,34			0,48	1,18

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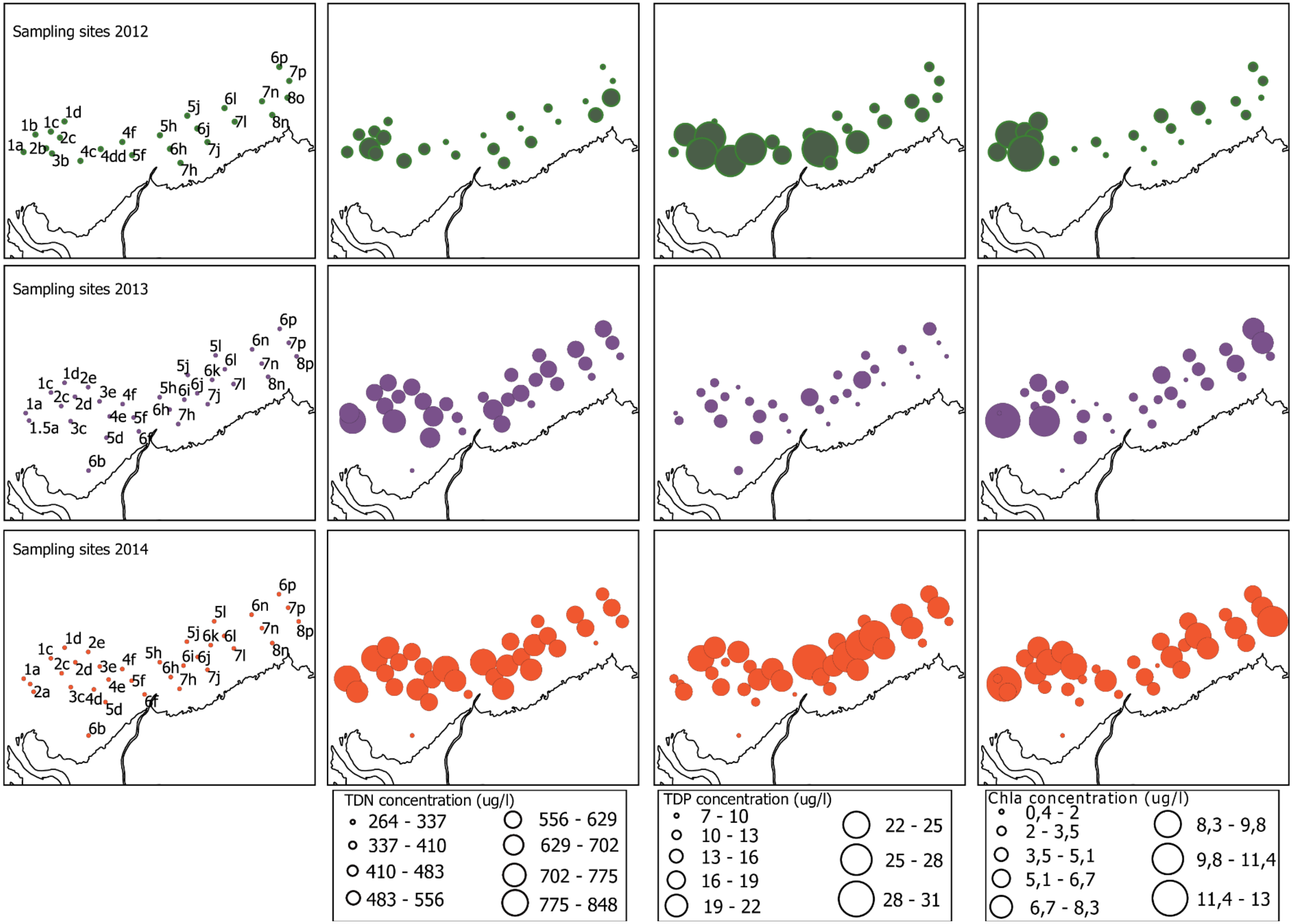

Figure S1. Spatio-temporal variation in biotic and abiotic variables.

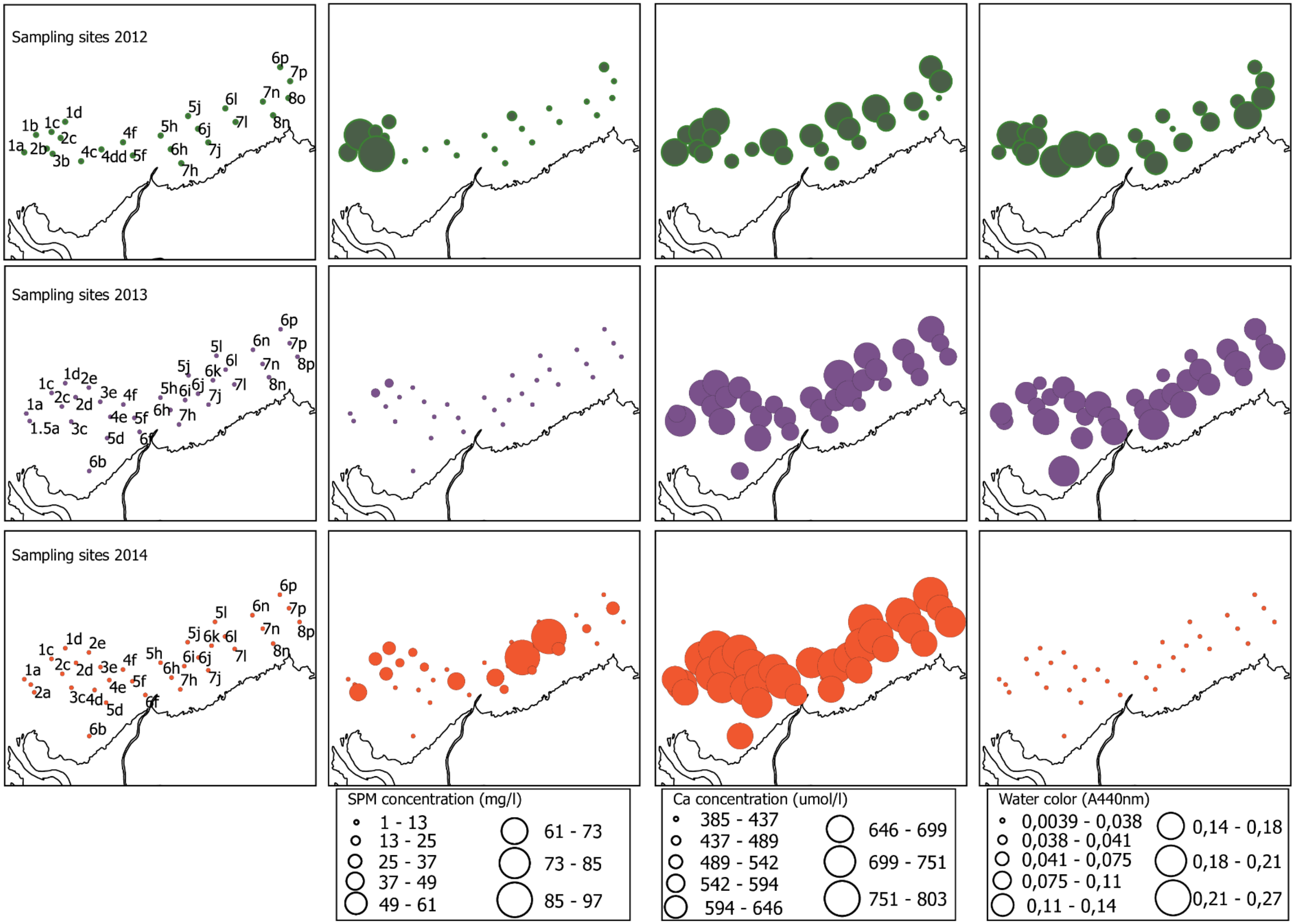

Figure S1. Spatio-temporal variation in biotic and abiotic variables (Suite)

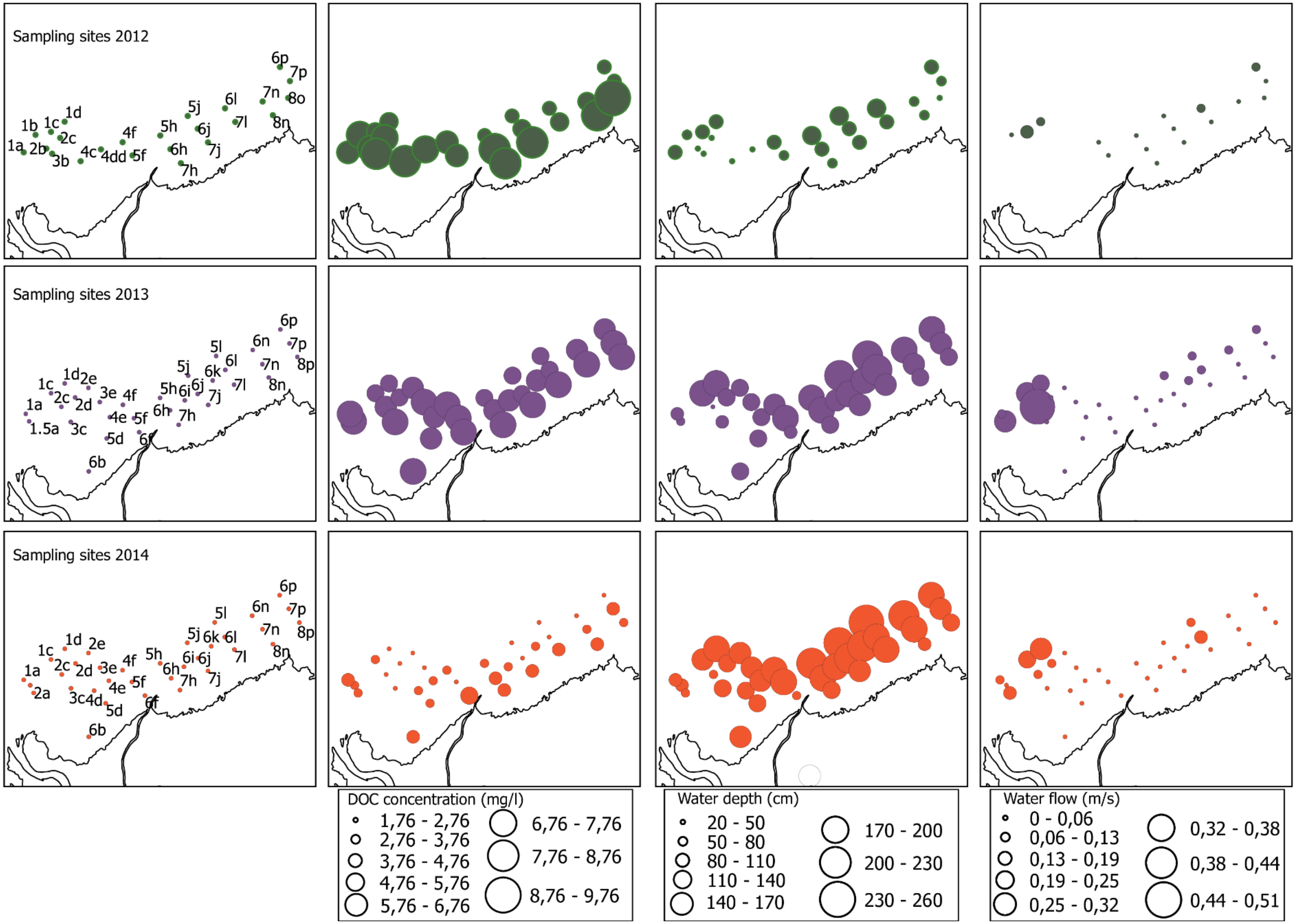

Figure S1. Spatio-temporal variation in biotic and abiotic variables (Suite)

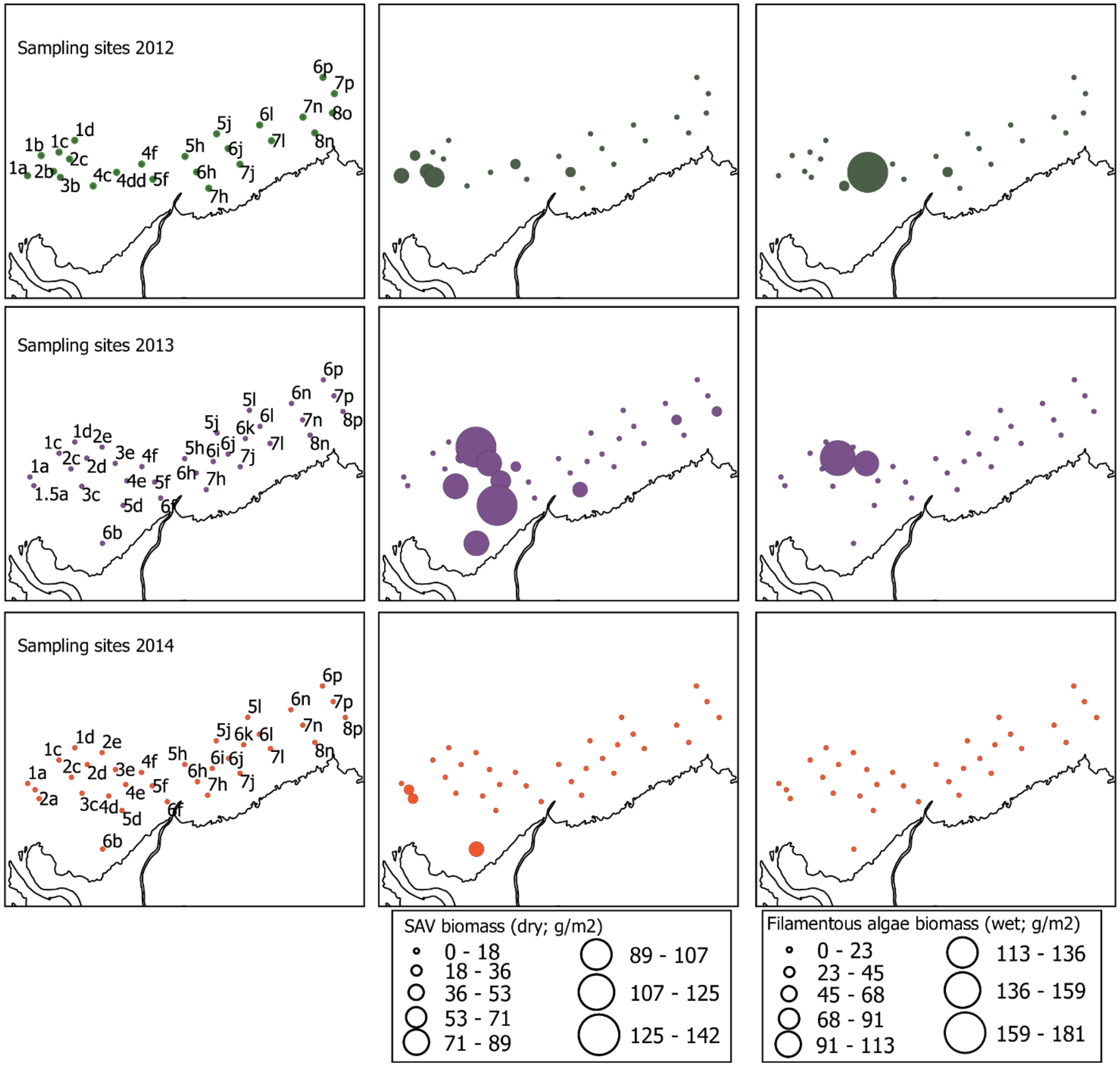

Figure S1. Spatio-temporal variation in biotic and abiotic variables (Suite)

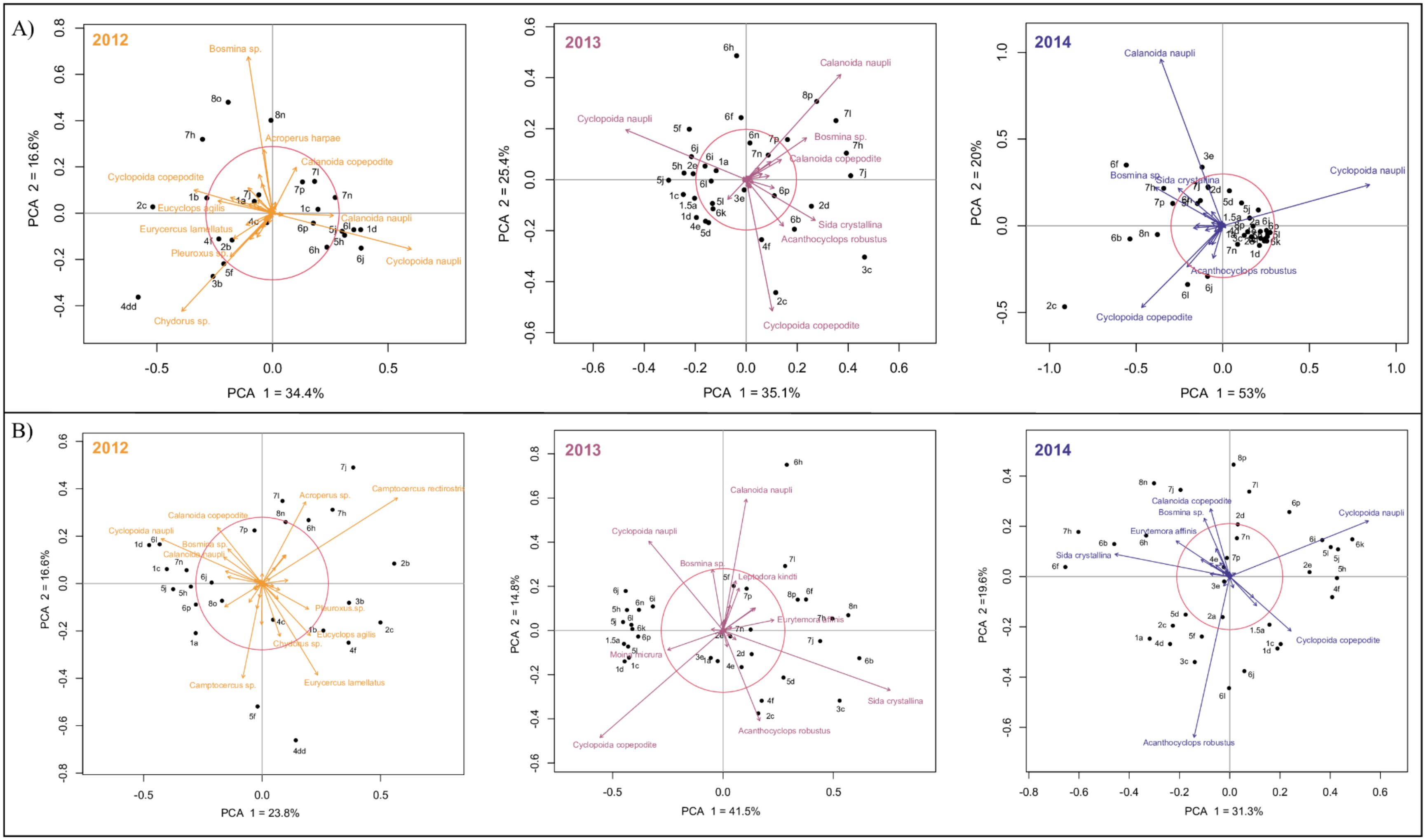

Figure S2. PCA based on zooplankton A) abundance and B) biomass for the three years of analysis. Taxa outside the circle are those contributing the most to the two PCA axes.

CHAPITRE 2

DOES SUBMERGED AQUATIC VEGETATION SHAPE ZOOPLANKTON COMMUNITY STRUCTURE AND FUNCTIONAL DIVERSITY? A TEST WITH A SHALLOW FLUVIAL LAKE SYSTEM

Cet article est publié dans la revue *Hydrobiologia*

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Référence complète :

Bolduc, P., A. Bertolo et B. Pinel-Alloul. 2016. Does submerged aquatic vegetation shape zooplankton community structure and functional diversity? A test with a shallow fluvial lake system. *Hydrobiologia*, *778*(1), 151-165.

2.1 Abstract

Submerged aquatic vegetation (SAV) plays important roles in shallow lakes. In addition to its refuge effect for zooplankton, one key role of SAV is to provide diverse ecological niches to these organisms. The reduction of habitat complexity due to loss of SAV might thus have huge effects on zooplankton communities. The objective of this study was to investigate the relationship between SAV abundance and composition and zooplankton functional diversity and community structure. We used as model system the littoral zone of Lake St. Pierre (Québec, Canada), a shallow fluvial lake experiencing dramatic changes in SAV cover. Our sampling protocol allowed us to analyse the relationship between SAV and zooplankton along a gradient of SAV abundance. We showed that SAV abundance explained 41% of the variation in the zooplankton community structure and 25% of the variation in zooplankton functional diversity. Our results also indicated that the presence of the benthic cyanobacterium *Gloeotrichia* sp. in SAV beds had a structuring effect within the dominant family of Chydoridae, being negatively correlated to the abundance of relatively large-bodied species. Our findings suggest that loss in SAV biomass and complexity can affect both community structure and functional diversity of zooplankton in shallow fluvial lakes.

Keywords

Zooplankton community structure · Functional diversity · Submerged aquatic vegetation · Fluvial shallow lakes

2.2 Introduction

Submerged aquatic vegetation (SAV) plays many ecological roles in the littoral zone of shallow lakes, where they can cover extensive areas. In Norwegian north temperate lakes, it has been shown that these productive habitats host a large part of the lake biodiversity, contributing to more than two-third of total crustacean zooplankton species richness (Walseng et al., 2006). SAV beds also help maintain a high density and biomass of zooplankton in shallow lakes (Scheffer, 2004).

Several mechanisms have been suggested to explain the positive relationship observed between SAV and zooplankton diversity and abundance, and much emphasis has been put on its potential role as an antipredator refuge (Timms & Moss, 1984; Jeppesen et al., 1997). Although the effectiveness of SAV as a refuge for zooplankton varies among north temperate (Denmark, Norway) and warm (subtropical and Mediterranean) lakes (Castro et al., 2007), SAV habitats have been widely recognized to contribute to maintaining a higher biodiversity, density and biomass of zooplankton compared to the open water (Scheffer 2004; Walseng et al., 2006; Meerhoff et al., 2007; Brucet et al., 2009; González Sagrario & Blaseiro, 2010).

Another key factor potentially explaining this positive relationship is the physical structural complexity of the SAV beds, which provides various ecological niches for zooplankton (Walseng et al., 2006; Van Onsem et al., 2010). Higher habitat heterogeneity within SAV beds should thus increase species richness and functional diversity by increasing niche availability (Heck & Crowder, 1991; Kelaher & Castilla, 2005; Willis et al., 2005; Matias et al., 2010). Despite the fact that SAV is not the more profitable habitat for some open-water zooplankter due to relatively low phytoplankton resources within SAV beds (Burks et al., 2002), it has been shown that SAV physical complexity is positively related to zooplankton diversity (Declerck et al., 2007; Meerhoff et al., 2007). These results give support to the hypothesis that SAV beds provide more niches compared to the open water habitat (Pennak, 1957; Basu et al. 2000; Walseng et al., 2006).

Despite the multiple ecological roles of SAV beds such as reducing sediment resuspension and maintaining a high water quality (Madsen et al., 2001; Horpilla & Nurminen, 2003; Jeppesen et al., 2012), anthropic activities are increasingly threatening these key habitats. During the last decades, several studies have reported a SAV-reduction in human-impacted lakes (Blindow, 1992; Körner, 2002). By using a paleoecological approach, Vermaire et al. (2012) suggested that nutrient inputs and water-level fluctuations were the main factors explaining the observed reduction of SAV abundance in southern Quebec lakes. Given that a high-grazing potential by filter-feeders in SAV beds has been suggested to be one key mechanism explaining the positive role of SAV in stabilizing a clearwater state in shallow lakes (Scheffer et al., 1993), it is crucial to better understand the association between SAV and zooplankton.

The aim of this study is to investigate the relationship between SAV biomass and composition and zooplankton community structure and functional diversity in a system experiencing spatio-temporal variations in SAV biomass. We predicted that SAV biomass i) would correlate with zooplankton total biomass, ii) would explain variations in zooplankton community structure, via its positive effect on structural complexity and refuge availability, and iii) would increase zooplankton functional diversity (FD), due to higher niche availability.

2.3 Methods

2.3.1 Study site

Our study was conducted on the littoral zone of Lake Saint-Pierre (LSP; Fig.1), the largest shallow fluvial lake of the St.-Lawrence River (Quebec, Canada). This atypical shallow lake (area: 300 km^2; mean depth: ca. 3 m) is an open system characterized by two shallow littoral vegetated zones covering around 70% of the lake area (Jean & Létourneau, 2014) separated by a deep navigation channel (11 m depth; Fig. 1). In LSP, nutrient inputs are highly variable (probably caused by water coming from farmland tributaries), and show average values of 0.4 mg·L^{-1} for nitrates (min-max: 0.1-3.3) and 0.3 mg·L^{-1} (min-max: 0.01-6.9) for total phosphorus (Tall et al., 2015). The draining basin on the south shore of LSP is mainly occupied by intensive agriculture, leading to potential high inputs of nutrients which can promote the development of benthic cyanobacteria (Lévesque et al., 2012). The occurrence of benthic cyanobacteria such as *Lyngbya wollei* (Farlow ex Gomont) Speziale & Dyck and *Gloeotrichia* sp. have been related with low SAV biomass in the south shores of LSP, and is considered as a symptom of ecosystem degradation (Lévesque et al., 2012; Hudon et al., 2014). The fish community is composed of up to 80 species (Laviolette et al., 2003), with a high abundance of potential planktivores such as juvenile yellow perch *Perca flavescens* (Mitchill, 1814) in the littoral zone (A. Bertolo, pers. obs), including our study site.

Samples of SAV, hereafter define as vascular macrophytes and benthic algae, and zooplankton were collected at 25 sites in the south shore of LSP within the plumes of two main tributaries, the St. François and Yamaska Rivers (Fig. 1). This area of approximately 26 km^2 is characterized by a gentle slope, very slow water current and important spatial variation in SAV cover from upstream to downstream. Sampling was performed in August 2012, a period corresponding to the maximum abundance and growth of SAV bed. Environmental variables (nutrients, phytoplankton chlorophyll, water colour and flow velocity, Table 1) were also measured at the sampling sites. To ensure that all sites were located in the plumes of the St. François and Yamaska water masses, we determined their position based on the analysis of Landsat 5 and Landsat 7 Enhanced Thematic Mapper satellite images taken 2 weeks before the field campaign. Sites were thereafter placed on a regular grid allowing a full coverage of the whole SAV gradient within a relatively small gradient of water depth (76.7 cm ± 33.8).

2.3.2 Zooplankton sampling, biomass and functional traits

Water was collected in SAV at each site using a submersible pump (Rule, model 1500) (Masson et al., 2004) connected to a digital water smart-flow meter (Gardena; model 9188) and filtered with a zooplankton net (153-µm mesh size). This method enabled us to sample zooplankton in large volumes of water in densely vegetated areas (approximately 200 L per station). Despite that the 153-µm mesh size could probably have underestimated the abundance of smaller zooplankton such as nauplii and rotifers, this filtering method was the most efficient to avoid clogging due to the large amounts of plant detritus. Zooplankton organisms were fixed in a 4% sugar-formaldehyde solution prior to identification (Prepas, 1978). Crustacean zooplankton identification was conducted at the species level when possible using Edmonston (1959), Amoros (1984) & Hebert (1995) for cladocerans, and Edmonston (1959), Smith & Fernando (1978), Hudson & Lesko (2003) and Haney et al. (2010) for copepods. The first 30 individuals of each crustacean species were measured to determine their mean biomass based on length-weight relationships (Malley et al., 1989). All cladocerans and copepods were identified and counted. Rotifers were only counted (no taxonomic identification) in order to have a rough estimate of their biomass (Bottrell et al., 1976). These counts were reported as number of individuals per liter of filtered water. Crustacean zooplankton species were grouped at the family level for the community structure analysis. As the Chydoridae are the dominant zooplankton taxa in our study area, we analyzed it more thoroughly (i.e., genus level). Nauplii and copepodite stages were considered as distinct "functional species" from adults for the analysis of zooplankton community structure and functional diversity because of traits differences in size and diet (Reid and Williamson, 2010). Each functional species, defined at different taxonomic resolution (e.g. *Bosmina* or a cyclopoid copepodite) was classified according to six functional traits based either on direct measurements (mean dry weight, maximum length) or derived from the literature (habitat, swimming capacity, feeding-type and trophic level) (Barnett et al., 2007; Massicotte et al., 2014). Given the lack of data about the swimming capacity of the different species of zooplankton, the taxonomic group was used as a proxy of the swimming capacity (i.e., cladocerans, calanoids, cyclopoids and harpacticoids) (Drenner & McComas, 1980). For more details about the traits used, see Table S1 (supplementary information) in Massicotte et al. (2014). Variation in functional traits among sites was computed to quantify the FD of zooplankton communities using the *dbFD( )* function in the "FD" package in R (Laliberté et al., 2014). Four indices of functional diversity were calculated: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villeger et al., 2008) and functional dispersion (FDis) (Laliberté & Legendre, 2010). FRic is represented by the maximum convex hull including all the species of a community (Villeger et al., 2008). The other two indices (FEve and FDiv) are standardized between 0 and 1, where a FEve value of 1 indicates that species are evenly distributed in the space of traits with similar abundance and FDiv represents traits diversity with value of 1 indicating that the most abundant species have extreme functional trait values (Villeger et al., 2008). FDis values have no upper limits, with the higher FDis values represent a larger traits dispersion in the space of traits (Laliberte & Legendre, 2010). FDis is the mean distance of individual species to the centroid of all species in the community in the traits space and, in contrast to the other three indices, is by construction not correlated to species richness (Laliberte & Legendre, 2010).

2.3.3 SAV sampling

SAV biomass was estimated at each site with a double-headed rake (35 cm wide) (Yin et al., 2000) dragged over a distance of approximately 1 m (0.35 m^2 total sampling area). To reduce the variability between sites associated to different performances in plant sampling, the same person performed the scraping during the entire sampling period. SAV samples were rinsed and kept frozen until laboratory analysis. Vascular macrophytes were identified at the species level and subsequently dried (50ºC) and weight (to the nearest 0.1 mg). Dry weight of filamentous chlorophytes and benthic cyanobacterium *L. wollei* were also measured. The dry weight of each SAV taxon was used in the analysis. Presence or absence of the benthic colonial cyanobacterium *Gloeotrichia* sp. was recorded directly on the field. Given that benthic cyanobacteria could form large and dense mats, they can contribute to alter the physical structure of the habitat for zooplankton. For this reason, they were included in the analysis as a component of SAV.

2.3.4 Environmental variables

At each site, we measured water depth and transparency. As the average depth of the sites was 1.5 m, we used a Schnell tube instead of a Secchi disc to measure water transparency. We used a multiparameter sonde YSI model 556MPS (YSI Incorporated, USA) to obtain a vertical profile of temperature, dissolved oxygen, pH, conductivity and redox potential. Underwater light attenuation was measured using a Li-Cor (model LI-193SA Underwater Quantum Sensor) at each 0.25 m. Water samples were collected using a Tempest pump at 0.5 m below the water surface before zooplankton sampling. Whereas this might have caused some disturbance to zooplankton, this sequence was chosen to avoid the contamination of water samples by sampling zooplankton first. Both filtration and nutrients analysis methods (total phosphorus, total dissolved phosphorus, total nitrogen, total dissolved nitrogen, nitrate and ammonium) were already described in D'Arcy & Carignan (1997). To determine DOC concentration, water was filtered using a 0.45-µm syringe filter (Nalgene SFCA). Filters were then stored in acid-washed vials at 4ºC prior to analysis and placed in a wet persulfate oxidation solution. DOC analysis was performed with an Aurora 1030 TOC Analyzer equipped with an auto sampler (model 1088, IO Analytical Instruments). To determine phytoplankton chlorophyll-*a* and pheopigment concentrations, water was filtered through a 25 mm diameter Whatman GF/F filters (nominal pore size 0.7 mm). Filters were kept frozen until analysis when chlorophyll-*a* was extracted overnight with 95% ethanol in the dark. Spectrophotometric analyses of the solutions were performed as in Bergmann & Peters (1980). Chlorophyll-*a* and pheopigment concentrations were then calculated using equations of Lorenzen (1967). Water colour was measured at 440 nm absorbance following methods used by Cuthbert &

Del Giorgio (1992). Water flow was measured at each site using a current velocity indicator (model 3000, Swoffer Instruments Inc.).

2.3.5 Spatial variables

To better understand the importance of SAV and environmental variables in shaping zooplankton communities, it is important to control for the spatial autocorrelation between sites. Not taking into account spatial autocorrelation in the analysis of field data can in fact lead to biased results and inflated type I error (Legendre & Fortin 1989). Therefore, we combined geographical coordinates with information on water flow direction to create spatial variables by using a spatially explicit statistical method, the asymmetric eigenvector maps (AEM) (Blanchet et al., 2008b). This method allows modeling the directional spatial process influencing the distribution of species. In our study system, the water flow could have influenced the distribution of bulk zooplankton, but also affected differentially the distribution of different species within the community, depending on their specific swimming capacities. To measure the degree of correlation among neighbouring observations, we calculated the Moran's I coefficient for each eigenfunction (hereafter "AEM variable") produced by the AEM procedure (Legendre & Fortin, 1989). As we were interested in the patterns produced by spatially contagious processes, which can lead to positive spatial correlation, we choose to keep only positive and significant variables according to Moran's I coefficient for further analysis (Borcard et al., 2011). Sites were georeferenced with a *Differential Global Positioning System* (DGPS), allowing accuracy in the range of decimeters.

2.3.6 Statistical analyses

Detrended correspondence analysis (DCA) was used to verify the length of the gradient of the zooplankton community data prior to analysis. As the range of the ordination score obtained was lower than three standard deviations, we used redundancy analysis (RDA) to model our data, since assuming a linear relationship between zooplankton and explanatory variables is appropriate in this case (Jongman et al., 1995).

Both zooplankton community structure (assessed from the biomass of the different taxa present in the sample) and functional diversity (four FD indices; see above) were modeled using partial redundancy analysis (pRDA) where SAV, environmental and spatial variables were used as explanatory datasets. Taking into account these three components allowed us to separate their role in shaping zooplankton community structure and functional diversity.

To avoid multicollinearity, only explanatory variables with a variance inflation factor below ten were kept in the analysis. Subsequently, we used a two-steps forward selection procedure (significance level: $\alpha = 0.05$; Blanchet et al., 2008a) to select the environmental and SAV variables to be included in the RDAs explaining zooplankton community structure and functional diversity. The statistical significance of selected variables was tested by a Monte Carlo permutation test ($n = 999$).

Variation partitioning was performed through multiple RDAs and pRDAs (Borcard et al., 1992) to partition the amount of explained variation of the zooplankton community structure and functional diversity attributable to independent and confounded effects of the three different explanatory datasets (Fig. S1-Online resource). These components were computed using the *varpart( )* function in "vegan" [R] package (Oksanen, 2013).

For the analysis of SAV, we modeled zooplankton data with both total SAV biomass and SAV biomass by taxon (7 taxa). Only the models explaining the largest part of the variation are presented in the results section. Prior to analysis, zooplankton species abundance was transformed using the Hellinger transformation (square root of the relative abundance of each species in the site), allowing the reduction of the relative weight of abundant species in the analysis (Legendre & Gallagher, 2001). SAV and ENV variables were log-transformed. Numerical analyses were performed using the [R] graphical and statistical computing environment (R Core Team, 2015).

2.4 Results

In our study system, mean depth was 76.7 cm (± 33.8), mean chlorophyll a was 3.8 $\mu g \cdot L^{-1}$ (± 2.9), mean water colour was 0.1 (± 0.05) while mean water flow was 0.03 $m \cdot sec^{-1}$ (± 0.04). Environmental variables describing the study site including those not selected for the RDA are presented in Table 1. SAV community was dominated by *Vallisneria americana* Michx. (60.7 ± 36.6 % of total biomass), followed by *Potamogeton richardsonii* (A. Benn.) Rydb. (17.0 ± 25.1 % of total biomass) and *Elodea nuttallii* (Planch.) H. St. John (3.6 ± 10.3 % of total biomass). The remaining four species (*Stuckenia pectinata* (L.) Börner, *Chara* sp., *Heteranthera* *dubia* (Jacq.) MacMill., *Myriophyllum* sp.) present in the community represented each less than 3.5%.

2.4.1 Zooplankton community structure

Despite their underestimation due to the mesh size of the zooplankton net, the most abundant zooplankton functional groups in our samples were cyclopoid nauplii, followed by rotifers and cyclopoid copepodites (Table 2). Cyclopoids (Cyclopidae) and calanoid (Temoridae) adults were rarely found in our study system and accounted on average for only 0.08 and 0.03 $ind \cdot L^{-1}$ respectively. Cladocerans were mainly represented by the Bosminidae, Chydoridae and Sididae families (0.87-0.27 $ind \cdot L^{-1}$). Despite their relatively low abundance, Chydoridae accounted for the largest share of the biomass in our study system (47.9 % of total zooplankton biomass) due to the relatively large size of some genera, such as *Camptocercus*, *Chydorus*, *Eurycercus*, and *Acroperus* (Table 3), which were the largest in our study system. Within this family, the genus *Camptocercus* (median length of 0.55 mm), *Chydorus* (median length of 0.21 mm) and *Eurycercus* (median length of 0.63 mm) were the most abundant and those contributing most to the Chydoridae family biomass. Finally, we also found a positive relationship between total SAV biomass and total zooplankton biomass (Spearman's $r = 0.63$).

Among all variables, the forward selection procedure retained two environmental variables (ENV), two SAV variables and five spatial variables (AEM) to explain zooplankton community structure based on biomass: a) water colour and water flow predicting 37.7 % (based on adjusted-R^2); b) the biomass of the most abundant macrophyte *V. americana*, representing 60% of SAV biomass in our study system), and the presence of the cyanobacterium *Gloeotrichia* sp. explaining together 41.3 %; and c) the five spatial variables predicting 7.9 % of the total variation in zooplankton biomass (Table 4).

We performed a pRDA including SAV and ENV variables, with AEM variables as covariables in order to understand how zooplankton families were related to both environmental and SAV variables while controlling for spatial autocorrelation (Fig. 2a). This model explained 44.1 % of the total variation in zooplankton community structure (Table 4), with the first two axes explaining, respectively, 37.1 % and 4.5 % of this variation. The first axis represented a gradient of higher biomass of *V. americana*, the occurrence of the benthic cyanobacterium *Gloeotrichia* sp, and higher water colour. We also detected a strong negative relationship between SAV biomass (mainly *Vallisneria*) and the water flow (Fig. 3). In the same way, we found a strong relationship between *V. americana* and water colour (Spearman's r = 0.70). The first RDA axis shows that *V. americana* was strongly related to the Chydoridae family (Pearson's r = 0.73), and inversely related to cyclopoids nauplii. Greater occurrence of the cyanobacterium *Gloeotrichia* sp. in more coloured water was related to higher biomass of the Bosminidae and Sididae families, and lower abundance of cyclopoid nauplii along Axis 2.

Variation partitioning revealed that SAV, ENV and AEM variables explained together 42.9 % of the total explained variation in zooplankton community structure (see Table 4 for the variation explained by each component). The variation explained by AEM variables alone resulted to be negligible (less than 1 %), whereas their effect confounded with SAV and the ENV variables was of 7.9 % (sum of the SAV + AEM and ENV + AEM columns in Table 4). The variation of zooplankton community structure explained by SAV alone (i.e., after controlling for both environment and spatial variables) was 9.1 % (Fig. S2- Online resource). The variation explained by ENV factors alone was 7.2 % while the shared variation of SAV with ENV variables explained 27.4 %.

As the Chydoridae family was the most important in terms of biomass (Table 2), we examined more closely the relationship between the main genera of the Chydoridae family and total SAV biomass using the same approach used for the whole community (Fig. 2b). The total amount of variation explained by SAV, ENV and AEM was 38.3 %, whereas the pure contribution of SAV was of 19.4 % (Table 4), with the first two RDA axes explaining 16.0 % and 3.7 % respectively. Axis 1 was strongly associated with the cyanobacteria *Gloeotrichia* sp. and was correlated with *Acroperus* sp. but inversely related to *Eurycercus* sp. Axis 2 was related to total SAV biomass and was strongly associated to the genera *Pleuroxus* sp. and *Chydorus* sp., and inversely related to *Alona* sp. The portion of variance in Chydoridae community structure explained by SAV alone (i.e., controlling for both ENV and AEM variables) represented 19.4 % of the total explained variation (Table 4). Despite a slightly better explanatory power, the result obtained using total SAV biomass is in accordance with the result obtain using only *V. americana*, giving the fact that this species is the most important SAV component in our system. ENV variables, taken alone, accounted for 7.1 %, a similar amount as for the whole community. Compared to what was found for the whole zooplankton community, the shared portion of SAV and ENV variables was relatively low (3.6 %). The variation explained by the spatial variables (AEM) was negligible (1.3 %) whereas their confounded parts with SAV and the ENV variables were 9.4 % (sum of the SAV + AEM and ENV + AEM columns in Table 4).

2.4.2 Zooplankton functional diversity

Whereas FRic showed values near zero and small variation (s.d.< 0.01), all the other indices of functional diversity showed a relatively higher degree of variation. FEve mean value was 0.66 ± 0.08 (mean ± s.d.), FDiv mean value was 0.93 ± 0.04 and FDis mean value was 0.28 ± 0.02.

The model including SAV, ENV and AEM for the explanation of variance of zooplankton functional diversity (FD) accounted for 25.5 % of the total variation (Table 4). The forward selection procedure included *V. americana* among the SAV variables (sum of columns SAV, SAV+ENV, SAV+AEM and SAV+ENV+AEM in Table 4 accounting for 24.5 %) and water depth among the environmental variables (sum of columns ENV, SAV+ENV, ENV+AEM and SAV+ENV+AEM in Table 4 accounting for 13.0 %). The five selected AEM variables were also included but they explained a relatively low share of the total variation in zooplankton functional diversity (6.0 %). The pRDA including functional diversity indices in relation with SAV (ENV and AEM as covariables) showed that *V. americana* was represented along Axis 1, accounting for 12.5 % of explained zooplankton FD variation (Fig. 2c). SAV was inversely related to FEve, indicating that functional evenness was relatively low when *V. americana* biomass was high. On the opposite, functional dispersion (FDis) was directly related to *V. americana* biomass. The FDiv index was inversely related to *V. americana* but showed relatively low variation in our study system. No variation in FRic was apparent. The variation partitioning showed that the portion explained only by the SAV, after removing the combined effect with ENV and AEM variables, accounted for 12.5 % of the explained variation (Table 4). The shared portion explained by SAV and environmental variable accounted for 7.1 % while the shared portion of SAV, environmental and spatial variable was 4.8 %.

2.5 Discussion

Our results showed that SAV, together with environmental variables, is an important factor influencing not only zooplankton total biomass but also zooplankton community structure and functional diversity. These results, in accordance with another study on copepods in the St. Lawrence River (Pinel-Alloul et al., 2011), confirm our initial hypotheses and suggest that SAV are key habitat for maintaining diverse functional traits in crustacean zooplankton in shallow fluvial lakes.

2.5.1 Zooplankton total biomass and community structure

As predicted, total zooplankton biomass correlated directly with SAV abundance, in part due to the large number of plant-associated species in our samples. This positive relationship also confirms the key role of SAV habitats in maintaining a high abundance of zooplankton in lacustrine food webs. Moreover, the abundance of *V. americana* in SAV beds is the strongest factor explaining the relationship between SAV biomass and zooplankton community structure. Chydoridae seem in fact to find a good habitat in *V. americana* beds whereas the nauplii of cyclopoids were more frequent in the open water under higher water flow. In both cases, the sign of the relationships between SAV habitat and zooplankton could be easily explained by the ecological traits of these two functional groups. Beside their supposed flexibility and tolerance to environmental gradients, Chydoridae can respond to environmental gradients by showing a high degree of segregation across the littoral zone in macrophyte beds (Adamczuk, 2014). In our case, the strong positive relationship found between *V. americana* and the Chydoridae suggests a preferential habitat and potentially a possible refuge effect against fish predation. Moreover, these relatively large-bodied epiphytic and benthic cladocerans apparently found in vegetated complex habitat optimal conditions with low water flow velocity. This effect is probably behind the positive relationship between SAV and total zooplankton biomass. In contrast, the negative relationship observed between Cyclopidae nauplii and SAV biomass is probably explained by their pelagic lifestyle (Chullasorn et al., 2009). Whereas these effects might be interpreted *per se* as a physical-biological forcing of SAV on zooplankton community structure, the large share of variation confounded with environmental factors indicates important interactions between habitat resources and water flow and quality within *V. americana* beds. Given that our study area showed a relatively reduced variation in water depth within the plumes of the tributaries in the south shores of the LSP, the negative relationship between SAV biomass and flow velocity could be interpreted as a direct negative effect of SAV beds on water flow. Therefore, the confounded effect of water flow velocity and SAV on zooplankton could be seen as an indirect effect of SAV (as shown by the negative SAV biomass-water flow relationship; Fig. 3). Consequently, by slowing down the water flow, SAV further improve habitat quality for Chydoridae that are considered as bad swimmers (Barnett et al., 2007). This is consistent with previous studies showing that SAV beds could prevent zooplankton from being exported by the water flow (Basu et al., 2000).

Another important driver of the zooplankton community structure besides SAV biomass and water flow is the presence of the benthic cyanobacterium *Gloeotrichia* sp., which is known to be associated with ecosystem degradation (Hudon et al., 2014). The effects of the presence of benthic cyanobacteria on zooplankton community structure have not been widely documented compared to those of planktonic filamentous and colonial cyanobacteria (Havens, 2008). However, recent studies on macroinvertebrates in LSP indicated that lower abundance of macroinvertebrate grazers was related to benthic cyanobacteria, which reduce food and habitat availability (Tourville Poirier et al., 2010). Lévesque et al. (2012) showed that the presence of high benthic cyanobacteria abundance was related to low SAV biomass in LSP. The negative relationship between *Eurycercus* sp. and the presence of the benthic cyanobacterium *Gloeotrichia* sp. could be explained by the fact that *Eurycercus* sp. appears to be an obligatory periphyton scraper (Masclaux et al., 2014) and thus cannot feed on *Gloeotrichia* sp. which has a gelatinous sheet. However, the interpretation of the positive relationship observed between *Gloeotrichia* sp. and the genus *Acroperus* sp. is less obvious as this relationship has never been reported in the literature. While it has been shown that some zooplankton species (e.g. *Daphnia pulex*) can survive by feeding on this cyanobacteria (Fey et al., 2010), this has never been demonstrated for Chydoridae. Further studies are needed to confirm how to interpret these relationships.

The genera *Pleuroxus* and *Chydorus* were strongly related to the SAV biomass which could be explained by the fact that they need substrata to attach their diapausing eggs (Gyllström & Hansson, 2004). Therefore, more SAV biomass could be associated with more diapausing sites available. A positive relationship between *Chydorus* sp. and SAV biomass has also been reported by Lauridsen et al. (1996), which showed that *Chydorus* sp. were mainly macrophyte-associated and did not perform diel horizontal migration toward the open water. Contrary to what was reported in the literature, we found a negative relationship between SAV biomass and *Alona* sp. which is a puzzling result knowing that they are known to be also an epiphytic cladoceran (Sakuma et al., 2004).

2.5.2 Zooplankton functional diversity

Our results showed that *V. americana* biomass was the most important variable explaining zooplankton functional diversity, explaining alone 12.5 % (25% jointly with AEM and ENV) of FD variation. This result suggests that SAV increase the number of ecological niches, thus promoting the presence of zooplankton species with different functional traits (Barnett & Beisner, 2007). *V. americana* biomass was in fact positively related to zooplankton functional dispersion (FDis), meaning that *V. americana* is associated with zooplankton communities functionally more diversified compared to those found in the open water. However, an apparently contradictory result was obtained with zooplankton functional evenness (FEve) which was inversely related to *V. americana* biomass. The FDis index indicates the dispersion of the traits of a given community in the functional space and FEve is considered as an indicator of how the functional space is occupied within a community (Villéger et al., 2008). Therefore, our results suggest that zooplankton functional traits, despite a relatively wider distribution within the space of traits, were more irregularly distributed where SAV were more abundant. Whereas this might be interpreted as a direct negative effect of SAV on evenness, we suspect that this result might be due to the poor representation of functional diversity within the Chydoridae family. Only poorly detailed information exists about the functional traits of different Chydoridae species, and their contribution to total community functional diversity is probably underestimated. Among the different traits available, only mean dry weight and maximum length were calculated directly from our samples, whereas other traits were derived from general information about the family (e.g., habitat, swimming capacity, feeding-type, trophic level). Therefore, the higher representation of Chydoridae within SAV beds (i) widened the space of traits occupied by the whole community (higher FDis) on one side because of their higher size and biomass than the other families, and (ii) reduced the overall regularity of the traits distribution because of the low resolution of our traits database for this species-rich family. However, we cannot exclude that the available details about Chydoridae traits allowed indeed a proper estimation of their contribution to zooplankton functional diversity. If this will be proven correct by further studies, our results may simply indicate a high degree of habitat filtering when SAV is more abundant (Mouchet et al., 2010). This result could also be interpreted as a mechanism of competitive exclusion, where the Chydoridae family members outcompete other functional groups. This pattern was observed in some plant community, where reduced FEve was associated with high standing biomass of primary producers (Pakeman 2011). Massicotte et al. (2014) observed the same pattern with the zooplankton community of the St. Lawrence River, where they showed that FEve was negatively related to habitat heterogeneity.

In this study, variation partitioning allowed us to disentangle the importance of SAV, environmental (ENV) and spatial (AEM) process in shaping zooplankton community structure and functional diversity. Our results highlight that a change in the SAV abundance could have a direct effect on zooplankton total biomass, community structure and functional diversity. SAV biomass is an important component in maintaining high biomass of Chydoridae, thus promoting a relatively high total zooplankton biomass and functional diversity. Thus, the reduction of SAV beds could have a negative impact on zooplankton biomass and functional diversity, with potential large effects on ecosystem functions due to the key role of zooplankton as filter-feeders/scrapers in aquatic systems. This study shows for the first time the importance of SAV beds in shaping zooplankton functional diversity, confirming the importance of habitat heterogeneity in determining ecological functions within zooplankton communities (Massicotte et al., 2014). More research is now needed to expand our knowledge on zooplankton functional traits in order to have more realistic estimates of zooplankton functional diversity and thus better understand their potential effect on ecosystem functioning.

2.6 Acknowledgments

We would like to thank Ginette Méthot and Myriam Boisvert for their technical assistance for zooplankton identification. We also thank Philippe Massicotte, Raphaël Proulx and Guillaume Rheault for discussion about the experimental design and the statistical analysis. We also thank Captain Alain Ledoux for safely driving our team on the lake and the members of Jean-Jacques Frenette and Simon Bélanger laboratories who have helped during the sampling campaign as well as Christiane Hudon's team members who collected SAV data. Financial support was provided by the Fond Québécois de la Recherche Nature et Technologie (ISI-FQRNT), the RIVE-UQTR research centre, and the Groupe de Recherche Interuniversitaire en Limnologie et en environnement aquatique (GRIL), who also made possible data sharing between the researchers. Thanks to Morgan Botrel for the coordination during sampling and laboratory analysis. Finally, we thank the three reviewers and Mariana Meerhoff, associate editor, for their useful and constructive comments that help us improve significantly this paper. The authors declare that there is no conflict of interest.

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2.8 Tables

Table 1. Environmental variables describing the study site. The variables that were included in the zooplankton community structure and functional diversity analysis are in bold.

Environmental variables	Mean	Min-Max	Units
Water depth	76.7	20.0 - 137.0	cm
Water colour	0.1	0.04 - 0.3	-
Water flow	0.03	0 - 0.13	$m \cdot s^{-1}$
Chlorophyll-*a*	3.8	0.4 - 12.9	$\mu g \cdot L^{-1}$
Water transparency	62.2	20.0 - 111.0	cm
Water temperature	23.7	22.4 - 25.7	ºC
Dissolved oxygen	9.2	6.7 - 13.3	$mg \cdot L^{-1}$
pH	8.9	8.1 - 9.8	-
Conductivity	220	179 - 269	$\mu S \cdot cm^{-1}$
Redox potential	90.4	59.8 - 149.7	mV
Underwater light attenuation	2.2	0.02 - 5.6	$\mu mol \cdot m^{-2} \cdot s^{-1}$
Total phosphorus	48.9	27.1 - 105.7	$\mu g \cdot L^{-1}$
Total dissolved phosphorus	16.6	9.5 - 29.1	$\mu g \cdot L^{-1}$
Total nitrogen	525.0	340.9 - 890.1	$\mu g \cdot L^{-1}$
Total dissolved nitrogen	408.3	264.1 - 639.7	$\mu g \cdot L^{-1}$
Nitrate	31.2	< 0.1 - 157.8	$\mu g \cdot L^{-1}$
Ammonium	13.6	< 0.1 - 83.5	$\mu g \cdot L^{-1}$
Dissolved organic carbon	6.4	3.9 - 9.3	$mg \cdot L^{-1}$
Pheopigments	0.1	< 0.1 - 3.2	$\mu g \cdot L^{-1}$

Table 2. Zooplankton families included in the partial RDA of community structure, their relative abundance and their biomass within the study area. Family names in bold type are those appearing on Fig. 2. Rare taxa (< 0.01 ind·L-1 or µg·L-1) not shown are part of the Macrothricidae, Ilyocryptidae and Moinidae (Cladocera), the benthic group of the Harpacticoida (nauplii, copepodites, Laophontidae and Campthocamptidae families) and the fish parasites (Ergasilidae and Argulidae families).

Families	Family acronyme	Median abundance (ind·L^{-1}) (quartile 25% - quartile 75%)	Median biomass (µg·L^{-1}) (quartile 25% - quartile 75%)
ROTIFERA*	**Rot**	3.83 (1.05 - 6.52)	< 0.01
CLADOCERA			
Chydoridae	**Chy**	0.30 (0.04 - 1.81)	3.08 (0.50 - 3.07)
Sididae	**Sid**	0.27 (0.10 - 0.78)	0.55 (0.19 - 0.64)
Daphniidae	**Dap**	0.10 (0.03 - 0.30)	0.07 (0.03 - 0.08)
Bosminidae	**Bos**	0.87 (0.33 - 1.51)	0.20 (0.1 - 0.29)
COPEPODA			
Calanoid nauplii	**NaCa**	1.10 (0.00 - 1.89)	0.10 (0.00 - 0.11)
Calanoid copepodites	**CoCy**	0.14 (0.05 - 0.43)	0.28 (0.07 - 0.29)
Calanoid Temoridae (adults)	**Tem**	0.03 (0.01 - 0.29)	0.21 (0.07 - 0.26)
Cyclopoid nauplii	**NaCy**	29.83 (18.72 - 36.16)	1.72 (1.24 - 1.76)
Cyclopoid copepodites	**CoCy**	3.67 (1.16 - 13.42)	1.96 (0.77 - 2.48)
Cyclopoid Cyclopidae (adults)	**Cyclo**	0.08 (0.03 - 0.85)	0.91 (0.25 - 0.95)

*Rotifera included all rotifer's genera.

Table 3. Genera included in the partial RDA of the Chydoridae family, their relative abundance, biomass and median length within the study area. Genus name in bold type are those appearing on Fig. 2.

Chydoridae	Median abundance (ind·L^{-1}) (quartiles 25%-75%)	Median biomass (µg·L^{-1}) (quartiles 25%-75%)	Median length (mm) (quartiles 25%-75%)
Eurycercus	0.02 (0.00 - 0.31)	0.22 (0.00 - 5.83)	0.63 (0.60 - 0.75)
Acroperus	0.005 (0.00 - 0.15)	0.02 (0.00 - 0.42)	0.43 (0.40 - 0.53)
Camptocercus	0.15 (0.02 - 2.42)	0.90 (0.08 - 10.32)	0.55 (0.49 - 0.65)
Alonella	0.00 (0.00 - 0.08)	0.00 (0.00 - 0.08)	0.24 (0.20 - 0.28)
Alona	0.005 (0.00 - 0.17)	0.02 (0.00 - 0.20)	0.30 (0.25 - 0.43)
Chydorus	0.16 (0.05 - 1.39)	0.14 (0.01 - 0.57)	0.21 (0.20 - 0.27)
Pleuroxus	0.04 (0.00 - 0.13)	0.04 (0.00 - 0.18)	0.40 (0.33 - 0.46)
Disparalona	< 0.01	< 0.01	0.35 (0.33 - 0.43)
Monospilus	< 0.01	< 0.01	0.38 (0.33 - 0.38)
Rhynchotalona	< 0.01	< 0.01	0.30 (0.28 - 0.33)
Oxyurella	< 0.01	< 0.01	0.35 (0.35 - 0.48)
Pseudochydorus	< 0.01	< 0.01	0.43 (0.43 - 0.43)
Biapertura	< 0.01	< 0.01	0.50 (0.50 - 0.50)
Treptocephala	< 0.01	< 0.01	0.38 (0.38 - 0.38)
Dunhevedia	< 0.01	< 0.01	0.48 (0.48 - 0.48)

Table 4. Variation partitioning between SAV, spatial (AEM) and environmental (ENV) variables explaining the community structure of zooplankton (families biomass), the structure of Chydoridae family (genera biomass) and zooplankton functional diversity (FD). Numbers are express in percent of variance explained.

	SAV	AEM	ENV	SAV+ AEM	SAV+ ENV	ENV+ AEM	SAV+ENV+ AEM	Total variation explained
Community structure (covariables: ENV + AEM)	9.1	< 0.1	7.2	4.8	27.4	3.1	< 0.1	42.9
Community structure (covariable : AEM)	-	< 0.1	-	-	44.0	-	3.1	42.9
Chydoridae family	19.4	1.3	7.1	6.6	3.6	2.8	< 0.1	38.3
FD	12.5	< 0.1	< 0.1	< 0.1	7.1	1.0	4.8	25.5

2.9 Figures

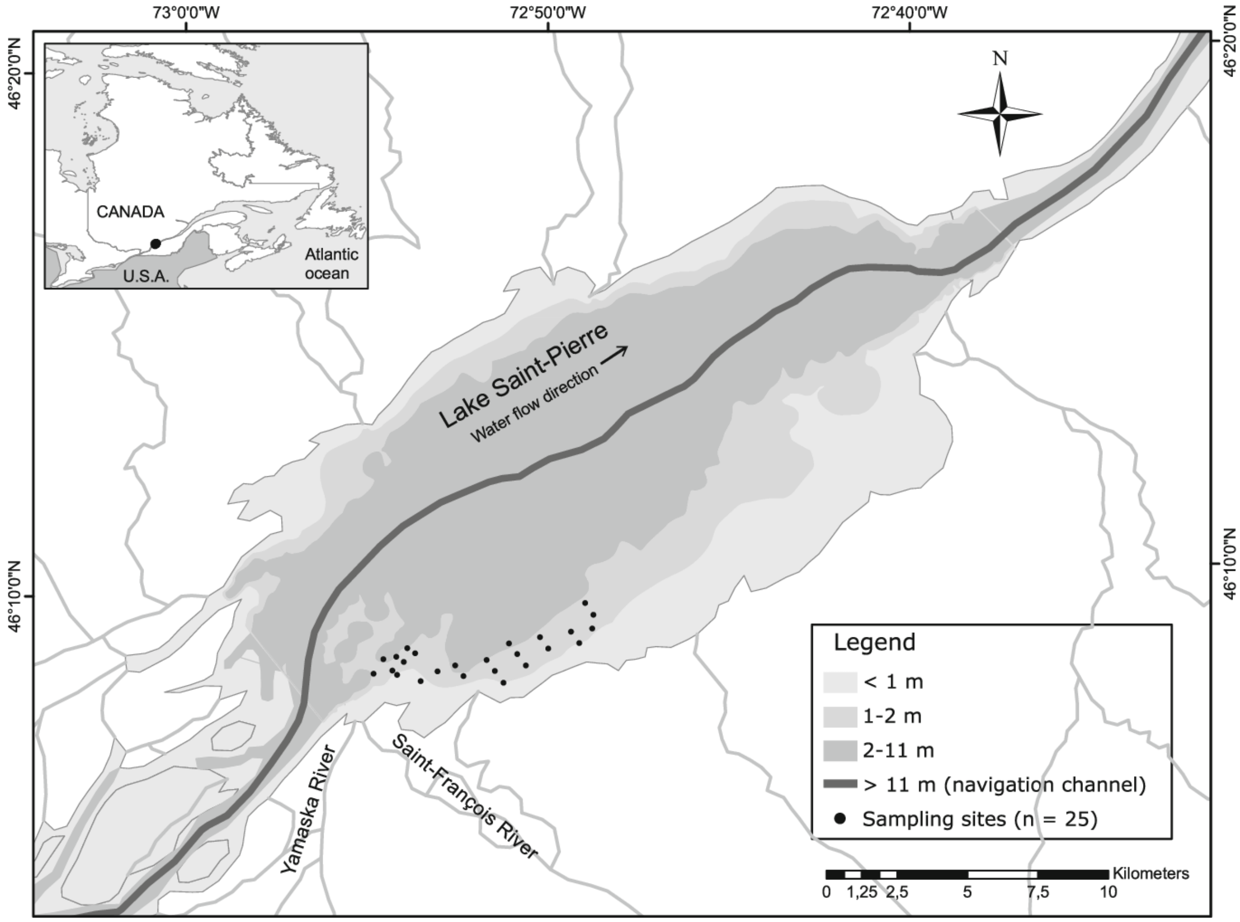

Figure 1. Map of the study area showing the bathymetry of the LSP and the location of the navigation channel. Sampling sites (dots) are located in the plume of Yamaska and Saint-François River.

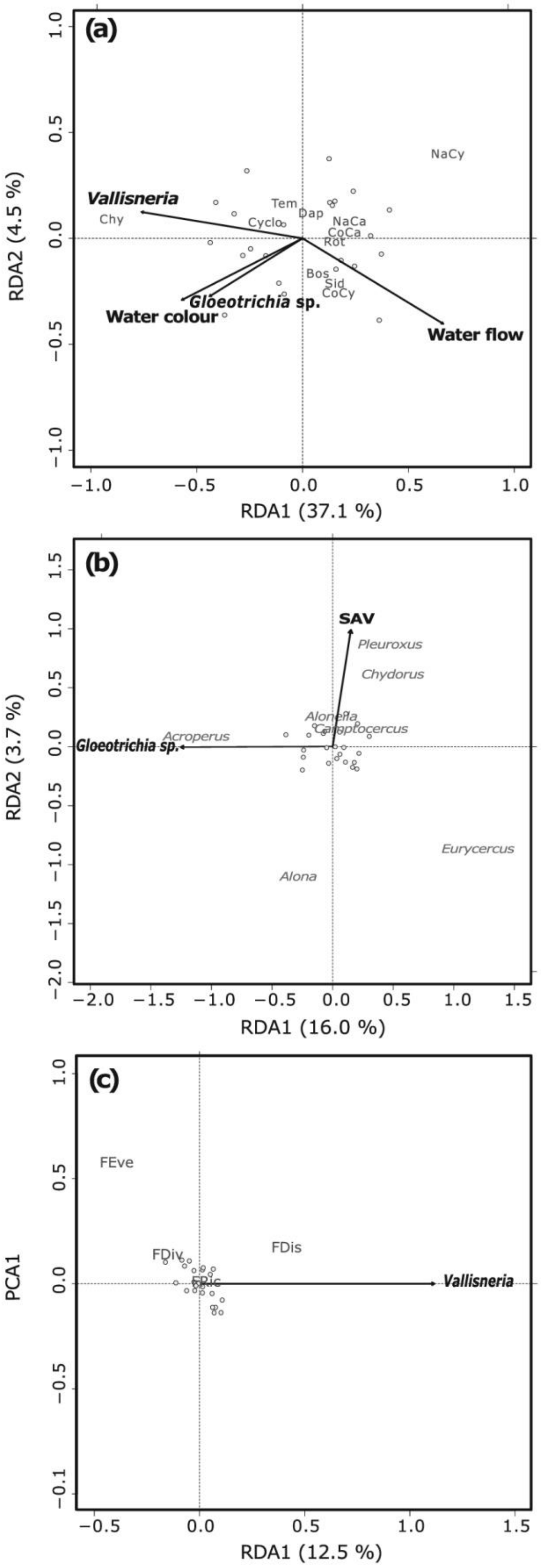

Figure 2. Partial redundancy analysis of a) major zooplankton families (grey) in relation with SAV and environmental variables (black). Spatial variables (5 AEM variables) were used as covariables; b) Chydoridae's genera (gray) in relation with SAV (black), environmental and spatial variables (5 AEM variables) attributes of the habitat used as covariables; **c)** pRDA of zooplankton functional diversity in relation with SAV (black), environmental and spatial attributes (5 AEM variables) of the habitat used as covariables. Functional indices are: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). To allow a better graphical representation, only most abundant families and genera are shown. For a complete list of family included in the analysis, see Table 2. For a complete list of the genera included in the analysis, see Table 3. Dots represent the study sites.

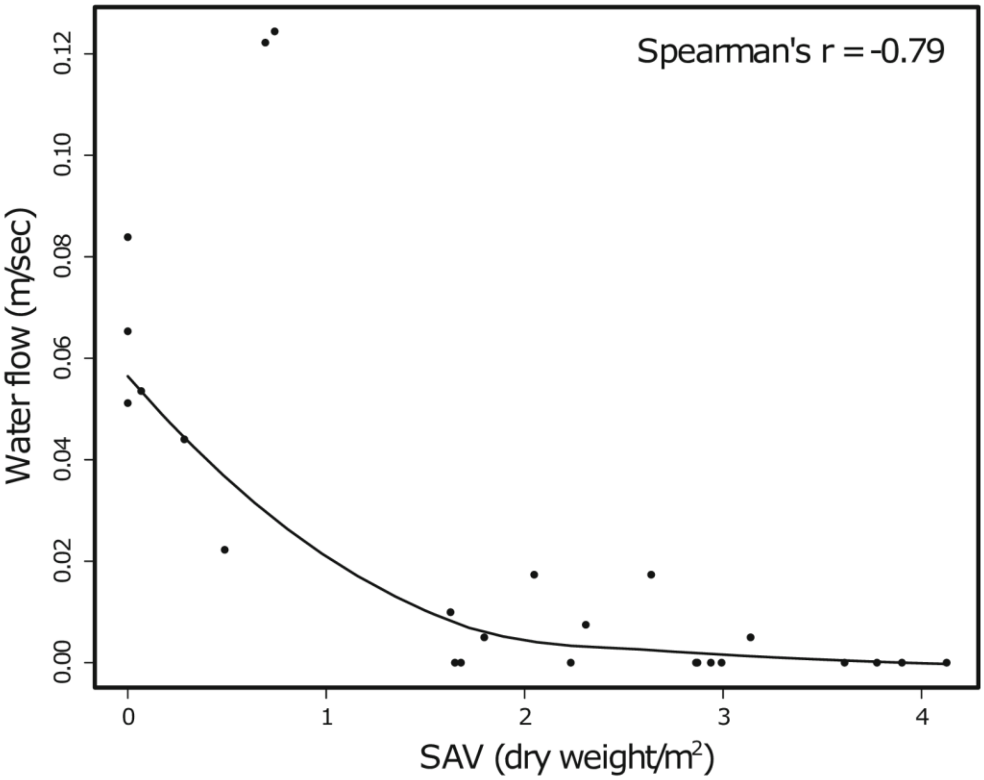

Figure 3. Relationship between water flow and total SAV biomass in the study system. The smooth curve was applied using a local polynomial regression (loess curve fitting).

2.10 Supplementary material

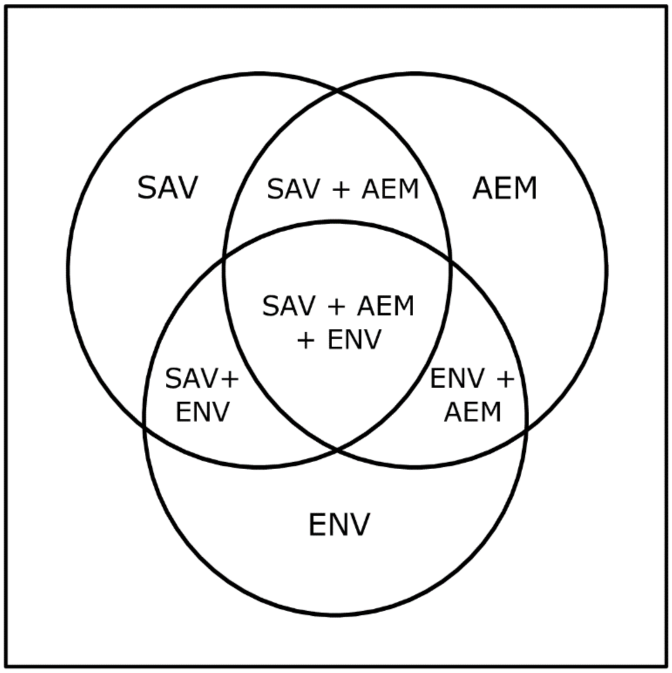

Figure S1. Venn diagram showing the decomposition of the variance of the zooplankton community data set explained by nine different components representing the independent and confounded effects of three subsets of variables. Circles correspond to the total variance accounted for by each individual variable subset (SAV, ENV and AEM variables). The areas of overlap among circles represent the variance of the zooplankton community that is jointly explained by the associated set of SAV, ENV and AEM. SAV is represented by Vallisneria sp. and Gloeotrichia sp., ENV is represented by water colour and water flow and AEM is represented by 5 asymmetric eigenvector map (AEM).

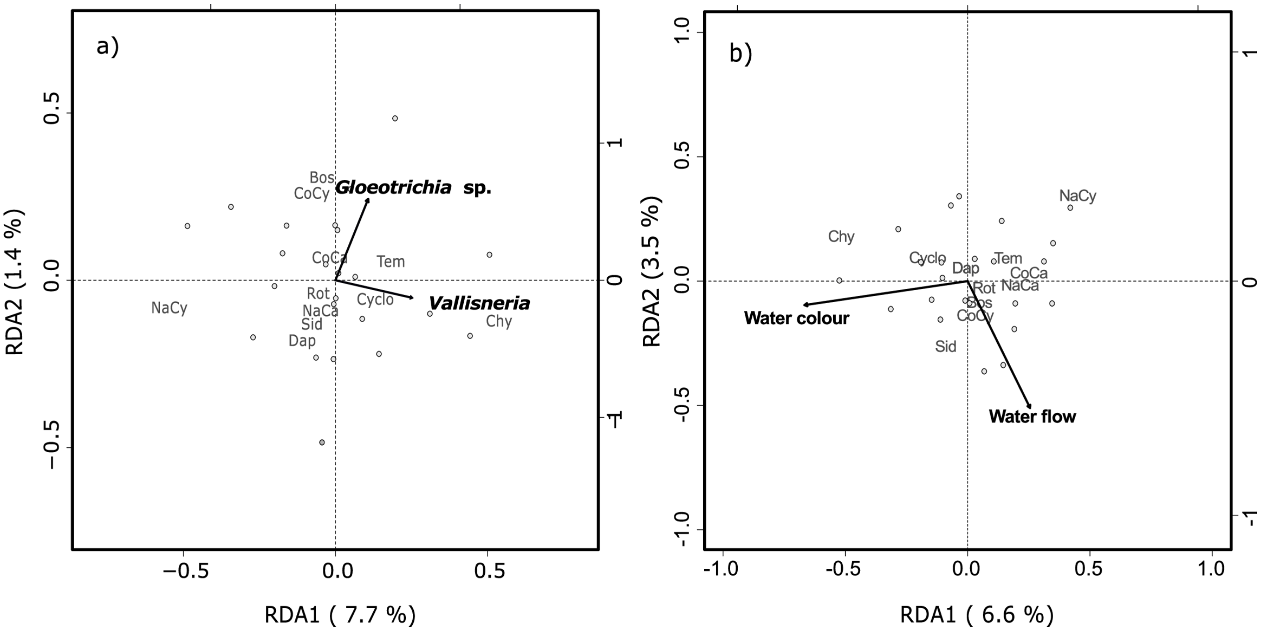

Figure S2. Partial RDA of the major zooplankton families (gray) in relation with a) SAV (black) alone (environmental (A440 nm and water flow) and spatial attributes (5 AEM) used as covariables); b) ENV alone (SAV (*Vallisneria* sp. and *Gloeotrichia* sp.) and spatial attributes (5 AEM) used as covariables). To allow a better graphical representation, only most abundant families are shown. For a complete list of family included in the analysis, see Table 2.

CHAPITRE 3

SUBMERGED AQUATIC VEGETATION COVER AND COMPLEXITY DRIVE CRUSTACEAN ZOOPLANKTON COMMUNITY STRUCTURE IN A LARGE FLUVIAL LAKE: AN IN SITU APPROACH.

Cet article est publié dans la revue *Journal of Great Lakes Research*

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Référence complète :

Bolduc, P., A. Bertolo, C. Hudon et 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*(4), 767-779.

3.1 Abstract

Submerged aquatic vegetation (SAV) is considered an important driver of the zooplankton community, owing to the refuge offered by its structural complexity. However, non-destructive *in situ* approaches to assess quantitatively the features of SAV beds and their effects on zooplankton community are still lacking. This study aims to: 1) estimate SAV cover and complexity using subaquatic upward photographs (SUP) and 2) analyse the relationship between SAV variables and crustacean zooplankton composition and functional diversity (FD). SAV biomass and zooplankton were sampled at 52 stations in a large fluvial lake. Two metrics based on SUP were used to quantify SAV cover and complexity: 1) the percentage of the underwater landscape occupied by SAV (PLAND: SAV cover), and 2) its perimeter-area fractal dimension (PAFRAC: SAV complexity). Zooplankton composition and functional diversity were estimated based on crustacean species assemblages and functional traits. We used linear models to describe the relationships between SAV indices, environmental variables and zooplankton abundance, biomass and FD. SUP was an effective method to estimate *in situ* SAV cover and complexity. PLAND and PAFRAC were positively related to SAV biomass and zooplankton abundance, yielding a non-destructive assessment of the SAV-zooplankton relationships. Our study partially supports the habitat complexity-ecological niche availability hypothesis, as SAV cover and complexity influenced zooplankton functional groups and diversity indices. However, water transparency and depth also had important effects in interaction with PLAND and PAFRAC, and it remains difficult to fully disentangle the effects of SAV complexity from SAV cover on crustacean zooplankton community structure.

Keywords

Submerged aquatic vegetation, SAV cover and complexity, zooplankton community structure, underwater photography, large fluvial lake

3.2 Introduction

Large lakes provide ecosystem services such as drinking water and fisheries. Vegetated habitats are important to maintain the functioning of such ecosystems, especially in large shallow lakes, where extensive aquatic vegetation beds provide substrate to epiphytes as well as food resources and habitats for invertebrates and vertebrates (*e.g*. Hudon et al., 2012; Jeppesen et al., 2012). Moreover, it is widely recognized that submerged aquatic vegetation (SAV) is generally related to lake health and ecological integrity (Scheffer et al., 1993; Jeppesen et al., 2012). For example, water quality improvement in Lake Balaton, the largest shallow lake in Central Europe, was strongly related to the rehabilitation of its SAV beds (Istvánovics et al., 2007, 2008). In the large fluvial lakes of the St. Lawrence system (Canada), vegetated areas can occupy up to 70% of the littoral zone (Hudon, 1997; Jean and Letourneau, 2014). These habitats are sensitive to anthropogenic pressures, climate change and the introduction of exotic species, which are known to cause SAV decline in lakes worldwide (Zhang et al., 2017). Water level fluctuations have also been identified as a major stressor for SAV in the St. Lawrence system (Hudon, 1997; Hudon et al., 2000, 2005), coincident with the proliferation of dense mats of benthic cyanobacteria, further indicative of ecosystem degradation (Lévesque et al., 2012, 2017).

Since MacArthur and MacArthur in 1961, many studies have shown that structurally complex habitats can support a greater abundance and diversity of species than homogeneous habitats, independently of the number of structures and/or surface available for organisms (Lapointe and Bourget, 1999; Bracewell et al., 2018). The hypothesis, predicting a positive relationship between habitat complexity and biodiversity, is based on the ecological niche concept where habitat complexity contributes to ecological niche availability, sustaining the diversity of organisms that can coexist within a given habitat (Pennak, 1957; St. Pierre and Kovalenko, 2014). In aquatic ecosystems, it is widely recognized that SAV is one of the key drivers of habitat complexity (Van Onsem et al., 2010; Kovalenko et al., 2012). Reynolds et al. (2018), for example, showed the importance of habitat cover and complexity in seagrass beds in predicting predation pressure on macroinvertebrates in marine systems. In freshwaters, it has been suggested that SAV complexity could also affect macroinvertebrates because submerged vegetation supported higher biomass than emergent vegetation which has a relatively simpler structure than the former (Cremona et al., 2008; Tessier et al., 2008); however, SAV with a complex architecture did not host significantly greater macroinvertebrate biomass than plants with a simpler architecture (Cremona et al., 2008).

In lakes, SAV is also an important habitat for zooplankton, with more than two-thirds of crustacean zooplankton species inhabiting the littoral zone either because of their epiphytic lifestyle (*e.g.*, *Sida crystallina*; Fairchild, 1981) or because SAV acts as daytime refuge against predation (Lauridsen et al., 1996; González Sagrario and Balseiro, 2010). In addition, in the fluvial lakes of the St. Lawrence River, SAV could also prevent zooplankton downstream advection, as it supports nine-fold more biomass of crustacean zooplankton than the open water (Basu et al., 2000). For littoral zooplankton species, habitat availability depends on the overall complexity of SAV architecture, such as leaf area or the amount of leaf edges (Bergström et al., 2000). Moreover, complex architecture in SAV (*e.g*. dissected *vs* broad leaves) has been shown to be related to high zooplankton diversity in experimental field studies (Declerck et al., 2007; Meerhoff et al., 2007). Recent studies have suggested that habitat complexity has the potential to drive zooplankton taxonomic and functional diversity also at the scale of whole lakes and rivers (Walseng et al., 2006; Massicotte et al., 2014). Whereas for macroinvertebrates it has been shown that this effect could be due to a complexity effect *per se* (i.e., independent of leaf surface; Warfe et al., 2008), in the case of zooplankton, it is still unclear if the effect of SAV architectural complexity could be disentangled from that of SAV cover based on leaf surface availability (Zeng et al., 2017). To our knowledge, only a few studies focused on the effect of habitat complexity within SAV patches on zooplankton abundance and diversity and their results are somewhat contradictory. For example, whereas Lucena-Moya and Duggan (2011) showed that rising SAV complexity at the scale of individual plant enhanced zooplankton abundance and diversity, Zeng et al. (2017) did not find any relationship between SAV structural complexity and either zooplankton abundance or diversity. Thus, there is yet no clear evidence of a relationship between SAV architecture and zooplankton diversity at the SAV patch scale.

Ecological research in the last decades has increasingly made use of new technologies, which offer a cost-effective approach and a high spatio-temporal resolution for field data collection. Close-range remote sensing is getting a lot of attention as an efficient tool to monitor and quantify the complexity of terrestrial habitats (*e.g*. Proulx and Parrott, 2009). The potential of close-range remote sensing to assess underwater habitat complexity has also been recognized, but has mostly been shown in clear oceanic waters for measuring coral reefs and artificial structure complexity (*e.g*. Mellin et al., 2009). The potential use of these novel techniques remains to be tested in freshwater systems where water transparency can be limiting. Here, we propose a method to overcome some of these issues by testing the potential of close-range digital underwater photography to assess SAV habitat cover and complexity and test their relationships with zooplankton community structure and functional diversity.

Traditionally, SAV cover and complexity were assessed at the individual or at the species level by harvesting the vegetation on a known surface (*e.g.* quadrat) (Hudon, 1997), or using hand-rake methods (*e.g*. Bolduc et al., 2016). In some cases, SAV complexity was assessed using SAV species and their morphological attributes providing qualitative description of the complexity of each species (*e.g*., *Myriophyllum* spp. is more complex than *Vallisneria* spp.; Zeng et al., 2017). Others used proxies of SAV structural complexity by taking direct measures of distance between leaves on harvested plants of different species (*e.g*. St. Pierre and Kovalenko, 2014). Some studies recognized the potential of using fractals to assess the difference in the complexity among species based on measures of the edge length of their photosynthetic structures (Tokeshi and Arakaki, 2012). The fractal attributes of each species present within each macrophyte beds were then weighted by their abundances to calculate an average fractal index representative of the community complexity (*e.g*. McAbendroth et al., 2005; Wolters et al., 2018). However, none of these methods captured the natural arrangement of SAV structure *in situ* which is the more direct proxy of the real niche habitat complexity within SAV beds available for zooplankton.

The aim of this study was to investigate with a non-destructive approach the relationship between SAV habitat features, namely cover and complexity, and crustacean zooplankton community structure based on the diversity of species assemblages and functional groups according to functional traits (*e.g*. maximum length, habitat, swimming capacity, trophic level) of recorded species. Functional diversity has the potential to link zooplankton communities with ecosystem functions (Barnett et al., 2007). SAV complexity was measured *in situ* using a novel approach based on subaquatic upward photography (SUP). Here we used the SAV bed of Lake Saint-Pierre (Québec, Canada), a large shallow lake of the St. Lawrence River, as our model system. Our objectives were to: 1) evaluate the potential of SUP as an efficient tool to assess SAV cover and complexity, when compared to harvested SAV biomass and 2) disentangle the effects of SAV cover and complexity on the composition and functional diversity of crustacean zooplankton communities. We hypothesized that high SAV cover would increase crustacean zooplankton abundance and biomass because of the larger area available for microinvertebrates and their algal resources while a high SAV complexity would increase zooplankton functional diversity because of higher niche availability for microinvertebrates (*e.g.* to avoid predation), independently from SAV cover (Pennak, 1957; Walseng et al., 2006).

3.3 Methods

3.3.1 Study system and sampling design

The study sites were located on the south shore of Lake Saint-Pierre (LSP) which is a large (≈ 300 km^2) and shallow (mean depth of 3 meters) fluvial lake of the St. Lawrence River (Quebec, Canada). The lake is an open system characterized by two extensive shallow littoral zones, separated by a deep (> 11 m) navigation channel. Zones of emergent and submerged vegetation cover around 70 % of the lake area (Jean and Létourneau, 2014). Submerged vegetation is mainly dominated by *Vallisneria americana* Michx. and *Potamogeton richardsonii*.(A. Benn) Rydb (Bolduc et al. 2016). The drainage basins on the south shore of LSP are extensively occupied by farmlands, leading to high inputs of nutrients (Bolduc et al. 2016), and to increase in SAV biomass (Lévesque et al., 2012). In the last decade, this area was found to be largely colonized by benthic cyanobacteria, which coincided with reduced SAV biomass, a phenomenon considered as a symptom of ecosystem degradation (Lévesque et al., 2012; Hudon et al., 2014). The fish community comprises up to 80 species (Laviolette et al. 2003) including a high abundance of planktivorous species such as juvenile yellow perch *Perca flavescens* (Mitchill, 1814) inhabiting the littoral zone and our study site (P. Bolduc, per. obs.).

In this study, we sampled 52 stations over a two-year period (24 stations in 2013 and 28 stations in 2014) (Electronic Supplementary Material (ESM) Fig. S1,). Sampling was performed at two sampling areas (0.04 km^2 each year) selected in order to maximize SAV heterogeneity in terms of cover and complexity, while trying to minimize the variability of other environmental factors in the water. Because of changes in water levels between 2013 and 2014, the two sampling area were located at about 1 km from each other. Within each sampling area, sampling stations were distributed approximately on a regular grid (~30 meters). Each station represented an area covering three 900 cm^2 SAV quadrats spaced at ca. 4-m intervals. Sampling was carried out during daytime (between 7 a.m. and 5 p.m.) over a single week in mid-August (12-16 Aug. 2013 and 11-15 Aug. 2014) for both years.

3.3.2 Water physical and chemical environment

Water depth and flow were measured at each station. Water flow was measured with a current velocity meter (model 3000, Swoffer Instrument Inc.). We assessed physico-chemical water conditions (pH, conductivity, oxygenation and temperature) using a multiparameter probe (YSI, model 556MPS, YSI incorporated, USA) and we measured underwater light using a Li-Cor (model LI-193SA Underwater Quantum Sensor) along a profile, where each measurement was taken at 0.25 m intervals. The light attenuation was then calculated from the photosynthetically active radiation obtained regressed on depth of measurement (K_{PAR}, Table 1). As the average depth was 1.5 m, we used a Schnell tube, which consists of a small black and white disc lowered into a black PVC tube filled with the water sample, instead of a Secchi disc to measure water transparency.

3.3.3 Crustacean zooplankton sampling and analyses

Prior to SAV manipulations, crustacean zooplankton community was sampled using a submersible pump (Rule^{TM}, model 1500) (Masson et al., 2004) in a way to integrate both vertically and horizontally (by gently oscillating the pump up and down the water column while moving it from one side to the other of the boat) an area covering the three SAV quadrats (described in the next section) as well as between the quadrats. The volume of water collected to sample zooplankton (ca. 0.3 m^3) was comparable to the volume of water (0.4 m^3) covering the three quadrats for SAV sampling. In order to avoid disturbing and resuspending the sediments, zooplankton sampling was carried out before taking SUP pictures and harvesting SAV biomass (see next section). The pump was connected to a digital water smart-flow meter (Gardena^{TM}, model 9188) to get a precise estimation of the volume of water collected, which was subsequently filtered with a zooplankton net (153 μm mesh size). This method allowed us to collect all crustaceans from a large volume of water (approx. 300 L per station) in order to offset the low density of crustacean zooplankton previously reported in LSP (Bolduc et al., 2016). Zooplankton organisms were collected in sampling bottles (250 ml) and fixed in a 4% sugar-formaldehyde solution prior to identification (Prepas, 1978). Crustacean zooplankton identification was conducted at the species level when possible using the identification keys of Edmondson (1959), Haney (2013), and Thorp and Covich (2009) for the cladocerans, and Edmondson (1959), Smith and Fernando (1978), and Haney (2013) for the copepods. Within each sample, the length of the first 30 individuals of each crustacean species was measured to determine the mean biomass of each species based on length-weight specific relationships (Malley et al., 1989). All cladocerans and copepods species were identified and counted (reported as a number of individuals per liter of filtered water). To get a perspective of species assemblages and community composition, frequencies of occurrence, abundance and biomass of each species were established (ESM Table S2).

To determine the functional groups (FG) of crustacean zooplankton, each species was classified according to five functional traits based either on direct measurement (body size: maximum length) or data retrieved from the literature (habitat, swimming capacity, feeding-type and trophic groups) (Barnett et al., 2007; Massicotte et al., 2014) (ESM Table S2). The functional traits of zooplankton are rather scarce in the literature. We therefore selected these traits to get the most complete database possible. Given the lack of precise information at the species/genus level for most taxa, the broad taxonomic group (i.e., cladocerans, calanoids, cyclopoids and harpacticoids) of each individual was used as a proxy of the swimming capacity (Drenner, 1980).

3.3.4 Submerged aquatic vegetation (SAV) habitat features

SAV cover was estimated using two different approaches: SAV cover estimated from the SUP method and SAV biomass estimated from plants harvested by SCUBA divers. For each station, three quadrats were systematically sampled at fixed locations behind and on both sides of the boat, separated from each other by about 4 meters during mid-August, when SAV biomass was the highest. The mean values of SAV biomass, cover and complexity in these three quadrats were thereafter used to represent SAV habitat features in each station. Prior to SAV harvesting in each quadrat, an upward-oriented underwater photograph (model Pentax Optio WG-1) was taken from the middle of each quadrat to quantify SAV canopy cover while minimizing sediment resuspension. All pictures were taken by divers at approximately 1.5 m depth. After SUP pictures were made, SAV was collected by divers within each quadrat, rinsed and kept frozen until laboratory analysis. Vascular macrophytes were identified at the species level, dried at 50°C, weighed to the nearest 0.1 mg, and their biomass was finally measured and reported as dry weight per m^2.

3.3.5 SUP image analysis

SUP pictures stored in JPEG format were modified manually with the wand (tracing) tool and the freehand selection to remove the background (water, clouds, etc.) in order to only keep SAV images. Pictures were then transformed into monochrome images (i.e., 8 bit black and white images). All pictures modifications were performed using the ImageJ software (Rueden et al., 2016). The complexity of each modified picture was analysed with the class-level pattern metrics of the FRAGSTAT software (McGarigal et al., 2012), usually used in landscape ecology (*e.g.* Tischendorf and Fahrig, 2000). Among all the FRAGSTAT class metrics, Wang et al. (2014) identified nine indices efficiently capturing landscape fragmentation. Among these, we selected the proportion of the picture occupied by SAV (PLAND) quantifying habitat cover, and the perimeter-area fractal dimension (PAFRAC) quantifying habitat complexity (shape index) independently from habitat cover. PAFRAC values approaching 1 were related to SAV shapes representing very simple perimeter such as circles, whereas values close to 2 represented highly convoluted perimeter shapes (McGarigal et al., 2012). Examples of SUP images in quadrats with low, medium and highly SAV cover and complexity are presented in Figure 1. Original and modified SUP images taken in each quadrat are presented in (ESM Table S1, together with corresponding SAV biomass and dominant species, as well as PLAND and PAFRAC indices.

In order to match the sampling scales of zooplankton and environmental variables, PLAND, PAFRAC and SAV biomass were averaged for the three quadrats sampled at each station before the analysis. As the relationships between PLAND and SAV dry weight biomass had similar slopes in 2013 and 2014 (ESM Fig. S2), the data from the two years were pooled.

3.3.6 Statistical analyses

Differences in environmental descriptors (physical and chemical variables) of the study stations between sampling years were tested using Student's tests. To determine the hierarchical clustering of crustacean zooplankton into functional groups (FGs), we computed a principal component analysis using the functional traits database and the functions *FAMD()* and *HPCP()* in the "FactoMineR" package (Pagès, 2004). The maximum number of clusters was set to five. The abundance and biomass of all species within each functional group was then summed for each cluster and for each station.

We calculated four functional diversity indices (FD) based on crustacean functional traits with the *dbFD*() function in the "FD" package (Laliberté et al., 2014). The variation in functional traits among stations allowed us to compute the functional richness (FRic), functional evenness (FEve) (Villéger et al., 2008), and functional dispersion (FDis) (Laliberté and Legendre, 2010). FRic represents the maximum convex hull including all the species of the crustacean zooplankton community in the space of traits. FEve represents the evenness of the species traits in the space of traits and is standardized between 0 and 1, where FEve value of 1 indicates that species are evenly distributed in the space of traits with similar abundance (Villéger et al., 2008). FDis represents the mean distance of each species to the centroid within the traits space of all species of the community. FDis values do not have upper limits; higher FDis values represent a larger dispersion in the space of traits (Laliberté and Legendre, 2010). In contrast to FRic and FEve indices, FDis is independent of species richness (Laliberté and Legendre, 2010).

Crustacean zooplankton species abundances used to calculate FD indices were transformed using the Hellinger transformation (square root of the relative abundance of each species in the station), to reduce the relative weight of abundant species in the analysis (Legendre and Gallagher, 2001). Total density and biomass of crustaceans were log-transformed. The variance inflation factor (Neter et al., 1996; Graham, 2003) was computed to ensure that collinearity in SAV-zooplankton relationships was below the recommended threshold of 10 (all values were below 1.5).

Ten models were built to explain the effects of SAV and water variables on crustacean zooplankton total abundance, biomass and functional diversity indices (FRic, FEve and FDis). First, five models (hereafter called "full models") were built to describe the influence of SAV cover (PLAND), SAV complexity (PAFRAC), and water environmental variables (depth and transparency) on crustacean zooplankton abundance and biomass, and functional diversity indices. Then, to isolate the effect due only to PAFRAC on crustacean zooplankton abundance, biomass and FD indices, we built five partial models using the residuals of the relationships between each zooplankton variable and PLAND as the independent variables. Both water depth and transparency were included in the models to account for within-site variability in water conditions and their potential role as drivers of zooplankton community. We determined the best model based on the Akaike information criterion (AICc). When more than two models were below a ΔAIC of 2, the most parsimonious model was kept (Burnham and Anderson, 2003).

A redundancy analysis (RDA) was used to assess the relationships between each functional group of crustacean zooplankton, SAV habitat features (PLAND and PAFRAC) and environmental variables (water depth and transparency). A variance partitioning approach was used to isolate the contribution of the SAV cover (PLAND) and complexity (PAFRAC) from this of water environmental conditions on crustacean functional community structure. Prior to statistical analysis, SAV dry weight was log-transformed and PAFRAC was square root transformed in order to meet the normality and heteroscedasticity requirements.

All statistical analyses were performed within the R computing environment (R Core Team, 2017, version 3.4.3).

3.4 Results

3.4.1 Water environment and SAV habitat features

In accordance with our sampling design conceived to reduce environmental variability among sites, water depth (around 1.5 m), water flow (< 1cm/s), and dissolved oxygen content (> 10 mg/L) did not differ significantly between sampling years (Table 1). Nonetheless, there were small variations in water conditions between years of sampling. Water transparency, temperature, and conductivity were significantly higher in 2014 than in 2013, while pH and underwater light attenuation were lower. Water depth, transparency and conductivity were also more variable among stations in 2014. Also, despite our experimental design aimed at reducing the effect of the environmental variables, relatively important variations between the stations have nevertheless been observed.

SAV biomass was on average four-fold higher in the stations sampled in 2013 (115 d.w. g/m^2) than in the ones sampled in 2014 (25 d.w. g/m^2), thus maximizing the range of SAV biomass across the 2-years study period. The SAV community was dominated by four species (ESM Table S1). The higher water level observed in 2014 could explain why SAV coverage was significantly lower in 2014 than in 2013. The dominant species *Vallisneria americana* Michx. (63 % of total d.w. biomass) formed rosettes of ribbon-like linear leaves anchored to the bottom. The subdominant species *Potamogeton richardsonii* (A. Benn.) Rydb. (35 % of total d.w. biomass) formed branching stems covered with oblong leaves extending towards the surface, producing a nearly opaque canopy at high density. The last two species (*Heteranthera dubia* (Jacq.) MacMill and *Elodea nuttallii* (Planch.) H. St. John (< 2% of total d.w. biomass) completed the canopy in some stations. In some cases, SAV biomass measured in the quadrats may be very low (or null), despite the presence of SAV in the pictures, because branching stems extending towards the surface can be swept downstream by waves and current (ESM Table S1).

SAV cover (PLAND) was also significantly higher in 2013 (52% of coverage) than in 2014 (30%) (Table 1). Overall, PLAND was directly related to the biomass of SAV collected within all quadrats in 2013 and 2014 (Adj-$R^2 = 0.42$; ESM Fig. S2). Using the average value of PLAND and SAV biomass of the three replicate quadrats sampled in the 52 stations improved markedly this relationship ($r = 0.83$, $p < 0.0001$, Fig. 2-left panel). Mean biomass of SAV at each station ranged from 2.22 to 440.50 (mean 67.60 d.w. g/m^{-2} ± 69.34), reflecting the wide range of SAV cover (PLAND) from low (< 5%) to a nearly complete (75.6%) canopy.

SAV complexity (PAFRAC) was significantly higher in 2013 (1.37) than 2014 (1.25) as reported for PLAND; however, PAFRAC range of variation among-stations was generally lower (1.13 - 1.46), with a global mean value of 1.31 ± 0.07 (Table 1). SAV species composition did not affect PAFRAC index because it was neither correlated with the proportion of biomass of *V. americana* ($r = -0.1$, n.s., $p = 0.48$) nor of *P. richardsonii* ($r = 0.21$, n.s., $p = 0.14$). In fact, PAFRAC was positively related with SAV biomass ($r = 0.68$, $p < 0.0001$, Fig. 2-middle panel) as seen for PLAND. This can be explained by the relatively strong correlation observed in our study between the two SAV indices ($r = 0.67$, $p < 0.0001$, Fig. 2-right panel), even though the calculation of PAFRAC is by construction independent from PLAND (Wang et al., 2014).

3.4.2 Crustacean zooplankton community structure

The average abundance of zooplankton was higher in 2013 than in 2014, with respectively 14.25 and 8.60 ind/L. The difference comes mainly from cyclopoid copepods, which were three times more abundant in 2013 than in 2014. This difference is mainly attributed to the high abundance of nauplii and copepodites. The calanoid *Eurytemora carolleeae* and cladoceran species were more abundant in 2014 than in 2013, being respectively 0.44 and 2.58 times higher in 2014. This difference in terms of abundance was not reflected in the zooplankton biomass observed between the two years. In 2013, the average biomass of zooplankton per station was 7.82 µg/L while it was 8.38 µg/L in 2014. Some species were found only in 2013 or in 2014. *Homocyclops ater*, *Macrocyclops albidus*, *Mesocyclops americanus*, *Paracyclops poppei*, *Pseudochydorus* sp. and *Disparalona rostrata* were only present in 2013 while *Moina micrura*, *Alonella* sp., *Daphnia parvula* and *Rhynchotalona falcata* only occurred in 2014 although few individuals of these species were found.

When excluding the nauplii and copepodite stages, a total of 32 crustacean species were identified over the two sampling years (ESM Table S2). The mean number of species found at each station was approximately 15 (± 2). Eleven species were frequently encountered (> 20 stations); 6 species were found in 10-20 stations, and 15 species were quite rare (< 10 stations). Both the mean abundance (15.73 ind/L ± 65.76) and biomass (11.32 µg/L ± 41.92) of crustacean species within SAV beds exhibited high variability among stations (Table 2). In terms of abundance, copepods were dominant (82%), but were mainly composed of nauplii stages; whereas, cladocerans accounted only for 18% of total crustacean abundance. In terms of biomass, the dominance pattern was inverse as the cladocerans accounted for 68% and the copepods only for 32% of total crustacean biomass. Among the cladocerans, the most common species were *Bosmina* sp., *Sida crystallina*, *Alona* sp., *Diaphanosoma brachyurum*, *Ceriodaphnia* sp. and *Ilyocryptus* sp.. The dominant cladoceran taxa were *Bosmina* sp. (1.32 ± 1.81 ind/L) and *S. crystallina* (0.68 ± 0.81 ind/L), representing respectively 11.48% and 5.90% of total crustacean abundance (ESM Table S2). In terms of biomass, the large-bodied *S. crystallina* accounted for the largest contribution of the crustacean biomass (59.70 %) despite their relative low abundance, followed by the small-bodied *Bosmina* sp. (6.71 %). Copepods were mostly represented by cyclopoid and calanoid copepodites and nauplii (9.06 ± 6.90 ind/L), together accounting for 79% of the crustacean abundance but only for 17 % of their biomass. Adults of cyclopoids were mainly represented by *Eucyclops agilis* (0.15 ± 0.16 ind/L) and *Acanthocyclops robustus* (0.09 ± 0.29 ind/L). Adults of calanoids were represented by only one species, *Eurytemora carolleeae* (0.05 ± 0.06 ind/L). Harpacticoids were composed of epibenthic species such as *Nitokra* sp. (0.005 ± 0.01 ind/L). In terms of biomass, the most abundant copepods species (*A. robustus*, *E. agilis, E. affinis*) contributed moderately to the crustacean biomass (5.50, 4.78 and 4.95 %, respectively) (ESM Table S2).

The hierarchical clustering of crustacean assemblages based on their functional traits resulted in four distinct functional groups (FGs) (Fig. 3, Table 2; see also ESM Tables S2 and S3). FG1 was represented by small herbivorous species of chydorid cladocerans feeding on plant surfaces and epibenthic harpacticoids, all of them weak swimmers; it was the least important group both in abundance and biomass. Harpacticoid copepodites and nauplii accounted for 63 % of the abundance of the FG1 group while the chydorid *Ilyocriptus* sp. accounted only for 16 %. FG2 was represented by cladocerans of various sizes characterized by their strictly herbivorous diet and their low swimming capability. The small *Bosmina* sp. and the large *S. crystallina* were the two dominant species of the FG2 group, accounting for 52 % and 45 % of its abundance. Despite its relatively low abundance, FG2 group accounted for the largest part of the crustacean biomass due to the presence of the large species *S. crystallina*. FG3 was represented by the copepod cyclopoids, which are omnivores consuming algae, rotifers, and small crustaceans. FG3 was the most abundant group, mainly composed of nauplii (86 %) and copepodid (8 %) stages, and followed by adults of *E. agilis* (3 %) and *A. robustus* (2 %). FG3 was less important in biomass than FG2. Finally, FG4 was composed of the nauplii and copepodites of the calanoid *E. affinis* (94 % of total abundance). FG4 abundance and biomass were relatively low compared to FG2 and FG3, but higher than FG1. *E. affinis* is a pelagic species feeding on algae in suspension in water, and a good swimmer; the adults contributed for 6 % to the FG4 total abundance.

Zooplankton functional diversity indices (FRic, FEve and FDis) were derived from crustacean taxon-specific traits. Functional richness (FRic) ranged from 10 to 19, with a mean value of 15.00 ± 2.26 (Table 2), showing a large variation in the diversity of crustacean traits among stations. Mean values for functional evenness (FEve) and functional dispersion (FDis) were

0.65 ± 0.08 (0.49 to 0.84) and 0.47 ± 0.07 (0.30 to 0.55) (Table 2), and their 2-fold ranges of variation also reflect important differences in crustacean functional traits among stations, as observed for FRic.

3.4.3 SAV – crustacean zooplankton relationships

At the scale of the community, total abundance of crustacean zooplankton was positively related, albeit moderately, to SAV biomass (r = 0.42, p = 0.002), PLAND (r = 0.37, p = 0.007) and PAFRAC (r = 0.32, p = 0.019) (Fig. 4, left panels). Conversely, crustacean zooplankton total biomass was neither related to SAV biomass (r = 0.24, p = 0.09), PLAND (r = 0.26, p = 0.06) and PAFRAC (r = -0.17, p = 0.23) (Fig. 4, right panels). The proportion of littoral to total zooplankton showed a negative relationship with PLAND (r = -0.30, p = 0.003) and PAFRAC (r = -0.33, p = 0.017).

When considering the community structure based on crustacean functional groups, the RDA analysis showed that SAV cover (PLAND) and complexity (PAFRAC), and two environmental variables (water depth and transparency) explained together 36.51 % of the total variation, with the first two axes explaining respectively 32.31 % and 4.04 % (Fig. 5, left upper panel). The abundance of cyclopoids (FG3) was positively related to SAV indices (PAFRAC and PLAND) while the abundances of the other groups (FG1, FG2 and FG4) were inversely related. Variance partitioning showed that PAFRAC alone explained 6% of the total variance in FGs abundance, whereas PAFRAC and PLAND together shared 12% (Fig. 5, upper right panel). Water transparency and depth alone explained 10% of the total variance in FGs abundance, and up to 19% when combined with SAV indices. The RDA analysis based on the biomass of the crustacean FGs explained only 20.61 % (Fig. 5, lower left panel), with the first two axes accounting for 15.94 % and 4.40 % respectively. The biomass of large cladocerans (FG2: positively) and of calanoids (FG4: negatively) were both related to PLAND, and the biomass of cyclopoids (FG3: positively) to PAFRAC. For the FGs biomass, environmental factors (water depth and transparency) explained the largest fraction (8% alone and up to 14% when combined with SAV indices) of total variance while the effects of SAV indices were weak (4% and up to 10% when combined with water variables) (Fig. 5, lower right panel).

The best models (full and partial models) obtained for crustacean zooplankton abundance, biomass and functional diversity indices (FRic, FEve and FDis) revealed that SAV cover (PLAND) and/or complexity (PAFRAC) always explained a significant fraction of the total variance among stations in crustacean abundance and biomass and functional diversity indices (Table 3). The proportion of total variance explained by the full models was always higher for the three indices of functional diversity (Adj-$R^2 > 0.31$) than for crustacean zooplankton abundance (Adj-$R^2 = 0.18$) and biomass (Adj-$R^2 = 0.26$). In the three full models (zooplankton abundance, FRic, FEve), adding environmental variables such as water transparency and water depth increased the explanatory power, suggesting a combined effect of SAV habitat and water environment. Nonetheless, a large fraction (> 67%) of the variation in zooplankton variables remained unexplained. By removing the effect of SAV cover (PLAND; "Partial model" in Table 3), SAV complexity (PAFRAC) was retained as a significant explanatory variable in only two models. In fact, SAV complexity was negatively related to crustacean zooplankton biomass (Adj-$R^2 = 0.11$) and FDis index (Adj-$R^2 = 0.10$).

3.5 Discussion

Our study showed that SUP is a reliable method to estimate *in situ* SAV biomass and cover in shallow lakes, despite being relatively time-consuming in terms of image analysis processing. The SUP approach also provided key information about the *in situ* complexity of natural SAV assemblages. Our results partially supported the hypothesis that SAV cover (PLAND) and complexity (PAFRAC) sustain higher abundance (in terms of density only) and drive functional community structure and diversity in crustacean zooplankton communities. However, models relating SAV habitat features to crustacean zooplankton functional groups had relatively low explanatory power (< 35% of the total variation explained), even when adding other local environmental predictors. Higher SAV cover was associated with higher abundances and functional richness (FRic) of crustacean zooplankton. In contrast, SAV complexity was associated with lower biomass of crustacean zooplankton, higher FEve index, and lower FDis index, even when controlling for the effect of SAV cover. SAV habitat features also affected crustacean functional groups. Both the abundance and the biomass of copepod cyclopoids (FG3), mainly nauplii and copepodid stages, were positively related to SAV cover and complexity. The biomass of large herbivorous cladocerans (FG2), mainly *S. crystallina*, also increased with SAV cover, while the biomass of calanoids (FG4), mainly *E. affinis,* decreased.

3.5.1 SUP: a reliable method to assess in situ SAV cover and complexity

Although remote sensing has long been used in terrestrial ecosystems to assess *in situ* habitat complexity (Proulx and Parrott, 2009), those techniques have only seldom been applied to aquatic ecosystems (but see Mellin et al., 2012). In the current context of SAV-reduction in human-impacted lakes worldwide (Körner, 2002), underwater photography could allow wider spatial monitoring of SAV biomass. We have shown that SAV cover and complexity measured from SUP were well correlated with SAV harvested biomass in our study system. As these indices displayed a high spatial variability at the scale of our study, the use of the averaged values of SAV biomass over the three quadrats improved the reliability of the method. As shown in previous studies (McAbendroth et al., 2005), we were expecting that differences in SAV species composition would lead to greater SAV complexity due to morphological differences between plants leaves among species. However, we did not find any effect of SAV species composition on SAV complexity. This result is probably due to the low plant diversity within SAV patches, as our study system was mainly dominated by only two, albeit structurally different, species (i.e. *V. americana* and *P. richardsonii)*. Moreover, these two dominant species are not considered structurally complex, as they do not have dissected leaves such as, *e.g.*, *Myriophyllum spicatum*. Hence, this SAV species composition may not represent a sufficiently high gradient of complexity to generate an answer of the zooplankton communities to complexity. Here, the PAFRAC index was probably more related to the spatial arrangement of individual plants within the SAV patch than to the species present. This could also explain the strong relationships between the two indices, SAV cover and complexity; even though, PLAND and PAFRAC are calculated independently from each other (Wang et al., 2014). This narrow gradient of complexity could hide the effect of structural element diversity on zooplankton diversity. Future studies would benefit from being performed in lakes with wider SAV diversity.

The SUP approach is a promising avenue to assess SAV features in a non-destructive way. Although this technique provides a good estimate of plant biomass, its limitations should be taken into account. For example, the camera seldom detected SAV cover within the water column even in the absence of SAV biomass within the quadrat itself (*e.g*. Table S1, site X6Y6 in 2014). In most cases, this was attributable to wind and/or wave action on plants reaching the surface, causing the stems to bend over or to drift above the quadrat. Using multiple replicate SUP images should thus be recommended to overcome this issue. Moreover, water turbidity made it difficult to automate image processing based on colour and contrast, imposing a time-consuming manual analysis to isolate SAV from the picture background. Whereas some techniques exist to perform underwater image enhancement (e.g., Zhao et al., 2015), they are not very efficient in situations such as ours where the background and the plants have similar colours; and there is limited contrast between them. Novel approaches such as machine-learning might hopefully bridge this gap in the near future. Another potential issue related to our approach is the reduction of a three-dimensional information into only two-dimensions, leading to an underestimation of SAV habitat complexity. Recently, new techniques were developed to capture three-dimensional habitat features, providing a more accurate representation of the habitat (*e.g*. Figueira et al., 2015). However, the advantage of the use of 2D cameras is its easy application which can be especially needed for the development of large-scale studies involving citizen science (Foster et al., 2017). Given the good relationship found here between SAV biomass collected by divers and SAV cover measured in the pictures , it is now possible to get relatively good estimates of SAV cover using underwater imagery only. The use of inexpensive devices such an extensible pole in replacement of the divers should further ease the application of this technique and open the way to innovative low-cost citizen science projects.

3.5.2 SAV effects on zooplankton community structure and functional groups

Our results support the hypothesis that the abundance of crustacean zooplankton increased with SAV biomass and cover, as well as complexity, albeit this relationship was weaker than what was observed at a larger scale (Bolduc et al., 2016). This finding was expected because our small-scale sampling design aimed at understanding the effects of cover and complexity within SAV patches, which make the relationship less pronounced than on a large scale. At a small scale, detectable gradients of SAV cover and complexity are reduced by the noise induced by small-scale spatial variability.

At larger scale (study area of 26 km^2), the strong relationship between SAV biomass and zooplankton community has been explained by the protection provided by SAV against current (Basu et al., 2000; Bolduc et al., 2016), which was markedly higher in those studies (mean velocity: 30 cm/s) than in the present study (velocity < 1 cm/s). Thus, at the scale of our study, the observed higher total abundance of crustacean zooplankton in SAV patches was determined by the dominant taxa, mostly cyclopoid copepods, which are known to live in dense macrophyte beds (Jeppesen et al., 1998). In systems showing high predation risk in the littoral zone, SAV beds have been shown to benefit small-bodied zooplankton which would be less vulnerable to predation by insect larvae and small fish (González Sagrario and Balseiro, 2010). Although we did not assess predation risk in our study, a similar mechanism might operate in our system, where medium- and small-sized species such as *E. agilis*, *A. robustus* (adults, copepodites and nauplii) and *Bosmina* sp. were more abundant within SAV beds. In contrast, another trait that may explain the low abundance of large-bodied calanoid species (*E. affinis*) observed in SAV beds is its ability to swim fast, and thus the ability to escape predators in open water (Mahjoub et al., 2011). The low abundance of medium-sized cladocerans such as *D. brachyurum* could also be explained by their predator-avoidance behavior through daytime hiding within the sediments (Gonzàlez Sagrario and Balseiro, 2010). Because our study was performed over different years, the spawning success of fish, and thus the number of predatory larvae, could have masked the potential SAV-crustacean zooplankton relationship. Moreover, as some chydorid species tend to attach themselves on SAV, using a pump to collect zooplankton may not harvest all species present, which would also have an impact on the detection of the SAV-zooplankton relationship.

In accordance with the results obtained by Zeng et al. (2017), the regression models showed that high SAV cover correlated with crustacean abundance, but there was no simple effect of SAV complexity. However, when considering crustacean functional groups, we found a positive effect of SAV cover and complexity on the abundance of copepod cyclopoids (FG3), and a positive effect of SAV cover alone on the biomass of large cladocerans (FG2: *S. crystallina*). This positive effect of SAV cover on cladoceran biomass might be related both to the larger surface available for plant-associated species such as *S. crystallina* and chydorids, as observed at a large scale in Lake St.-Pierre (Bolduc et al. 2016). Cladoceran chydorid species also showed a high degree of segregation within littoral SAV beds in deep and shallow lakes in Europe (Jeppesen et al., 1998; Adamczuk, 2014).

More complex SAV habitats were reported to coincide with high zooplankton biomass by providing refuge for large zooplankton species against predation by fish in both field and experimental conditions (Jeppesen et al., 1998; Manatunge et al., 2000; Meerhoff et al., 2007). Unexpectedly, we did not observe a significant positive relationship between crustacean zooplankton biomass and SAV complexity in our study system. Although habitat complexity can influence fish-prey interactions (Crowder and Cooper, 1982), our results indicate that SAV complexity at the scale of SAV patches in our study system is not a guarantee of safety for large cladoceran species. Indeed, whereas the biomass of the functional group composed by large cladocerans (FG2) was positively related to high SAV cover, it was not related to SAV complexity. These results indicate that FG2 was more influenced by the area of plant surfaces available than by their architectural complexity, and thus not related to the refuge effect provided by high complexity SAV beds. This was also reported in temperate lakes by Gonzàlez Sagrario and Balseiro (2010) who showed that the effectiveness of SAV as a refuge for zooplankton may depend on the presence and identity of their predators (macroinvertebrates and fish). Our results may thus reflect complex interactive trophic cascades mediated by both invertebrate and vertebrate predators.

3.5.3 SAV effects on crustacean zooplankton functional diversity

Our study gave only a partial support to the niche habitat diversity concept because SAV habitat features have relatively weak effects on crustacean zooplankton functional diversity indices. Considering the full models, SAV cover was positively related to the higher functional richness (FRic) whereas SAV complexity was positively related to functional evenness (FEve) and negatively to functional dispersion (FDis). However, when controlling for SAV cover effects, only the negative effect of SAV complexity on FDis remained. Thus, in our study system, increasing SAV cover had a positive effect on crustacean FRic and FEve whereas both SAV cover and complexity decreased crustacean FDis. This refutes the complexity-diversity hypothesis, where an increase in habitat complexity should be related to an increase in functional diversity. As the FDis index indicates the dispersion of the crustacean traits from the centroid in the total space of traits (Laliberté and Legendre, 2010), our results showed that variation in crustacean traits was lower in more complex SAV habitats. This could be explained in two ways: 1) by the over-representation of one taxon, such as the nauplii of copepods in dense and complex SAV habitat as in our study system, which would attract the centroid close to this taxon, and therefore decrease the sum of the distance of taxa's traits to the centroid, or 2) by the presence of multiple species having similar traits in the community, which would reduce the space of traits. Whereas we also observed a higher FEve with increasing SAV complexity in our study system, our results suggest overall that dense SAV beds, by offering a habitat for specialists, narrows, rather than broadening, niche availability.

In a previous large-scale study, Bolduc et al. (2016) showed that crustacean zooplankton functional traits in SAV beds were more dispersed compared to those found in the open water. These authors argued that the dominance of chydorid species in SAV beds could widen the functional space by competitive exclusion. At a smaller scale, our study yielded a similar species pool but in different proportions among stations. The high abundance of nauplii in complex SAV habitats apparently reduced the crustacean functional dispersion (FDis). When the abundances of nauplii and copepodites were low, other crustacean taxa (harpacticoids, cladocerans and calanoids) were present in more or less equal abundance, which increased the value of FRic, and therefore agrees with the complexity-diversity hypothesis. Inclusion of nauplii in the assessment of functional diversity is interesting since the dominance of this functional group could exert a strong impact in the evaluation of the complexity-diversity relationship. Although rarely considered in zooplankton community studies, nauplii fulfill an important ecological role since they are at the base of the food chain (Porter et al. 1988). Our results were similar to those of McAbendroth et al. (2005) which reported that complex habitats enhanced the number of small-bodied macroinvertebrates.

3.6 Conclusions

The use of close-range remote sensing methods is now widely recognized as an efficient tool to monitor terrestrial ecosystems. However, the use of these new techniques underwater is still recent. Here we provide an example of the opportunities provided by using SUP methods as a reliable non-destructive method to assess SAV habitat features. We showed how SAV cover and complexity were strongly related to each other, and to SAV biomass estimated by harvesting plants.

Our study gave a partial support to our hypothesis based on the ecological niche concept. Total crustacean abundance and biomass increased with SAV cover but not with SAV complexity. Zooplankton functional diversity was higher in dense SAV cover, but high SAV complexity *per se* did not favor more functionally diverse crustacean community. Unexpectedly, some effects of SAV complexity were observed, but our results pointed towards negative, rather than positive, effects on zooplankton functional diversity. SAV habitat features influenced the functional structure of crustacean zooplankton, increasing the abundances of small copepod cyclopoids and the biomass of large cladocerans. However, the models relating SAV features to zooplankton abundance, biomass and functional diversity were relatively weak, and confounded by interactive effects of water environments. Our approach should open the way to a larger test of the complexity-diversity hypothesis by taking advantage of the cost effectiveness of digital photography. Using an improved and automatized method such as SUP could provide new opportunities to expand SAV monitoring to shallow lake habitats and benefit future citizen science programs.

3.7 Acknowledgments

This study is a contribution of the Groupe de Recherche Interuniversitaire en Limnologie (GRIL) and the Canada-Québec St. Lawrence Action Plan. Financial support was provided by the NSERC (Discovery grant to BPA: RGPIN-2015-04875), the Fond Québécois de la Recherche Nature et Technologie (ISI-FQRNT 186430), the RIVE-UQTR Research centre, and the GRIL, which supported P. Bolduc doctoral studies. We would like to thank Lucas Deschamps, Annie Picard and Joëlle Guitard for their technical assistance for zooplankton identification. We also thank Guillaume Rheault for the discussions about the sampling design and the statistical analysis and the technical staff of Environment and Climate Change Canada for SAV data collection. Thanks to Morgan Botrel and Stéphanie Massé for the coordination during sampling and laboratory analysis. The authors declare that there is no conflict of interest.

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3.9 Tables

Table 1. Environmental descriptors (mean ± SD) of the study stations sampled in 2013 and 2014. Submerged aquatic vegetation (SAV) refers to all submerged aquatic vegetation plants, including filamentous algae. Proportion of landscape occupied by SAV in the picture (PLAND) and perimeter-area fractal dimension (PAFRAC) are habitat features calculated from subaquatic upward photography (SUP), representing respectively SAV cover and complexity. Variables in bold are used in the RDA analysis (see Fig. 5). Probability values ($\alpha < 0.05$) indicate significant differences between years.

Variables	2013 (n = 24)		2014 (n = 28)		p-value
	Mean	± SD	Mean	± SD	
ENVIRONMENTAL VARIABLES					
Water depth (cm)	148.3	5.3	145.8	35.2	0.70
Water transparency (cm)	25.6	6.5	35.5	8.8	< 0.01
Water flow (cm/s)	0.3	0.4	0.5	0.9	0.16
Dissolved oxygen (mg/L)	13.2	19.4	9.8	2.0	0.17
pH	8.45	0.37	7.84	0.39	< 0.01
Conductivity (µS/cm)	152.5	11.2	258.8	60.8	< 0.01
Light attenuation (K_{PAR}; ln m^{-1})	2.1	0.4	1.6	0.5	< 0.01
Water temperature (°C)	19.8	1.1	24.1	1.9	< 0.01
SAV BIOMASS					
SAV dry weight (g/m^2)	115.0	76.9	24.6	18.4	< 0.01
SAV HABITAT FEATURES FROM SUP					
PLAND (%)	51.8	13.2	30.3	16.2	< 0.01
PAFRAC	1.37	0.05	1.25	0.08	< 0.01

Table 2. Mean abundance and biomass of species for the total crustacean zooplankton and for each taxonomic group, mean abundance and biomass of the crustacean functional groups and mean values of FD indices based on their functional traits. Crustacean species included in each FG group are shown in Figure 4. For more details on species traits and functional groups, see ESM Table S2 and Table S3.

Zooplankton	Dominant taxa	Species mean abundance (ind/L) ± SD	Species mean biomass (µg/L) ± SD
Total crustaceans	Cyclopoids nauplii; *S. crystallina*	15.73 ± 65.76	11.32 ± 41.92
Cladocerans	*Bosmina* sp.; *S. crystallina*	6.01 ± 17.67	16.21 ± 60.41
Copepod calanoids	Copepodites; *E. carolleeae*	14.99 ± 10.76	16.69 ± 12.77
Copepod cyclopoids	Nauplii; Copepodites; *E. agilis*; *A. robustus*	34.01 ± 110.87	6.73 ± 10.59
Copepod harpacticoids	Copepodites; *Nitokra* sp.	0.64 ± 0.63	0.21 ± 0.27

Functional groups	Principal traits	FG mean abundance (ind/L) ± SD	FG mean biomass (µg/L) ± SD
FG1	Herbivore-detritivores, surface feeding, bad swimmers	0.07 ± 0.29	0.03 ± 0.08
FG2	Herbivores, C-Filtration, bad swimmers	2.06 ± 1.96	5.59 ± 5.76
FG3	Omnivores, grasping, intermediate swimmers	8.50 ± 7.07	1.68 ± 1.84
FG4	Pelagic species, stationary suspension feeding, good swimmers	0.86 ± 0.94	0.96 ± 0.86

Functional indices	Definition	Range	Mean ± SD
FRic	Maximum convex hull including all species in the space of traits	10 - 19	15 ± 2.26
FEve	Evenness of species traits	0.49 - 0.84	0.65 ± 0.08
FDis	Mean distance of each species to the centroid of all species	0.30 - 0.55	0.47 ± 0.07

Table 3. Full and partial models relating crustacean zooplankton abundance, biomass and the functional diversity indices (FRic, FEve and FDis) to SAV cover (PLAND), SAV complexity (PAFRAC) and to environmental descriptors (water depth and transparency). The full model used these four independent variables while the partial models used the residual variance not explained by PLAND. Zooplankton abundance and biomass were log-transformed. PAFRAC was square-root transformed.

	Full models				Partial models			
Parameter	Estimate	SD	Adj.-R^2	p-value	Estimate	SD	Adj.-R^2	p-value
ZOOPLANKTON ABUNDANCE			0.18	<0.01			0.06	0.04
Intercept	0.27	0.71		<0.01	-1.17	0.57		0.04
PLAND	0.02	0.01		<0.01				
Water transparency	0.24	0.11		<0.01	0.21	0.10		0.04
ZOOPLANKTON BIOMASS			0.26	<0.01			0.11	<0.01
Intercept	16.30	3.83		<0.01	8.57	3.15		<0.01
PLAND	0.03	0.01		<0.01				
PAFRAC	-13.54	3.50		<0.01	-7.48	2.74		<0.01
FUNCTIONAL RICHNESS (FRic)			0.33	<0.01			0.29	<0.01
Intercept	2.86	0.17		<0.01	0.20	0.14		0.14
PLAND	0.002	<0.01		0.02				
Water depth	-0.30	0.07		<0.01	-0.30	0.07		<0.01
Water transparency	0.04	0.02		0.04	0.04	0.02		<0.01
FUNCTIONAL EVENNESS (FEve)			0.34	<0.01			0.16	<0.01
Intercept	0.15	0.23		0.51	0.12	0.04		<0.01
PAFRAC	0.46	0.18		0.02				
Water depth	-0.05	0.02		0.04				
Water transparency	-0.02	0.01		0.01	-0.02	<0.01		<0.01
FUNCTIONAL DISPERSION (FDis)			0.31	<0.01			0.10	0.01
Intercept	1.31	0.19		<0.01	0.52	0.20		0.01
PAFRAC	-0.80	0.17		<0.01	-0.45	0.18		0.01

3.10 Figures

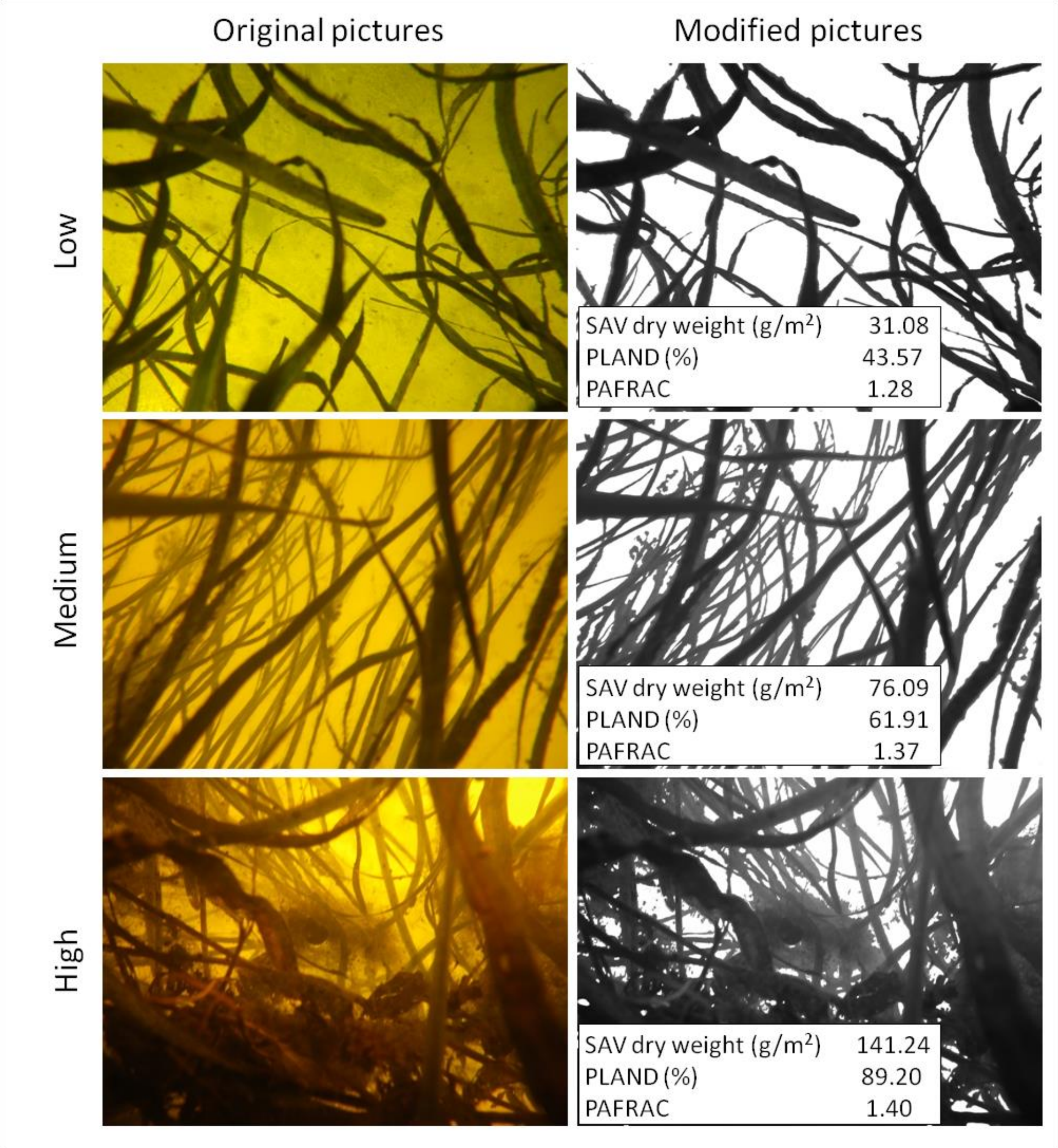


Figure 1. Example of subaquatic upward photography of a low, medium and highly vegetated quadrats, comparing the original pictures (left panels) with manually modified pictures (right panels). PLAND represents the proportion of landscape occupied by the submerged aquatic vegetation (SAV) in the modified picture and PAFRAC represents the perimeter-area fractal dimension, a complexity index of the SAV in the modified picture. See ESM Table S1 for more details.

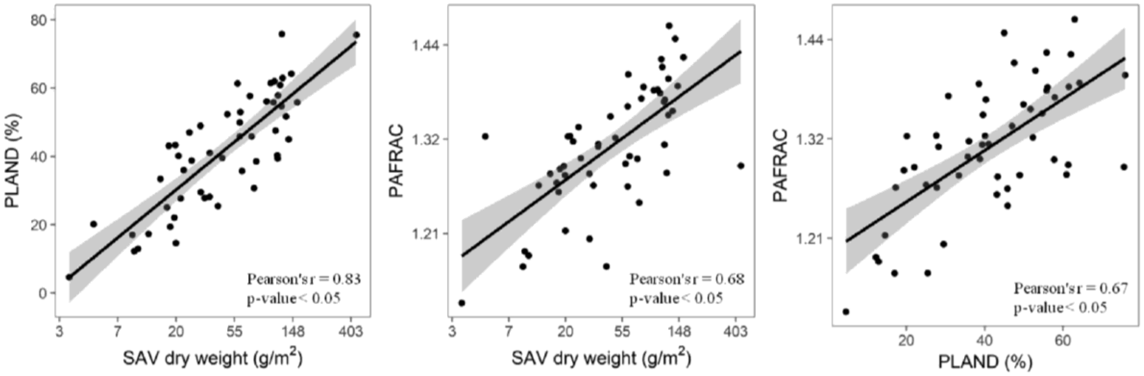


Figure 2. Relationship between submerged aquatic vegetation (SAV) biomass expressed in dry weight per m2 (log-transformed data) and the percentage of landscape occupied by SAV in the picture (PLAND; right panel), relationship between SAV biomass and the perimeter-area fractal dimension (PAFRAC; square-root transformed; middle panel); and relationship between PLAND and PAFRAC (left panel). Scale of the axes represents non-transformed data.

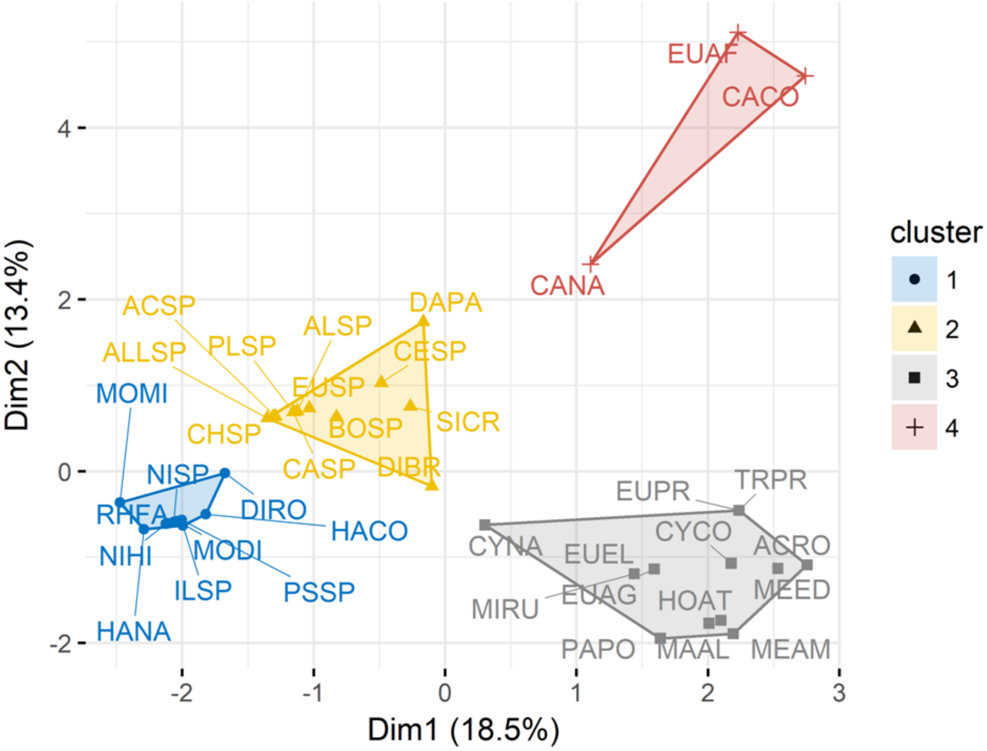


Figure 3. Zooplankton functional groups (FGs) calculated from the species traits in the community (see ESM Table S1). FGs were obtained by a hierarchical clustering on principal components analysis using categorical (swimming capacity, habitat, feeding type, trophic levels) and continuous data (maximum length). FG1: *Disparalona rostrata* (DIRO), *Ilyocryptus* sp. (ILSP), *Moina micrura* (MOMI), *Monospilus dispar* (MOMI), *Pseudochydorus* sp. (PSPS), *Rhynchotalona falcata* (RHFA), *Harpacticoida* copepodite (HACO), *Harpacticoida* naupli (HANA), *Nitokra hibernica* (NIHI), *Nitokra* sp. (NISP); FG2: *Acroperus* sp. (ACSP), *Alona* sp. (ALSP), *Alonella* sp. (ALLSP), *Bosmina* sp. (BOSP), *Camptocercus* sp. (CASP), *Ceriodaphnia* sp. (CESP), *Chydorus* sp. (CHSP), *Diaphanosoma brachyurum* (DIBR), *Daphnia parvula* (DAPA), *Eurycercus* sp. (EUSP), *Pleuroxus* sp. (PLSP), *Sida crystallina* (SICR); FG3: *Acanthocyclops robustus* (ACRO), *Cyclopoida* copepodite (CYCO), *Cyclopoida* naupli (CYNA), *Eucyclops agilis* (EUAG), *Eucyclops elegans* (EUAL), *Eucyclops prionophorus* (EUPR), *Homocyclops ater* (HOAT), *Macrocyclops albidus* (MAAL), *Mesocyclops americanus* (MEAM), *Mesocyclops edax* (MEED), *Microcyclops rubellus* (MIRU), *Paracyclops poppei* (PAPO), *Tropocyclops prasinus* (TRPR); FG4: *Calanoida* naupli (CANA), *Calanoida* copepodite (CACO), *Eurytemora carolleeae* (EUAF).

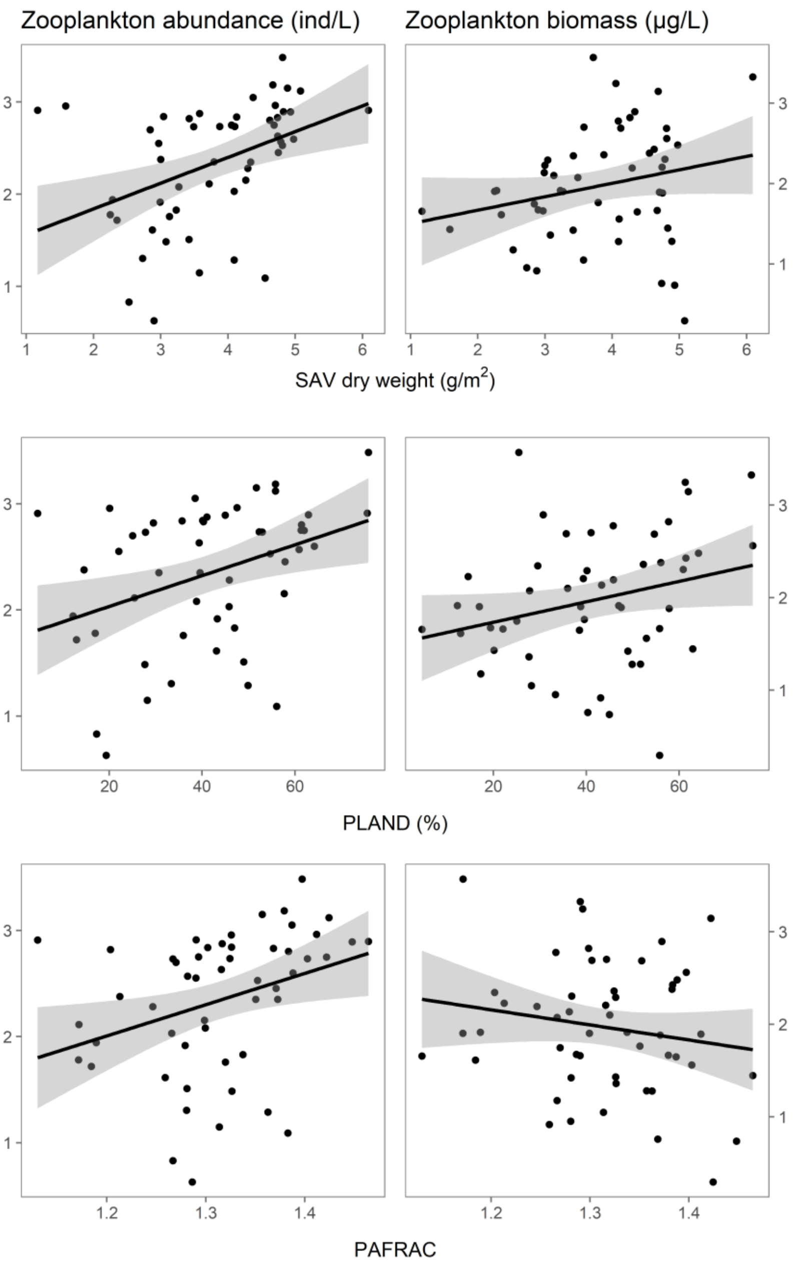


Figure 4. Relationships between zooplankton abundance (left panel) and zooplankton biomass (right panel) with submerged aquatic vegetation (SAV) biomass (dry weight/m2 - log-transformed data; upper panels), the percentage of landscape occupied by SAV in the picture (PLAND; middle panels) and the perimeter-area fractal dimension (PAFRAC - square-root-transformed data; lower panels). Scale of the axes represents non-transformed data.

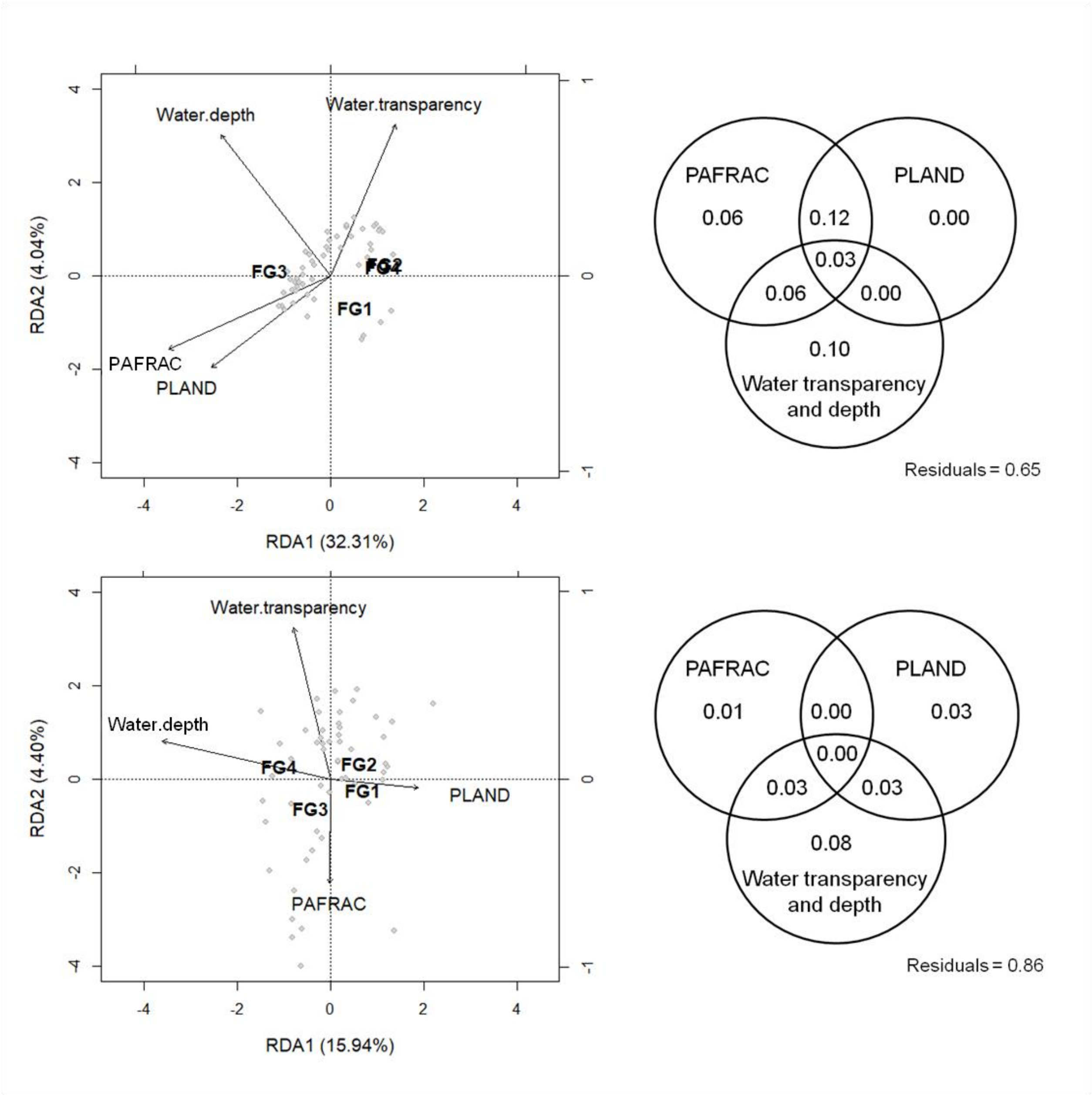
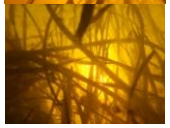
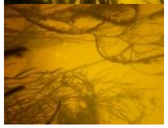


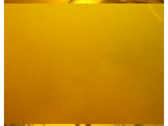
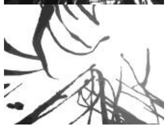
Figure 5. RDA on zooplankton functional group abundance (upper left panel) and variation partitioning (upper right panel) between the complexity index (PAFRAC), the percentage of landscape occupied by SAV in the picture (PLAND) and environmental variables (water depth and transparency); RDA on zooplankton functional group biomass (lower left panel) and variation partitioning (lower right panel) between the complexity index (PAFRAC), the percentage of landscape occupied by SAV in the picture (PLAND) and environmental variables (water depth and transparency).

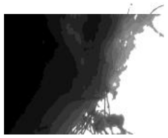
3.11 Supplementary material

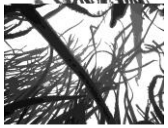
Table S1. SAV original and modified pictures for each quadrat, SAV biomass (dry weight/m2) associated and the proportion of SAV species calculated from the biomass data. Pictures were modified by manually removing the background and turn them into black and white images (8-bit images).

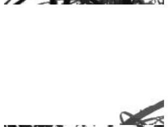
Year	Site	Quadrat	Original picture	Modified picture	SAV biomass	V. americana prop.	P.richardsonii prop.	H. dubia prop.	E. nuttallii prop.	Filamentous algae prop.	PLAND	PAFRAC
2013	X1Y5	1			288.04	0.09	0.59	0.08	0.00	0.25	50.29	1.4492
2013	X1Y5	2			66.43	0.27	0.70	0.00	0.00	0.03	47.67	1.4986
2013	X1Y5	3			150.88	0.24	0.63	0.00	0.01	0.12	37.02	1.3961
2013	X1Y7	1			173.06	0.68	0.31	0.00	0.00	0.01	73.39	1.3509
2013	X1Y7	2			179.17	0.15	0.63	0.00	0.00	0.22	27.89	1.4344
2013	X1Y7	3			169.66	0.11	0.87	0.00	0.00	0.01	66.12	1.4879
2013	X2Y4	1			186.95	0.34	0.53	0.00	0.00	0.13	76.36	1.4664

2013	X2Y4	2			117.75	0.50	0.43	0.03	0.00	0.05	73.23	1.4571
2013	X2Y4	3			101.00	0.95	0.01	0.00	0.00	0.05	39.20	1.4697
2013	X2Y6	1			116.03	0.52	0.38	0.00	0.00	0.09	10.43	1.2841
2013	X2Y6	2			110.49	1.00	0.00	0.00	0.00	0.00	83.06	1.433
2013	X2Y6	3			102.15	0.86	0.13	0.00	0.00	0.01	73.90	1.4204
2013	X2Y8	1			153.40	0.52	0.43	0.00	0.00	0.04	61.33	1.3778
2013	X2Y8	2			82.56	0.89	0.05	0.00	0.00	0.06	77.02	1.4162
2013	X2Y8	3			142.02	0.99	0.00	0.00	0.00	0.01	89.20	1.3977
2013	X3Y3	1			98.95	0.99	0.00	0.00	0.00	0.01	63.68	1.4621
2013	X3Y3	2			196.15	0.18	0.36	0.01	0.00	0.46	50.86	1.4703

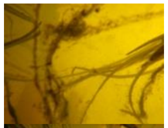
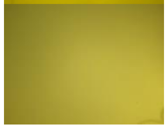
2013	X3Y3	3			119.00	0.99	0.00	0.00	0.00	0.01	71.41	1.3338
2013	X3Y5	1			40.64	0.52	0.28	0.00	0.00	0.20	48.82	1.48
2013	X3Y5	2			17.50	0.00	0.97	0.00	0.00	0.03	8.99	1.379
2013	X3Y5	3			2.31	0.97	0.02	0.00	0.00	0.01	0.31	NA
2013	X3Y7	1			206.74	0.19	0.52	0.00	0.00	0.28	35.58	1.3995
2013	X3Y7	2			171.92	0.24	0.75	0.00	0.00	0.02	41.96	1.3432
2013	X3Y7	3			81.56	0.34	0.58	0.00	0.00	0.08	77.48	1.3285
2013	X4Y2	1			135.78	0.43	0.55	0.00	0.00	0.03	70.48	1.3585
2013	X4Y2	2			72.69	0.95	0.00	0.00	0.00	0.05	72.35	1.4648
2013	X4Y2	3			165.23	0.12	0.11	0.75	0.00	0.02	21.15	1.2335

2013	X4Y4	1			32.69	0.97	0.00	0.00	0.00	0.03	49.71	1.4743
2013	X4Y4	2			85.18	0.90	0.07	0.00	0.00	0.03	63.07	NA
2013	X4Y4	3			103.93	0.99	0.00	0.00	0.00	0.01	24.76	1.2648
2013	X4Y6	1			66.45	0.99	0.00	0.00	0.00	0.01	29.50	1.4572
2013	X4Y6	2			225.87	0.95	0.04	0.00	0.00	0.02	83.17	1.3125
2013	X4Y6	3			41.99	0.95	0.00	0.00	0.00	0.05	29.92	1.4662
2013	X4Y8	1			76.09	1.00	0.00	0.00	0.00	0.00	61.91	1.3674
2013	X4Y8	2			258.16	0.59	0.34	0.01	0.00	0.06	57.59	1.4138
2013	X4Y8	3			19.71	0.06	0.25	0.66	0.00	0.03	1.43	1.324
2013	X5Y1	1			422.71	0.04	0.79	0.00	0.00	0.17	75.57	1.2902

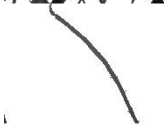
2013	X5Y3	1			55.37	0.97	0.00	0.00	0.00	0.03	86.03	1.385
2013	X5Y3	2			347.23	0.08	0.57	0.00	0.00	0.35	38.14	1.3899
2013	X5Y3	3			157.14	0.15	0.82	0.00	0.00	0.03	68.33	1.3892
2013	X5Y5	1			35.00	0.93	0.01	0.00	0.00	0.05	66.12	1.3665
2013	X5Y5	2			44.72	0.89	0.00	0.00	0.00	0.11	37.50	1.3667
2013	X5Y5	3			108.45	0.96	0.02	0.00	0.00	0.03	55.27	1.4749
2013	X5Y7	1			76.39	0.94	0.06	0.00	0.00	0.01	48.39	1.384
2013	X5Y7	2			123.63	0.94	0.04	0.00	0.00	0.02	25.81	1.4189
2013	X5Y7	3			38.53	0.35	0.62	0.00	0.01	0.02	41.32	1.358
2013	X6Y2	1			101.67	1.00	0.00	0.00	0.00	0.00	60.64	1.4233

2013	X6Y2	2			110.21	1.00	0.00	0.00	0.00	0.00	45.12	1.3596
2013	X6Y2	3			131.48	1.00	0.00	0.00	0.00	0.00	67.85	1.33
2013	X6Y4	1			59.04	0.95	0.00	0.00	0.00	0.05	60.21	1.4117
2013	X6Y4	2			43.96	0.98	0.00	0.00	0.00	0.02	55.91	1.3652
2013	X6Y4	3			31.15	0.91	0.08	0.00	0.00	0.01	2.56	1.2745
2013	X6Y6	1			108.19	0.87	0.00	0.05	0.00	0.08	26.34	1.4364
2013	X6Y6	2			46.98	0.98	0.00	0.00	0.00	0.02	72.21	1.3496
2013	X6Y6	3			32.46	0.96	0.00	0.00	0.00	0.04	51.12	1.3023
2013	X7Y1	1			94.08	0.97	0.00	0.00	0.00	0.03	58.43	1.4554
2013	X7Y1	2			93.07	1.00	0.00	0.00	0.00	0.00	52.64	1.3665

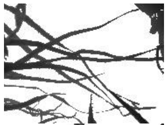
2013	X7Y1	3			120.90	0.97	0.00	0.00	0.00	0.03	73.23	1.3286
2013	X7Y3	1			136.65	1.00	0.00	0.00	0.00	0.00	76.19	1.4246
2013	X7Y3	2			67.30	1.00	0.00	0.00	0.00	0.00	48.68	1.3259
2013	X7Y3	3			78.05	1.00	0.00	0.00	0.00	0.00	43.30	1.3981
2013	X7Y5	1			201.99	0.63	0.25	0.00	0.00	0.12	43.02	1.2554
2013	X7Y5	2			73.98	0.54	0.37	0.00	0.00	0.09	21.22	1.3477
2013	X7Y5	3			103.48	0.71	0.21	0.00	0.00	0.07	53.91	1.3442
2013	X8Y2	1			97.78	0.62	0.34	0.00	0.00	0.04	54.72	1.4353
2013	X8Y2	2			58.57	0.06	0.93	0.00	0.00	0.01	51.23	1.4095
2013	X8Y2	3			208.87	0.30	0.67	0.00	0.00	0.02	76.67	NA

2013	X8Y4	1			122.51	0.41	0.40	0.02	0.00	0.17	33.58	1.4531
2013	X8Y4	2			92.16	0.96	0.00	0.03	0.00	0.01	43.38	1.384
2013	X8Y4	3			33.12	0.75	0.25	0.00	0.00	0.00	15.20	1.2807
2014	X1Y1	1			7.17	1.00	0.00	0.00	0.00	0.00	11.83	1.2682
2014	X1Y1	2			24.71	0.99	0.00	0.00	0.00	0.01	56.53	1.3202
2014	X1Y1	3			44.19	1.00	0.00	0.00	0.00	0.00	48.01	1.3097
2014	X1Y3	1			0.20	0.87	0.00	0.00	0.00	0.13	NA	NA
2014	X1Y3	2			9.23	0.96	0.00	0.00	0.00	0.04	NA	NA
2014	X1Y3	3			0.00	0.00	0.00	0.00	0.00	0.00	3.93	1.3745
2014	X1Y5	1			0.00	0.00	0.00	0.00	0.00	0.00	NA	NA

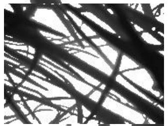
2014	X1Y5	2			0.00	0.00	0.00	0.00	0.00	0.00	NA	NA
2014	X1Y5	3			0.00	0.00	0.00	0.00	0.00	0.00	NA	NA
2014	X1Y7	1			105.05	0.00	0.98	0.02	0.00	0.00	54.49	1.2677
2014	X1Y7	2			15.54	0.07	0.93	0.00	0.00	0.00	21.90	1.2475
2014	X1Y7	3			0.00	0.00	0.00	0.00	0.00	0.00	NA	NA
2014	X2Y2	1			16.40	0.88	0.00	0.00	0.00	0.12	22.58	1.2655
2014	X2Y2	2			74.30	1.00	0.00	0.00	0.00	0.00	81.11	1.3215
2014	X2Y2	3			81.03	1.00	0.00	0.00	0.00	0.00	80.26	1.2911
2014	X2Y4	1			0.00	0.00	0.00	0.00	0.00	0.00	NA	NA
2014	X2Y4	2			3.33	1.00	0.00	0.00	0.00	0.00	3.27	1.211

2014	X2Y4	3			0.00	0.00	0.00	0.00	0.00	0.00	NA	NA
2014	X2Y6	1			16.79	1.00	0.00	0.00	0.00	0.00	26.09	1.2766
2014	X2Y6	2			14.43	1.00	0.00	0.00	0.00	0.00	16.30	1.2887
2014	X2Y6	3			3.33	1.00	0.00	0.00	0.00	0.00	9.51	1.235
2014	X2Y8	1			10.35	1.00	0.00	0.00	0.00	0.00	39.87	1.3197
2014	X2Y8	2			8.43	0.99	0.00	0.00	0.00	0.01	32.77	1.1957
2014	X2Y8	3			31.56	1.00	0.00	0.00	0.00	0.00	56.64	1.2612
2014	X3Y1	1			4.91	0.99	0.00	0.00	0.00	0.01	19.36	1.2842
2014	X3Y1	2			31.08	1.00	0.00	0.00	0.00	0.00	43.57	1.2778
2014	X3Y1	3			19.58	1.00	0.00	0.00	0.00	0.00	3.27	1.3078

2014	X3Y3	1			67.74	1.00	0.00	0.00	0.00	0.00	52.79	1.347
2014	X3Y3	2			53.28	1.00	0.00	0.00	0.00	0.00	63.70	1.3081
2014	X3Y3	3			20.84	1.00	0.00	0.00	0.00	0.00	40.44	1.3177
2014	X3Y5	1			8.75	1.00	0.00	0.00	0.00	0.00	9.28	1.2771
2014	X3Y5	2			16.01	1.00	0.00	0.00	0.00	0.00	29.18	1.2759
2014	X3Y5	3			3.73	1.00	0.00	0.00	0.00	0.00	0.39	NA
2014	X3Y7	1			30.24	1.00	0.00	0.00	0.00	0.00	10.86	1.3233
2014	X3Y7	2			7.21	1.00	0.00	0.00	0.00	0.00	72.69	1.238
2014	X3Y7	3			19.15	1.00	0.00	0.00	0.00	0.00	46.31	1.276
2014	X4Y2	1			14.88	0.33	0.20	0.47	0.00	0.00	28.64	1.3225

2014	X4Y2	2			22.14	1.00	0.00	0.00	0.00	0.00	42.10	1.3464
2014	X4Y2	3			22.78	1.00	0.00	0.00	0.00	0.00	49.65	1.3088
2014	X4Y4	1			0.13	1.00	0.00	0.00	0.00	0.00	NA	NA
2014	X4Y4	2			24.91	1.00	0.00	0.00	0.00	0.00	28.03	1.3487
2014	X4Y4	3			1.38	0.97	0.00	0.00	0.00	0.03	8.63	1.2191
2014	X4Y6	1			59.56	1.00	0.00	0.00	0.00	0.00	71.12	1.3203
2014	X4Y6	2			86.58	1.00	0.00	0.00	0.00	0.00	64.44	1.2699
2014	X4Y6	3			64.38	0.47	0.53	0.00	0.00	0.00	37.57	1.3058
2014	X4Y8	1			115.44	1.00	0.00	0.00	0.00	0.00	90.64	1.2679
2014	X4Y8	2			51.08	1.00	0.00	0.00	0.00	0.00	32.80	1.2668

2014	X4Y8	3			10.06	0.99	0.00	0.00	0.00	0.01	13.99	1.2617
2014	X5Y1	1			21.66	0.93	0.06	0.00	0.00	0.00	37.19	1.2979
2014	X5Y1	2			11.01	1.00	0.00	0.00	0.00	0.00	5.61	1.2509
2014	X5Y1	3			15.85	1.00	0.00	0.00	0.00	0.00	32.31	1.2607
2014	X5Y3	1			2.30	1.00	0.00	0.00	0.00	0.00	0.80	NA
2014	X5Y3	2			47.53	1.00	0.00	0.00	0.00	0.00	61.09	1.3495
2014	X5Y3	3			39.12	0.26	0.74	0.00	0.00	0.00	26.70	1.2613
2014	X5Y5	1			2.31	1.00	0.00	0.00	0.00	0.00	4.05	1.2896
2014	X5Y5	2			51.08	1.00	0.00	0.00	0.00	0.00	52.17	1.3539
2014	X5Y5	3			51.22	0.69	0.30	0.00	0.00	0.00	66.85	1.3063

2014	X5Y7	1			48.84	0.73	0.27	0.00	0.00	0.00	35.14	1.3348
2014	X5Y7	2			93.24	0.35	0.65	0.00	0.00	0.00	40.91	1.3038
2014	X5Y7	3			41.07	1.00	0.00	0.00	0.00	0.00	31.03	1.2669
2014	X6Y2	1			15.56	1.00	0.00	0.00	0.00	0.00	15.90	1.1974
2014	X6Y2	2			23.49	0.99	0.00	0.00	0.00	0.01	66.93	1.3392
2014	X6Y2	3			4.13	1.00	0.00	0.00	0.00	0.00	17.27	1.305
2014	X6Y4	1			4.68	1.00	0.00	0.00	0.00	0.00	2.14	1.2383
2014	X6Y4	2			0.27	0.87	0.00	0.00	0.00	0.13	0.15	NA
2014	X6Y4	3			20.53	1.00	0.00	0.00	0.00	0.00	48.67	1.2761
2014	X6Y6	1			24.44	1.00	0.00	0.00	0.00	0.00	35.34	1.3163

2014	X6Y6	2			29.41	0.84	0.16	0.00	0.00	0.00	NA	NA
2014	X6Y6	3			3.33	1.00	0.00	0.00	0.00	0.00	8.39	1.3233
2014	X6Y8	1			10.18	1.00	0.00	0.00	0.00	0.00	6.57	1.2571
2014	X6Y8	2			26.64	1.00	0.00	0.00	0.00	0.00	52.62	1.373
2014	X6Y8	3			28.86	1.00	0.00	0.00	0.00	0.00	48.72	1.3296
2014	X7Y1	1			9.80	0.99	0.00	0.00	0.00	0.01	6.98	1.2986
2014	X7Y1	2			2.77	0.70	0.00	0.00	0.00	0.30	4.609	1.3592
2014	X7Y1	3			0.00	0.00	0.00	0.00	0.00	0.00	48.75	1.3197
2014	X7Y3	1			23.96	1.00	0.00	0.00	0.00	0.00	42.36	1.4182
2014	X7Y3	2			8.59	1.00	0.00	0.00	0.00	0.00	8.65	1.1954

2014	X7Y3	3			29.64	1.00	0.00	0.00	0.00	0.00	32.01	1.3655
2014	X7Y5	1			33.21	1.00	0.00	0.00	0.00	0.00	11.32	1.214
2014	X7Y5	2			33.11	1.00	0.00	0.00	0.00	0.00	38.07	1.3018
2014	X7Y5	3			29.00	1.00	0.00	0.00	0.00	0.00	33.99	1.2845
2014	X7Y7	1			14.43	1.00	0.00	0.00	0.00	0.00	41.95	1.3119
2014	X7Y7	2			17.30	1.00	0.00	0.00	0.00	0.00	56.71	1.3072
2014	X7Y7	3			41.07	1.00	0.00	0.00	0.00	0.00	42.33	1.3931
2014	X8Y2	1			6.89	0.97	0.00	0.00	0.00	0.03	13.79	1.3904
2014	X8Y2	2			0.54	0.00	0.00	0.00	0.00	1.00	NA	NA
2014	X8Y2	3			0.46	0.00	0.00	0.00	0.00	1.00	NA	NA

2014	X8Y4	1			41.17	1.00	0.00	0.00	0.00	0.00	61.27	1.3089
2014	X8Y4	2			11.89	1.00	0.00	0.00	0.00	0.00	20.35	1.2843
2014	X8Y4	3			35.52	1.00	0.00	0.00	0.00	0.00	65.26	1.2496
2014	X8Y6	1			43.29	1.00	0.00	0.00	0.00	0.00	46.92	1.3038
2014	X8Y6	2			57.72	0.92	0.08	0.00	0.00	0.00	17.61	1.3222
2014	X8Y6	3			2.87	1.00	0.00	0.00	0.00	0.00	20.08	1.3147
2014	X8Y8	1			22.21	1.00	0.00	0.00	0.00	0.00	59.47	1.3334
2014	X8Y8	2			15.81	1.00	0.00	0.00	0.00	0.00	28.93	1.3973
2014	X8Y8	3			50.12	0.95	0.00	0.00	0.00	0.05	58.45	1.2153

Table S2. Species traits used in the determination of the five functional groups obtained with the hierarchical clustering. The maximum length of species was measured directly on individuals. Species traits were derived from the literature (swimming capacity, habitat, feeding type, trophic level) and from direct measurement (max length).

Identification	FG	Acronym	Occurence (/52)	Abundance (%)	Biomass (%)	Swimming capacity	Habitat	Feeding type	Trophic level	Max length (mm)
CLADOCERA										
Acroperus sp.	2	ACSP	3	<0.01	<0.01	Bad	littoral	C-Filtration	Herbivore	0.65
Alona sp.	2	ALSP	35	0.19	0.39	Bad	littoral	C-Filtration	Herbivore	0.925
Alonella sp.	2	ALLSP	10	0.02	0.02	Bad	littoral	C-Filtration	Herbivore	0.55
Bosmina sp.	2	BOSP	51	11.48	6.71	Bad	generalist	B-Filtration	Herbivore	0.45
Camptocercus sp.	2	CASP	21	0.03	0.31	Bad	littoral	C-Filtration	Herbivore	0.88
Ceriodaphnia sp.	2	CESP	23	0.11	0.11	Bad	generalist	D-Filtration	Herbivore	0.75
Chydorus sp.	2	CHSP	11	0.02	0.12	Bad	littoral	C-Filtration	Herbivore	0.625
Diaphanosoma brachyurum	2	DIBR	34	0.13	0.10	Intermediate	littoral	S-Filtration	Herbivore	0.80
Daphnia parvula	2	DAPA	1	<0.01	<0.01	Bad	pelagic	D-Filtration	Herbivore	0.65
Disparalona rostrata	1	DIRO	2	<0.01	0.02	Bad	littoral	C-Filtration	herbivore-detritivore	0.775
Eurycercus sp.	2	EUSP	10	0.03	0.09	Bad	littoral	C-Filtration	Herbivore	1.075
Ilyocryptus sp.	1	ILSP	26	0.11	0.04	Bad	littoral	Surface Feeding	Detritivore	0.63
Moina micrura	1	MOMI	1	<0.01	<0.01	Bad	Littoral	S-Filtration	herbivore-detritivore	0.25
Monospilus dispar	1	MODI	11	0.03	0.07	Bad	littoral	Surface Feeding	herbivore-detritivore	0.60
Pleuroxus sp.	2	PLSP	9	0.01	0.07	Bad	littoral	C-Filtration	Herbivore	0.875
Pseudochydorus sp.	1	PSSP	1	<0.01	0.03	Bad	littoral	Surface Feeding	herbivore-detritivore	0.65
Rhynchotalona falcata	1	RHFA	6	0.04	0.04	Bad	littoral	SurfaceFeeding	herbivore-detritivore	0.48
Sida crystallina	2	SICR	52	5.90	59.70	Bad	littoral	S-Filtration	Herbivore	2.175
COPEPODA										
Acanthocyclops robustus	3	ACRO	44	0.82	5.50	Intermediate	pelagic	Grasping	Omnivore	1.175
Cyclopoida copepodite	3	CYCO	52	4.47	6.21	Intermediate	generalist	Grasping	Omnivore-Herbivore	1.1
Cyclopoida naupli	3	CYNA	51	67.27	3.59	Bad	littoral	Grasping	Omnivore-Herbivore	0.40
Calanoida naupli	4	CANA	41	3.39	0.53	Bad	pelagic	StationarySuspension	Omnivore-Herbivore	0.30
Calanoida copepodite	4	CACO	47	3.70	6.17	Good	pelagic	StationarySuspension	Omnivore-Herbivore	1.03
Eucyclops agilis	3	EUAG	50	1.32	4.78	Intermediate	littoral	Grasping	Omnivore-Herbivore	0.875
Eucyclops elegans	3	EUEL	2	<0.01	0.01	Intermediate	littoral	Grasping	Omnivore-Herbivore	0.875
Eucyclops prionophorus	3	EUPR	1	<0.01	<0.01	Intermediate	pelagic	Grasping	Omnivore-Herbivore	0.58
Eurytemora carolleeae	4	EUAF	47	0.44	4.95	Good	pelagic	StationarySuspension	Herbivore	1.4
Harpacticoida copepodite	1	HACO	43	0.24	0.14	Bad	littoral	SurfaceFeeding	herbivore-detritivore	0.95
Harpacticoida naupli	1	HANA	7	0.15	<0.01	Bad	littoral	SurfaceFeeding	herbivore-detritivore	0.18
Homocyclops ater	3	HOAT	2	<0.01	0.03	Intermediate	littoral	Grasping	Omnivore-Carnivore	1.45
Macrocyclops albidus	3	MAAL	3	<0.01	0.03	Intermediate	littoral	Grasping	Omnivore-Carnivore	1.3
Mesocyclops americanus	3	MEAM	1	<0.01	<0.01	Intermediate	generalist	Grasping	Omnivore	0.875
Mesocyclops edax	3	MEED	22	0.04	0.13	Intermediate	pelagic	Grasping	Omnivore-Carnivore	0.80
Microcyclops rubellus	3	MIRU	18	0.02	0.03	Intermediate	littoral	Grasping	Omnivore-Herbivore	0.625

Nitokra hibernica	1	NIHI	4	<0.01	<0.01	Bad	littoral	SurfaceFeeding	herbivore-detritivore	0.45
Nitokra sp.	1	NISP	17	0.04	0.05	Bad	littoral	SurfaceFeeding	herbivore-detritivore	0.55
Paracyclops poppei	3	PAPO	2	<0.01	<0.01	Intermediate	littoral	Grasping	Omnivore	0.7
Tropocyclops prasinus	3	TRPR	4	<001	<001	Intermediate	pelagic	Grasping	Omnivore-Herbivore	0.58

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Table S3. Zooplankton species contributing to the biomass and abundance of functional groups. Only species contributing for 2% or more are listed with their relative contribution. See table S2 for zooplankton species acronym.

Functional group	Species contributing to abundance (%)	Species contributing to biomass (%)
FG1	HACO (41%), HANA (22%), ILSP (16%), RHFA (7%), NISP (6%),MODI (4%)	HACO (36%), MODI (16%), NISP (11%), ILSP(11%), RHFA (10%), PSSP (6%), DIRO (5%)
FG2	BOSP (52%), SICR (45%)	SICR (92%), BOSP (7%)
FG3	CYNA (86%), CYCO (8%), EUAG (3%), ACRO (2%)	CYCO (30%), EUAG (27%), ACRO (26%), CYNA (15%)
FG4	CACO (54%), CANA (40%), EUAF (6%)	CACO (58%), EUAF (39%), CANA (4%)

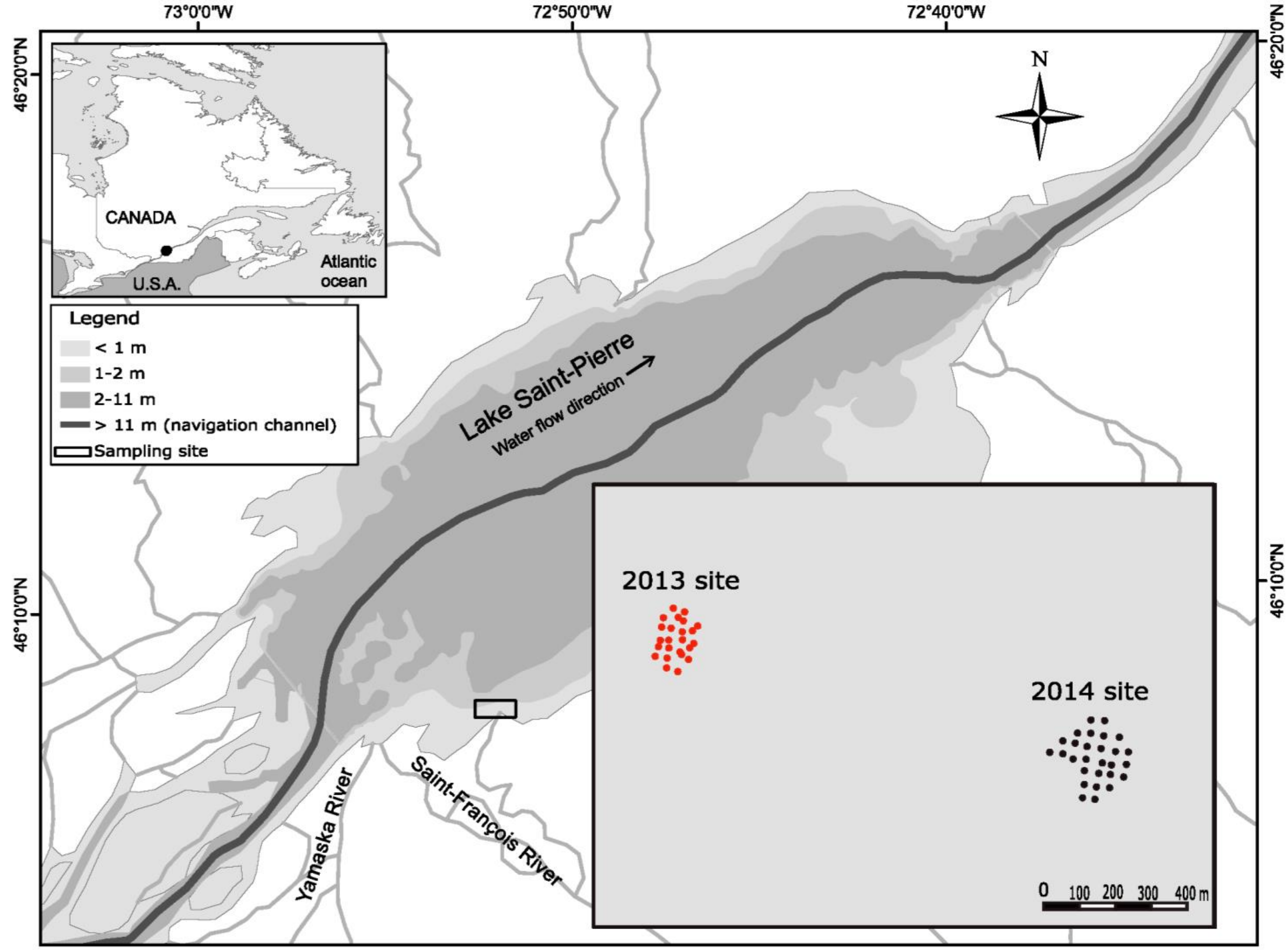

Figure S1. Map of the study sites and stations for the 2013 and 2014 sampling within the Lake St. Pierre, Canada.

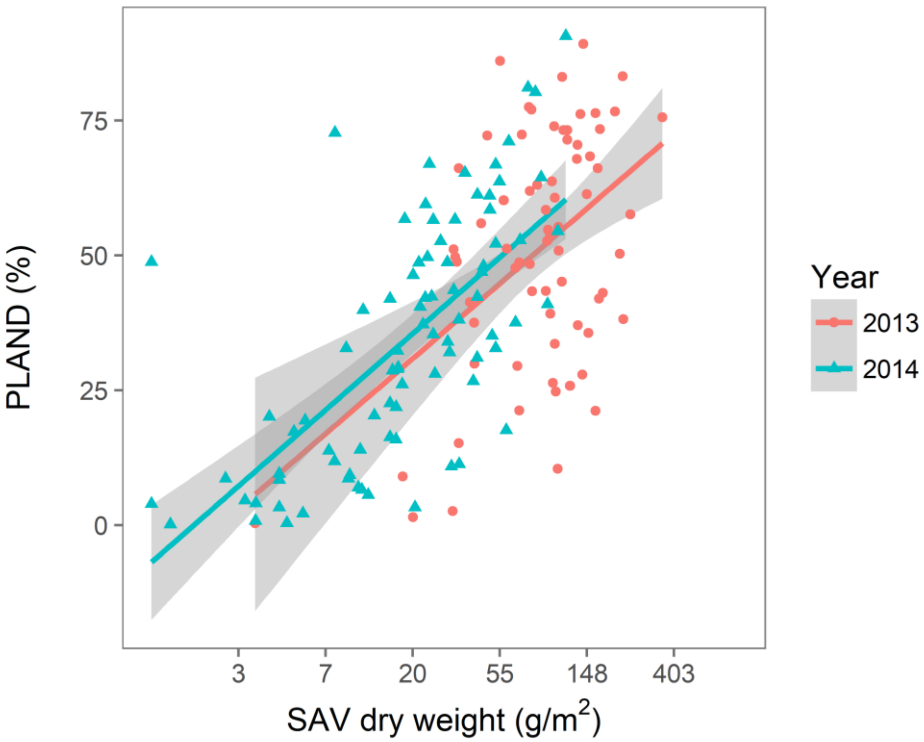

Figure S2. Percentage of landscape occupied by SAV in the picture (PLAND) in relation with submerged aquatic vegetation (SAV) dry weight per m2 harvested for each quadrat by a diver (log-transformed data; n = 140; adj-R2 = 0.42, p-value < 0.05). Scales represent real data (i.e., not transformed).

CHAPITRE 4
DISCUSSION GÉNÉRALE

4.1 Synthèse et contributions scientifiques de la thèse

Dans cette thèse, nous avons appliqué des concepts théoriques d'écologie des communautés pour évaluer l'importance relative des variables biotiques et abiotiques dans la structuration des communautés zooplanctoniques et de leurs traits fonctionnels dans le Lac Saint-Pierre (LSP), un système où les conditions environnementales varient beaucoup d'une année à l'autre. Nous avons montré, sur une période de 3 ans (2012-2014), que les taxa présents réagissaient de manière différente face aux conditions environnementales et qu'une même espèce pouvait avoir une réponse totalement opposée d'une année à l'autre, dépendamment de la variation des facteurs environnementaux (Chapitre 1). Bien que les filtres environnementaux aient sélectionné une diversité et une abondance d'espèces différente à chaque année, les traits présents dans les communautés (pondérés selon l'abondance des espèces) montraient une tendance similaire, suggérant une redondance fonctionnelle dans les traits malgré un environnement changeant. Contrairement à la majorité des études qui regardent à quel point les traits des espèces présentes dans la communauté se chevauchent dans des conditions fixes (Wellnitz et Poff, 2001), nous avons utilisé une mesure des traits pondérée par l'abondance des espèces pour montrer que globalement, même si l'identité des espèces changeait, les traits de la communauté répondaient essentiellement de la même manière aux facteurs environnementaux. Nous avons également confirmé que la végétation aquatique submergée (VAS) était un facteur biotique important dans la structuration des communautés zooplanctoniques en milieu naturel et nous avons mis en évidence que la VAS jouait un rôle important dans la structuration fonctionnelle du zooplancton, notamment en favorisant les taxons de plus grande taille. Ce résultat est en accord avec les études antérieures qui montrent que la pression de prédation sur les gros individus serait réduite dans la VAS (Brooks et Dodson, 1965; Manutunge et al. 2000). À l'échelle du paysage, les communautés zooplanctoniques seraient donc structurées par des facteurs biotiques et abiotiques. Étant donné l'importance de la variabilité interannuelle observée dans les conditions biotiques et abiotiques dans le LSP, notre étude suggère 1- l'importance de réaliser des suivis sur plusieurs années consécutives pour s'assurer de capturer un portrait juste des réponses des communautés zooplanctoniques face à différents facteurs environnementaux et 2- l'importance de réduire les facteurs qui contribuent à la réduction et à l'homogénéisation des communautés de VAS pour s'assurer de maintenir la diversité fonctionnelle des communautés de zooplancton et favoriser la redondance fonctionnelle. Dans un contexte de changements globaux, ce dernier point est très important pour s'assurer de maintenir l'adaptabilité de ce système face à des conditions changeantes.

Afin de mieux comprendre l'impact d'une diminution de la VAS, nous avons utilisé les données prélevées lors de l'été 2012 pour analyser plus spécifiquement la variation de la biomasse et de la diversité taxonomique et fonctionnelle du zooplancton le long d'un gradient de VAS (Chapitre 2). Un partitionnement de la variation nous a permis de voir que l'effet de la VAS était largement confondu avec les variables environnementales. Par exemple, l'abondance de la VAS était inversement reliée au courant, suggérant ainsi que la VAS empêchait que le zooplancton ne soit exporté par le courant (Basu et al. 2000). Lorsque nous avons isolé l'effet de la VAS , c'est-à-dire une fois que l'effet confondu des variables environnementales a été enlevé, la VAS expliquait 9% de la variation dans la biomasse de zooplancton, alors que c'était 13% de la variation dans la diversité fonctionnelle qui était expliquée. Le chapitre 2 de cette thèse montre donc l'importance de la VAS dans le maintien de la diversité taxonomique et fonctionnelle du zooplancton dans les lacs peu profonds. La plus grande représentation de la famille des Chydoridae dans la VAS élargissait l'espace de traits occupé par la communauté comparativement aux communautés se trouvant en dehors de la VAS, mais réduisait la régularité de la distribution de ces mêmes traits. La famille des Chydoridae était prédominante et composée en majorité de grosses espèces associées à la VAS. Ce résultat pourrait traduire un plus grand degré de filtres environnementaux dans la VAS comparativement aux endroits sans VAS, ou encore un mécanisme d'exclusion compétitive des Chydoridae sur les autres familles de zooplancton. Cette étude est la première en milieu naturel à mettre en évidence l'impact de la diminution de la VAS sur la diversité fonctionnelle du zooplancton. L'étude de Giacomazzo et al. (2020) montre que, dans le LSP, la diminution de la VAS est reliée à une diminution des stocks de poissons. Selon ces auteurs, les débarquements commerciaux de poissons sont fonction de la VAS et de la croissance des juvéniles qui en dépendent. Bien que le lien entre l'abondance de poissons et la diversité fonctionnelle de zooplancton n'a pas été explicitement exploré dans cette thèse, la diminution de la diversité fonctionnelle du zooplancton dans des habitats homogénéisés pourrait être le chaînon manquant expliquant les problèmes de recrutement des poissons au LSP, notamment celui de la perchaude.

La réduction de la VAS aurait donc un impact négatif sur la biomasse et la diversité fonctionnelle du zooplancton, pouvant avoir un effet négatif potentiel sur les fonctions écosystémiques en raison du rôle clé du zooplancton dans les écosystèmes aquatiques.

Plusieurs études tendent à montrer qu'en plus de l'abondance et de la densité de la VAS, la complexité structurelle de celle-ci aurait un impact dans la structuration des communautés zooplanctoniques (Declerck et al. 2007; Meerhoff et al. 2007). Traditionnellement, la couverture et la complexité de la VAS sont évaluées en récoltant la végétation sur une surface connue (ce que nous avons utilisé dans les Chapitres 1 et 2). Dans certains cas, la complexité de la VAS est évaluée en comparant les attributs morphologiques des espèces de plantes retrouvées sur les sites d'étude, permettant de fournir une description qualitative de la complexité de chaque espèce (St.Pierre et Kovalenko, 2014; Zeng et al. 2017). Certaines études ont également estimé la complexité à partir de mesures fractales prises sur chaque espèce de VAS qui sont pondérées par l'abondance des plantes pour obtenir un indice fractal moyen représentant la complexité de la VAS (McAbendroth et al. 2005; Wolters et al. 2018). Cependant, les effets du couvert de la végétation et de la complexité sont souvent confondus. Dans le 3^{e} chapitre de cette thèse, nous avons utilisé des mesures de fractales pour évaluer la complexité de la VAS à partir d'une méthode photographique afin de capter l'arrangement naturel de la structure de la VAS *in situ*, qui est un indice plus direct de la véritable complexité de l'habitat disponible pour le zooplancton. Cette mesure de complexité a ensuite été mise en relation avec différents groupes fonctionnels et indices de diversité fonctionnelle de zooplancton pour comprendre l'effet de la complexité sur la diversité taxonomique et fonctionnelle du zooplancton. Nous avons montré que l'approche photographique *in situ* est une méthode non destructrice qui permet d'évaluer rapidement à la fois le couvert et la complexité structurelle de la VAS et qui pourrait facilement être implantée dans les suivis de science citoyenne tel que le Réseau de surveillance volontaire des lacs du Québec. Cependant, les mesures de couvert de VAS étaient fortement corrélées aux mesures de complexité, rendant difficile de déterminer uniquement l'impact de la complexité sur les communautés zooplanctoniques. Tout comme l'étude de Wolters et al. (2018), nous ne sommes pas parvenus à pleinement séparer l'impact du couvert de VAS de l'impact de la complexité de la VAS. Seul l'indice de dispersion fonctionnelle était inversement relié à la complexité, montrant qu'une augmentation de la complexité était reliée à une plus grande abondance de petits individus. Ces résultats concordent avec ceux obtenus par

McAbendroth et al. (2005), qui a fait valoir qu'il était plus facile pour de petits taxa de se déplacer dans des environnements complexes comparativement aux grosses espèces. Dans ce cas-ci, une grande abondance de nauplies de copépodes a été observée dans les herbiers de VAS. Le Chapitre 3 de cette thèse est donc partiellement en accord avec l'hypothèse de complexité-diversité, puisque d'un côté la dispersion fonctionnelle du zooplancton diminue dans les habitats complexes, mais lorsque l'abondance des nauplies était faible, une augmentation de la complexité reflétait une augmentation de la richesse fonctionnelle. La dominance des nauplies dans le système d'étude n'a pas permis de bien cerner la relation complexité-diversité dans les communautés zooplanctoniques du LSP. Bien que l'approche photographique donne des résultats intéressants pour suivre facilement et efficacement les herbiers de VAS, la complexité demeure reflétée en deux dimensions, ce qui ne représente pas tout à fait la complexité tridimensionnelle en milieu naturel.

4.2 Perspectives de recherches

Une revue des articles publiés concernant l'analyse des traits fonctionnels appliquée au zooplancton en eau douce montre que cette approche est de plus en plus utilisée depuis 2016, mais que la plupart des études sont limitées au Canada, aux États-Unis, au Brésil et à l'Italie (Gomes et al. 2019). L'approche basée sur les traits et les fonctions aurait avantage à être utilisée dans plusieurs études empiriques, ce qui permettrait une augmentation des connaissances sur les processus dictant l'assemblage des communautés zooplanctoniques dans les lacs peu profonds. Comme souligné par Hébert et al. (2016), les connaissances concernant les traits du zooplancton progressent, mais il reste beaucoup de travail à faire afin d'avoir une base de traits complète. De plus, comme nous l'avons montré, la majorité des traits sont structurés phylogénétiquement. Il serait pertinent de continuer à mettre des efforts afin de bien déterminer les traits qui reflètent le fonctionnement des écosystèmes sans être reliés à la phylogénie. Selon Vincent et al. (2020), la phylogénie peut être utilisée pour remplacer l'approche par traits lorsque ceux-ci ne sont pas disponibles. Il arrive aussi fréquemment que la taxonomie est utilisée pour inférer les traits à partir des espèces. Pour être totalement efficace, cette approche devrait être totalement indépendante de la taxonomie, ce qui n'est pas le cas présentement. Deux avancées pertinentes seraient de 1) mieux cerner les fonctions écosystémiques en relation avec les traits fonctionnels et 2) continuer les études sur le fonctionnement des écosystèmes sans avoir recours à l'expertise de taxonomiste du zooplancton, cette compétence étant de plus en plus rare.

Durant cette thèse, la relation entre les communautés zooplanctoniques et leur diversité fonctionnelle a été étudiée au même moment durant trois années extrêmement variables, soit en août lorsque la VAS est à son maximum de croissance. Une étude récente montre que la contingence historique via des effets de priorité peut profondément façonner l'assemblage des communautés sous l'influence des changements environnementaux à travers les décennies (Garcia-Giron et al. 2021). Le LSP étant soumis à des périodes de crues extrêmement variables, il serait pertinent de faire le suivi de l'évolution des communautés zooplanctoniques durant toute l'année, permettant ainsi de documenter comment les stratégies reproductives et comportementales utilisées par les espèces présentes l'année précédente influence l'assemblage des communautés et la diversité fonctionnelle des communautés zooplanctoniques les années subséquentes. La variabilité intra- et interannuelle des conditions environnementales devrait être intégrée dans les études d'assemblage des communautés, permettant de mieux comprendre l'évolution des communautés, mais aussi leur réaction face aux changements environnementaux.

Les recherches effectuées dans le cadre de cette thèse n'ont pas permis de totalement séparer les effets du couvert de la VAS de celui de la complexité sur la diversité fonctionnelle du zooplancton. Comme mentionné précédemment, l'utilisation de l'approche photographique, couplée avec une analyse par machine learning, pourrait permettre un suivi rapide et efficace de la VAS dans les lacs du Québec. Cependant, afin de mieux faire ressortir l'effet de la complexité, une approche en 3D telles qu'utilisées sur les récifs coralliens serait plus appropriée (par ex. : Figueira et al. 2015). L'utilisation d'une bathymétrie multifaisceaux permettrait également d'avoir une meilleure conception de la complexité de l'habitat retrouvée sous l'eau.

CONCLUSION GÉNÉRALE

Cette thèse a permis non seulement d'augmenter nos connaissances par rapport aux facteurs structurant les communautés zooplanctoniques associés à la végétation aquatique submergée, mais a également permis de tester certaines théories écologiques. Le but ultime de ce travail de recherche était d'évaluer les impacts d’une perte de la VAS due aux activités anthropiques sur la structuration taxonomique et fonctionnelle du zooplancton dans un lac peu profond. Dans un premier temps, nous avons montré que les communautés zooplanctoniques avaient des réponses extrêmement variables face aux changements environnementaux, mais que les traits des espèces répondaient de manière relativement constante, suggérant la présence d’une redondance fonctionnelle dans les traits des espèces présentes. La VAS jouait un rôle important en tant que filtre biotique dans la structuration des communautés. Par la suite, nous avons partitionné les facteurs expliquant la structure des communautés de zooplancton dans un contexte de simplification de l'habitat, passant d'un habitat riche en VAS à un habitat dominé par les cyanobactéries benthiques. Finalement, nous avons mis en relation la diversité taxonomique et fonctionnelle du zooplancton avec la complexité structurelle de la VAS estimée à partir d’une méthode photographique. Cette méthode non-destructrice, du fait de sa facilité d’utilisation, et sa bonne correspondance avec les méthodes traditionnelles d’échantillonnage de la VAS, aurait avantage a être utilisée dans les programmes de suivi impliquant la science citoyenne. Dans un contexte global de perte de VAS, il est extrêmement pertinent de développer un programme de suivi qui pourra être instauré à grande échelle. La perte de la VAS observée au LSP a des impacts majeurs sur la diversité taxonomique et fonctionnelle du zooplancton, qui joue un rôle fondamental dans le transfert trophique vers les organismes tels que les larves de poissons.

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