UQAR

Université du Québec
à Rimouski

**Biodiversité du zooplancton côtier dans la zone
d'importance écologique de l'estuaire maritime
du Saint-Laurent :**

Utilisation d'une approche spécifique et fonctionnelle

Mémoire présenté

dans le cadre du programme de maîtrise en océanographie

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Avertissement

"Lorsque vous éliminez l'impossible, quoiqu'il reste, même plus qu'improbable doit être la vérité"
Star Trek

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RÉSUMÉ

Fortement dépendant des caractéristiques biotiques et abiotiques de son environnement, le zooplancton est considéré comme un groupe sentinelle. Le suivi des communautés zooplanctoniques permet ainsi de définir l'état des écosystèmes, notamment dans le cadre de la conservation et de la gestion des espaces protégés ou d'intérêt. La région côtière de l'estuaire maritime du Saint-Laurent (EMSL) présente une zone d'importance écologique et économique, mais n'a cependant été que très peu étudiée. L'objectif de cette étude était de déterminer la structure et le fonctionnement des communautés zooplanctoniques de cette zone, par l'étude des diversités spécifique et fonctionnelle en lien avec la variabilité des facteurs environnementaux. Pendant trois ans (2019 à 2021) en juillet et octobre, la communauté zooplanctonique a été échantillonnée à 35 stations sur la côte nord de l'EMSL et les paramètres environnementaux (*e.g.* température, salinité, chl *a* et nutriments) y ont été mesurés. Les individus du mésozooplancton ont été identifiés au plus bas rang taxonomique possible, et les traits fonctionnels (*e.g.* cycle de vie, régime trophique, stratégie d'alimentation, taille) leur ont été associés. La structure des communautés a montré une variabilité spatio-temporelle saisonnière entre les trois secteurs géographiques de la zone. Les « hotspot » de diversité étaient détectés à Baie-Comeau ou à Forestville selon la saison considérée, indiquant une influence de la variabilité saisonnière des paramètres environnementaux, notamment par la température et la chl *a*. Les zones de « hotspot » variaient également entre les diversités spécifique et fonctionnelle soulignant la complémentarité des deux approches. La communauté zooplanctonique était majoritairement composée par les Copepoda quel que soit le mois ou secteur. La communauté en juillet était composée en plus forte proportion par le méroplancton, notamment par les Bivalvia, et par les herbivores, et en octobre par les Appendicularia. La composition et l'abondance différaient avec le milieu plus profond de l'estuaire, et seraient liées aux conditions environnementales spécifiques de la zone côtière. Notre travail permet ainsi de dresser un état de référence de la zone côtière de l'EMSL pour de futures surveillances de changements potentiels liés aux activités anthropiques grandissantes et aux changements climatiques.

Mots clés : Zooplancton, Biodiversité, Zone côtière, Estuaire maritime du Saint-Laurent, Hotspots, Diversité spécifique, Diversité fonctionnelle.

ABSTRACT

Highly dependent on the biotic and abiotic characteristics of its environment, zooplankton is considered as a sentinel group. As such, monitoring the zooplankton communities allows to define the state of the ecosystems, particularly within the framework of the conservation and management of protected areas or areas of interest. The coastal zone of the Lower St. Lawrence Estuary (LSLE) has been determined as an ecologically and economically important area, but it has been scarcely studied so far. The aim of our study was to characterize coastal zooplankton diversity and its spatiotemporal variation using an integrated taxonomic and functional approach, in relation to the variability of environmental parameters, in order to establish a baseline of this coastal zone. For three years (2019 to 2021) in July and in October, the zooplanktonic community was sampled at 35 stations on the north coast of the LSLE and environmental parameters (*e.g.* temperature, salinity, chl *a* and nutrients) were measured. Mesozooplanktonic organisms were identified at the lowest possible taxonomic level, and functional traits (*e.g.* life history, trophic type, feeding strategy, size) were associated. The community structure showed a seasonal spatio-temporal variability between the three geographical sectors of the area. Hotspots of diversities were detected in Baie-Comeau or Forestville depending on the season, indicating an influence of seasonal variation of environmental parameters, especially temperature and chl *a*. Hotspot zones varied between taxonomic and functional diversity, underlining the complementarity of the two approaches. The zooplankton community was predominantly composed by Copepoda regardless of the month or sector. The community in July was composed in high proportion of abundance of meroplankton, especially Bivalvia, and of herbivores, and in October of Appendicularia. The composition and abundance differed when compared to the deeper environment of the estuary and could be related to coastal environmental conditions. Our work thus provides a baseline of the zooplankton communities of the LSLE coastal zone for future monitoring of potential changes related to increasing anthropogenic activities and climate change.

Keywords: Zooplankton, Biodiversity, coastal area, Lower St. Lawrence Estuary, Hotspots, Functional traits, Functional diversity, Taxonomic diversity.

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LSLE   Lower St. Lawrence Estuary

EMSL   Estuaire maritime du Saint-Laurent

GSL   Gulf of St. Lawrence

FRic   Functional richness - Richesse fonctionnelle

FDiv   Functional divergence - Divergence fonctionnelle

FEve   Functional evenness - Équitabilité fonctionnelle

INTRODUCTION GÉNÉRALE

BIODIVERSITÉ

Au cœur des préoccupations environnementales, la biodiversité est un terme fréquemment employé dans l'actualité pour représenter la santé des écosystèmes. Mais concrètement qu'est-ce que la biodiversité ?

La convention sur la biodiversité de 1992 (UN, 1992) a défini la biodiversité comme "la variabilité des organismes vivants de toute origine y compris, entre autres, les écosystèmes terrestres, marins et autres écosystèmes aquatiques et les complexes écologiques dont ils font partie ; cela comprend la diversité au sein des espèces, entre espèces ainsi que celle des écosystèmes".

La biodiversité est évaluée par trois composantes principales (Gaston and Spicer, 2004) :

    a) la diversité spécifique : basé sur la taxonomie des individus

    b) la diversité écologique ou fonctionnelle : basé sur la fonction des individus dans l'écosystème et définie à partir de traits fonctionnels

    c) la diversité génétique : à partir du « code » génétique des individus, qui ne sera pas abordé dans la présente étude.

La diversité spécifique

La diversité spécifique est basée sur la taxonomie des individus. La taxonomie permet de classer les individus selon différents caractères basés sur leur anatomie ou morphologie et autres caractéristiques (comprenant également des comparaisons génétiques) (Morrissey and Sumich, 2012; Castellani and Edwards, 2017). Cette classification basée sur un système

international (classification de Linnaeus), comprend différents niveaux, allant des caractéristiques les plus généraux aux plus précis (Fig. 1).
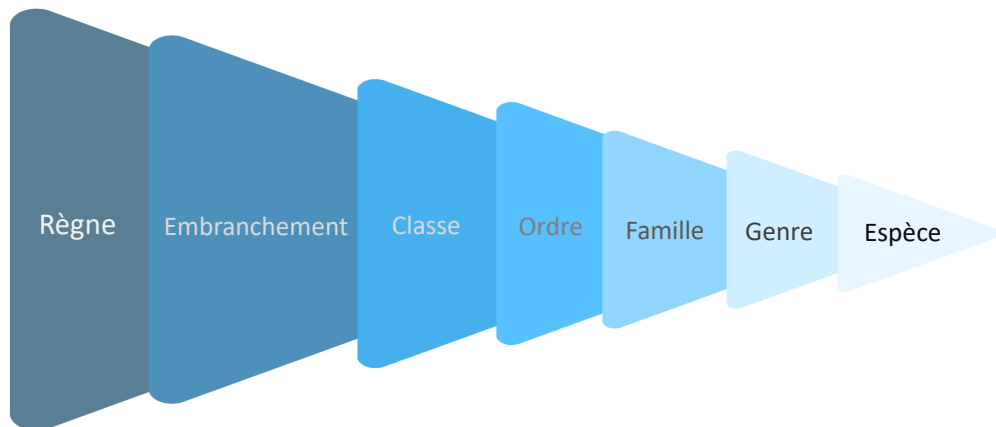
Fig. 1. Niveaux de classification de la taxonomie.

Les espèces, le niveau inférieur de la classification, sont alors des groupes d'individus d'apparence similaire, interféconds et avec des descendances fertiles (Morissey and Sumich, 2012). La diversité spécifique peut être évaluée par différents indices de diversité, tels que la richesse spécifique (S) basée sur le nombre d'espèces dans le milieu, l'indice de Shannon-Wiener (H') basé sur le nombre d'espèces et leur proportion relative, et l'indice d'équitabilité de Pielou (J') évaluant comment l'abondance est repartie entre les taxa. Ces indices sont des outils permettant d'évaluer facilement et rapidement la diversité d'un milieu et sont donc actuellement majoritairement utilisés pour l'évaluation de la biodiversité. Ils nécessitent une identification taxonomique précise, au plus bas rang taxonomique, avec des déterminations de densité et/ou abondance.

La diversité fonctionnelle

La diversité fonctionnelle est basée sur la fonction des individus dans l'écosystème et se définit à partir de traits fonctionnels. Les traits fonctionnels décrivent les individus du point de vue de leur caractéristiques morphologiques, physiologiques, comportementales et de leur

histoire de vie, et sont associés aux principales fonctions écologiques telles que l'alimentation, la croissance, la reproduction et la survie (Martini et *al.,* 2020, Fig. 2). Ces caractéristiques contrôlent la valeur adaptative des individus (« fitness »), ainsi que leur réponse à l'environnement et le fonctionnement de l'écosystème (Violle et *al*., 2007). Ils définissent ainsi le rôle écologique des espèces (Barnett et *al*., 2007 ; Benedetti, 2016).

Fig. 2. Classification des différents traits fonctionnels (Traduit et modifié de ©Martini et *al*., 2020). Les colonnes du tableau classent les traits par leur fonction écologique et les couleurs correspondent aux différents types de traits (lignes) dans lesquels ils sont classés.

Tout comme la diversité spécifique, des indices de diversité fonctionnelle ont été développés afin d'évaluer la diversité fonctionnelle d'un milieu. Parmi ces différents indices, la richesse fonctionnelle (FRic), l'équivalent de la richesse spécifique, basée sur le nombre de traits, mesure la quantité d'espaces de niche occupés par les espèces au sein d'une communauté. La divergence fonctionnelle (FDiv), l'équivalent fonctionnel de l'indice de Shannon-Wiener, mesure les différences fonctionnelles pondérées par l'abondance entre les espèces au sein d'une communauté. Et enfin, l'équitabilité fonctionnelle (FEve) décrit la répartition équitable des espèces (ou de l'abondance) d'une communauté dans l'espace de niche (Mason et *al.*, 2008) et est l'équivalent de l'indice d'équitabilité de Pielou.

Ces composants de biodiversité, bien qu'ils soient la plupart du temps présentés séparément, sont liés et non-indépendants (Gaston and Spicer, 2004). En effet, ils apportent de l'information complémentaire et chacun nécessite alors d'être évalué (Petchey and Gaston, 2006) afin de définir l'état d'un écosystème.

Pourquoi maintenir et étudier l'état de la biodiversité ?

Le maintien de la biodiversité permet de réduire le risque d'extinction des espèces, de maintenir les fonctionnalités des écosystèmes et de préserver l'histoire évolutive des organismes (Sala et *al.*, 2021). Généralement, les efforts sur la conservation de la biodiversité sont réalisés pour le maintien des fonctionnalités et des services que les écosystèmes peuvent fournir. La biodiversité marine apporte en effet différentes valeurs directes et indirectes, intervenant notamment dans les cycles biogéochimiques, la régulation atmosphérique et climatique, le cycle des nutriments, la photosynthèse (production d'oxygène), mais aussi au niveau économique (*e.g.* écotourisme, biomimétisme des produits industriels, contrôle biologique, médecine et nourriture) (Gaston and Spicer, 2004 ; Loreau and Kinne, 2010). Cependant, de nombreuses menaces pèsent sur la biodiversité marine, telles que la dégradation, la fragmentation ou la perte de l'habitat, le changement climatique, la

surexploitation directe ou indirecte, l'eutrophisation, la pollution, et l'introduction d'espèces invasives (Solan et *al*., 2012).

Un milieu est considéré comme stable et pouvant faire face à des perturbations (résilience) lorsque sa biodiversité est élevée (Beaugrand, 2014). De ce fait, le maintien d'une haute biodiversité est devenu une priorité pour la conservation des écosystèmes, notamment dans le cadre du changement climatique (Loreau, 2010). Mais, de nombreuses zones n'ont pas été encore étudiées, rendant également difficile l'évaluation de l'évolution de leur biodiversité (Lotze, 2021).

L'évaluation de la biodiversité est donc une composante importante afin de définir l'état d'un écosystème, et notamment dans les plans de protection et de gestion. La création d'un état de référence ("baseline") des écosystèmes est une étape primordiale afin de prévenir d'une modification de leur état et donc d'intervenir via différentes mesures de protection. Pour cela, et dans le cadre des études des BEF ("Biodiversity and Ecosystem Functioning"- « Biodiversité et fonctionnement d'écosystème »), différents outils ont été développés afin de quantifier l'état de la biodiversité d'un milieu, avec différents indices de diversité et avec la caractérisation de zones de haute diversité, dites "hotspot", ou de faible diversité, dites "coldspot", facilitant ainsi la prise de décision pour les gestionnaires de l'environnement (Gaston and Spicer, 2004 ; Martini et *al*., 2020).

La caractérisation de l'état de santé de ces zones va ainsi définir l'état des niches écologiques des espèces. Une niche écologique est l'ensemble des conditions environnementales abiotiques (facteurs environnementaux) et biotiques (*e.g.* compétition) dans lesquelles une espèce peut se développer (Hutchison, 1957). Elle comprend la niche fondamentale des espèces, réunissant toutes les composants et les conditions environnementales favorables et nécessaire à leur existence et développement. Chaque espèce va ainsi évoluer dans sa propre niche écologique déterminée par la combinaison de ces conditions environnementales, appelée la niche réalisée qui comprend ainsi leur niche fondamentale avec les contraintes des autres espèces présentes dans le même espace. Un changement de la répartition de ces espèces et donc de la structure des communautés, implique alors un changement des

conditions de leur niche. Le suivi de ces espèces en particulier est alors une indication de la modification de leur environnement. Ces espèces ou groupes d'espèces sont ainsi considérés comme des espèces sentinelles (Monaco et Prouzet, 2015).

ZOOPLANCTON

Petites espèces, grande importance : pourquoi utiliser ce groupe pour l'étude de l'état de santé des écosystèmes ?

Le zooplancton est un groupe d'organisme représenté par plus de 7000 espèces marines connues (Morissey and Sumich, 2012), de 15 phyla différents (Castellani and Edwards, 2017) et qui par définition ne peut s'affranchir des courants. Le zooplancton est catégorisé par classe de taille, on s'intéressera ici plus particulièrement au mésozooplancton (0.2 à 20 mm) (Fig. 3).
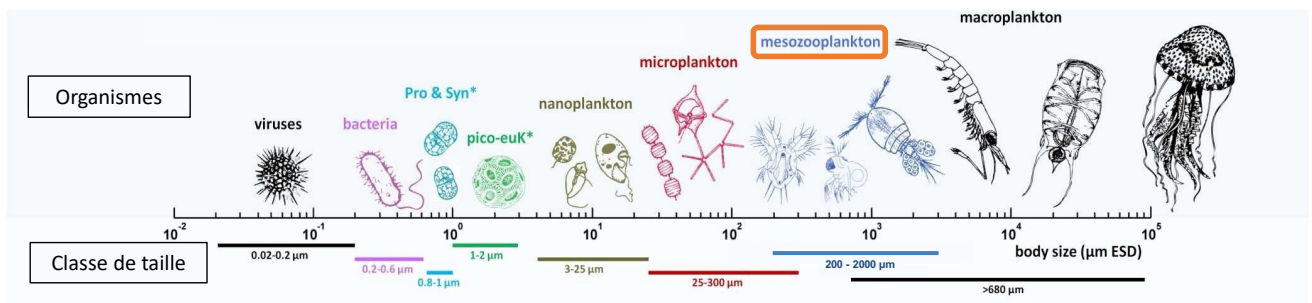
Fig. 3 Classification du zooplancton selon les classes de tailles (Modifié de © Romagnan 2013)

Le mésozooplankton comprend l'holoplancton, soit les organismes passant leur cycle de vie complet au sein du plancton, tels que les Crustacea (dont Copepoda, Diplostraca, Euphausiacea, Ostracoda), les Appendicularia, les Chaetognatha, les Ctenophora, et le méroplancton, les organismes passant une partie de leur cycle de vie au sein du plancton (généralement les stades larvaires des organismes benthiques) tel que les Decapoda, Amphipoda, Annelida, Mollusca, ainsi que les Teleostei et les Cnidaria.

Ce groupe tient une place importante dans les écosystèmes marins, d'une part car il est fortement dépendant des conditions environnementales de son milieu, tels que la température, la salinité, la quantité et la qualité de nourriture, et l'oxygène (Beaugrand et *al*., 2013 ; Helenius et *al*., 2017 ; Strand et *al*., 2020), et d'autre part pour sa place dans le réseau trophique. Ainsi, la composition spécifique des communautés zooplanctoniques sera alors fortement dépendante de la variation saisonnière des conditions abiotiques et biotiques du milieu (Laprise and Dodson, 1994). En tant que maillon clé intermédiaire du réseau trophique, le zooplancton constitue le lien entre les producteurs primaires et les niveaux trophiques supérieurs. Une modification dans les communautés zooplanctoniques aura alors des répercussions directes et indirectes sur tout le réseau trophique qui en dépend (Strand et *al*., 2020). Pour cela, le zooplancton est considéré comme un groupe sentinelle, et donc un groupe important pour le suivi de l'état des écosystèmes (Usov et *al*., 2019 ; Llope et *al*., 2020 ; Castellani and Edwards, 2017 ; Marques et *al*., 2006).

LES CÔTES DE L'ESTUAIRE MARITIME DU SAINT-LAURENT

Constituant l'un des plus grands estuaires au monde, l'estuaire du Saint-Laurent, situé à l'Est du Canada, relie le fleuve Saint-Laurent au golfe du Saint-Laurent (GSL). L'estuaire du Saint-Laurent est ainsi influencé par les flux d'eau douce du fleuve Saint-Laurent et des courants de marée de l'Atlantique et de l'Arctique (Dufour and Ouellet, 2007), définissant ses trois différentes sections : l'estuaire fluvial, l'estuaire moyen et l'estuaire maritime. Nous nous intéresserons plus particulièrement à l'estuaire maritime (EMSL), qui constitue l'interface directe entre l'estuaire moyen et le golfe (Plourde et *al*., 2002) (Fig. 4).
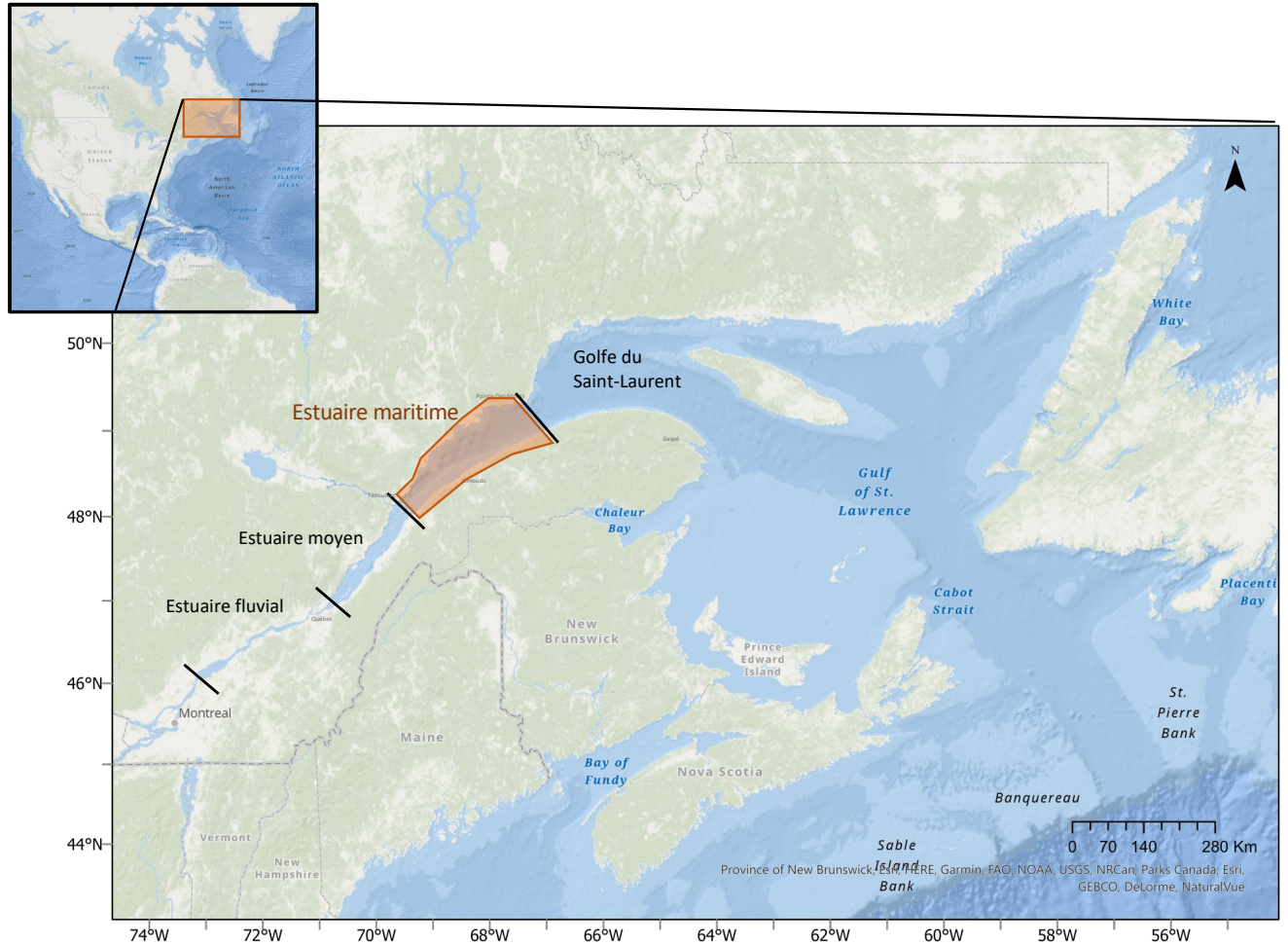
Fig. 4. Carte de l'estuaire du Saint-Laurent et des différentes sections de l'estuaire.

Long de 200 km sur 40 km de large avec une profondeur moyenne de 300 m (Savenkoff et *al*, 2017), l'estuaire maritime du Saint-Laurent, présente une forte variation spatio-temporelle de ses facteurs biotiques et abiotiques (Plourde et *al*., 2002). Sa dynamique est principalement liée aux apports d'eau saumâtre du fleuve et aux courants de marée, qui influent sur ses paramètres physico-chimiques, tels que la température et la salinité (Runge and Simard, 1990), et est soumise à la saisonnalité du couvert de glace pendant l'hiver (Blais et *al*., 2018). Cette caractéristique hydrodynamique induit un système spécifique comportant trois couches d'eau en été jusqu'à la fin de l'automne, soit la couche de surface, la couche intermédiaire froide (dite « CIF ») et la couche profonde, chacune différant dans ses

propriétés de salinité et de température et ayant une épaisseur qui varie selon les conditions annuelles (Galbraith et *al*., 2019).

La zone côtière de l'EMSL se définit par une zone de profondeur inférieure à 37 m (soit 20 brasses) (Gagné et *al*., 2013). La côte nord de l'EMSL est découpée par de nombreuses rivières affluentes (telles que la rivière Portneuf, la rivière Betsiamites, Rivière-aux-Outardes et la rivière Manicouagan) qui, en plus de l'effet du vent et de la marée, influent sur les caractéristiques physico-chimiques de l'environnement côtier (El Sabh, 1979; Pinet et *al*., 2011b). De plus, les caractéristiques géomorphologiques de cette région côtière évoluent d'est en ouest, passant d'une zone sableuse à rocheuse, avec des plateaux plus larges dans la zone la plus à l'ouest (vers Forestville) contrairement à la zone à l'est (vers Baie-Comeau) qui se différencie par une pente plus abrute et du sable plus grossier (Pinet et *al.,* 2011a).

PROBLÉMATIQUE

Pourquoi étudier la biodiversité du zooplancton de la zone côtière de l'estuaire maritime du Saint-Laurent ?

L'estuaire maritime est le refuge d'espèces emblématiques et clés, tel que le krill, les copépodes, les mammifères marins (Dufour et *al*., 2010), et est le lieu de nombreuses pêcheries commerciales (*e.g.* crabe des neiges, homard) et récréatives (*e.g.* éperlan, bar rayé), et d'activités touristiques (*e.g.* observation des baleines). Cependant, la partie côtière de l'estuaire n'a été que très peu étudiée, et représente pourtant une zone importante en tant que nurserie et refuge pour différentes espèces de poissons et de crustacés (Archambault et *al*., 1998). En tant qu'interface entre la terre et le milieu marin, les zones côtières sont soumises à de nombreuses pressions anthropiques (*e.g.* introduction d'espèces invasives, exploitation des ressources halieutiques, pollution par l'apport d'éléments nutritifs et de contaminants, bruits liés à la navigation) (Dufour et *al*., 2010) et sont sensibles aux impacts du changement climatique (*e.g.* variation de température et acidification des océans) (Lu et *al*., 2018).

C'est dans ce cadre que le « *Programme de données environnementale côtières de référence* » a été mis en place au niveau du Canada. L'estuaire maritime du Saint-Laurent a été déterminé comme l'un des sites importants à prioriser afin de caractériser les écosystèmes côtiers peu étudiés dans le cadre du changement climatique, en y dressant un état de référence. Notre étude s'inscrit alors dans ce projet, son but étant de définir un état de référence de ces zones côtières, en particulier au niveau des communautés zooplanctoniques, qui n'avaient jamais été étudiées jusqu'alors dans l'estuaire maritime. Ces données permettront ainsi de fournir un outil de référence pour de futures surveillances et mise en place de plan de gestion dans ces zones soumises à de nombreuses activités anthropiques et donc plus sensibles au changement climatique global.

OBJECTIF

Le but de la présente étude est la caractérisation de la structure et de la diversité du zooplancton de la côte nord de l'estuaire maritime du Saint-Laurent, via une approche couplant l'investigation de la diversité spécifique et de la diversité fonctionnelle, ainsi que la caractérisation de l'influence de paramètres environnementaux sur la composition des communautés zooplanctoniques. Durant trois années consécutives (de 2019 à 2021), les compositions spécifique et fonctionnelle, et les diversités de deux différentes saisons, de l'été et l'automne, seront décrites afin de déterminer la dynamique spatio-temporelle des communautés zooplanctoniques de la zone côtière de l'EMSL. Les diversités des communautés zooplanctoniques seront évaluées via une cartographie afin de mettre en évidence les sites de forte biodiversité, dits "hotspot", et de faible biodiversité, dits "coldspot". Cette approche complémentaire permettra de mieux comprendre le contrôle des conditions environnementales sur la dynamique du zooplancton côtier et de définir le premier état de référence des communautés dans cette zone côtière de l'EMSL.

Ce mémoire sera composé d'une introduction générale, de l'article scientifique, et d'une conclusion générale.

Ce projet s'inscrit dans le cadre du programme « des données côtière de référence », initié en 2018-19 par le MPO. L'échantillonnage ayant commencé en 2019 avec l'ISMER et le MPO, j'ai pris part de celui de 2021, puis effectué les analyses taxonomiques des échantillons de juillet 2021, les analyses des données (biologiques et environnementales) et la rédaction du présent mémoire et de l'article. Les co-auteurs.trices ont contribués à l'identification des organismes de 2019 à 2021, de l'aide et l'appui dans l'analyse des données et de la rédaction. L'article « Coastal zooplankton communities of the Lower St. Lawrence Estuary: a taxonomic and functional approach » sera soumis dans la revue « Journal of Plankton Reseach » co-rédigé.e par Gesche Winkler, Piero Calosi et moi-même en tant que première auteure.

Liste des communications :

Winkler, G., & Santo, M. (2022). Zooplancton de la zone côtière du nord de l'estuaire maritime du Saint-Laurent [Data set]. https://catalogue.preprod.ogsl.ca/dataset/ca-cioos_3e9c3887-d969- 4350-b405-ba65172eb67b?local=fr, https://doi.org/10.26071/ogsl-3e9c3887-d969

SANTO M.*, CHÉNARD L., BRAULT C., CALOSI P., WINKLER G. (2023) Biodiversity of coastal zooplankton of the Lower St. Lawrence Estuary: Specific and functional approach. CEBP National Partner Workshop, 22th - 25th January 2023, Ottawa, Canada. [Oral Presentation].

SANTO M.*, CHÉNARD L., BRAULT C., CALOSI P., WINKLER G. (2023) Le zooplancton côtier de l'estuaire maritime du Saint-Laurent: Diversités spécifique et fonctionnelle. Québec Océan- Réunion scientifique annuelle, 6h - 7th February 2023, Rivière-du-Loup, Canada [Poster].

SANTO M.*, CHÉNARD L., BRAULT C., CALOSI P., WINKLER G. (2023) What's in coastal waters? Taxonomic and functional diversity of coastal marine zooplankton in the Lower St. Lawrence Estuary. SCAS Montréal, 22th - 25th February 2023, Montréal, Canada. [Oral Presentation].

CHAPITRE 1

BIODIVERSITÉ DU ZOOPLANCTON CÔTIER DANS LA ZONE D'IMPORTANCE ÉCOLOGIQUE DE L'ESTUAIRE MARITIME DU SAINT-LAURENT : UTILISATION D'UNE APPROCHE SPÉCIFIQUE ET FONCTIONNELLE

Le zooplancton est un groupe important dans les écosystèmes, notamment pour sa position clé dans le réseau trophique, et est considéré comme un groupe sentinelle. L'étude des communautés zooplanctoniques permet ainsi de définir l'état d'un écosystème notamment dans les stratégies de conservation et de la gestion des espaces protégés ou d'intérêt. L'estuaire maritime du Saint-Laurent (EMSL) est considéré comme une "zone marine d'importance écologique et biologique". Cependant, très peu d'études sur la zone côtière de cette région subarctique ont été effectuées, limitant notre compréhension de la dynamique du zooplancton. Ainsi, le but de notre étude était de caractériser la structure et la diversité des communautés zooplanctoniques, ainsi que l'influence des facteurs environnementaux sur sa dynamique, via une approche couplant l'étude de la diversité taxonomique et de la diversité fonctionnelle. Pendant trois ans (2019 à 2021) en juillet et octobre, la communauté zooplanctonique a été échantillonnée à 35 stations sur la côte nord de l'EMSL avec un filet à plancton d'une maille de 200 μm, et les paramètres environnementaux tels que la température, la salinité, la concentration en chl a et les nutriments y ont été mesurés. Les individus du mésozooplancton ont été identifié au plus bas rang niveau taxonomique possible et les traits fonctionnels (cycle de vie, taille, régime trophique, stratégie d'alimentation) leur ont été attribués. La structure et la diversité des communautés zooplanctoniques ont révélés des variations spatio-temporelles entre les trois secteurs géographiques et entre les saisons, principalement lié à la température, à la concentration de Chl-a et à la salinité. Les diversités taxonomique et fonctionnelle ont montrées des zones de hotspots à Forestville ou à Baie-Comeau, variant de secteur selon la saison pour un même indice, indiquant une influence de la variabilité des facteurs environnementaux. Les zones de hotspot étaient différentes selon la diversité taxonomique et fonctionnelle soulignant la complémentarité des deux approches. Le couplage bentho-pélagique a été observé en juillet lorsque le méroplancton était plus abondant qu'en octobre. L'holoplancton était dominé par des espèces petites et abondantes, telles que *Oithona similis* et *Acartia longiremis* indépendamment de la saison et différaient de la zone plus profonde de l'EMSL, suggérant notamment une influence des caractéristiques physiques agrégatives de la zone côtière. Cette étude permet de dresser un état de référence de l'écosystème côtier de l'estuaire maritime du Saint-Laurent, apportant de nouveaux outils de référence pour de futures études de la zone dans le cadre du suivi des changements potentiels anticipés par l'augmentation des activités anthropiques et du changement climatique.

COASTAL ZOOPLANKTON COMMUNITIES OF THE LOWER ST. LAWRENCE ESTUARY: A TAXONOMIC AND FUNCTIONAL APPROACH

Zooplankton is an essential group in aquatic ecosystems, especially for its key position in the food web. As a sentinel group, studying zooplankton communities can inform about ecosystem health conditions, especially for conservation and management strategies. The Lower St. Lawrence Estuary (LSLE) is considered as an "ecologically and biologically significant marine area", however, the coastal zone of this sub-arctic region has been scarcely studied so far, limiting our understanding of zooplankton dynamics. Thus, the aim of our study was to characterize structure and diversity of coastal zooplankton communities and to determine the influence of environmental parameters on its dynamic, using an integrated taxonomic and functional approach. For three years (2019 to 2021) in July and October, the zooplankton community was sampled at 35 stations on the north coast of the LSLE with a 200 µm mesh plankton net, and environmental parameters such as temperature, salinity, chl-*a* concentration and nutrients were measured. Mesozooplankton individuals were identified at the lowest possible taxonomic level and assigned functional traits (life history, size, trophic type, feeding strategy). Zooplankton community structure and diversities revealed spatio-temporal variation among three different geographic sectors and between seasons. Differentiation was mainly driven by water temperature, Chl-*a* concentration and salinity. Zooplankton composition was dominated by copepods whatever the month or sectors, and secondly by bivalves in July and appendicularians in October. Zones of diversity hotspots were revealed in the sectors of Forestville or Baie-Comeau depending on the season for the same index considered, potentially due to the variability of environmental factors. Hotspots of taxonomic and functional diversities occurred in different zones in the same month, underlining the complementarity of the two approaches. Bentho-pelagic coupling was observed in July when meroplankton was more abundant than in October. The holoplankton was dominated by small and abundant species, such as *Oithona similis* and *Acartia longiremis,* that differed from the holoplankton composition in the deeper LSLE habitats, suggesting an influence of the aggregative physical characteristics of the coastal zone. This study will create the first baseline information on zooplankton communities in the coastal waters of the LSLE and will allow for future tracking of potential changes anticipated by the increase of anthropogenic activities and climate changes.

INTRODUCTION

According to the Convention on Biological Diversity (1992), "biological diversity means the variability among living organisms and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (UN, 1992). This definition implies that the loss of biodiversity will have a disruptive impact on the stability and resilience of marine ecosystems (Johnson et *al*., 2011). For this reason, biodiversity evaluation is commonly used to inform on the state of ecosystems in management strategies (Chiba et *al*., 2018). Biodiversity includes different elements, such as organismal diversity (taxonomic) and ecological diversity (functional). These elements are interlinked and not independent (Gaston and Spicer, 2004). Consequently, it is necessary to study each of these elements for ecosystem conservation management (Martini et *al*., 2020). Taxonomic diversity is based on individuals according to their taxonomic hierarchy (Gaston and Spicer, 2004), and functional diversity is based on taxa functional traits (Pomerleau et *al*., 2015). Functional traits define species in terms of their ecological role, *i.e.* their interaction with the environment and/or with other species (Barnett et *al*., 2007). Therefore, they represent morphological, physiological, life history and behavioral characteristics which are essential ecological functions of the individuals, such as growth, feeding, survival and reproduction.

As zooplankton is a major group in marine ecosystems, due to its pivotal position in food webs linking primary producers to carnivorous predators (Strand et *al*., 2020), this group is commonly used as an indicator or sentinel, to estimate ecosystem condition (Castellani and Edwards, 2017; Usov et al., 2019; Llope et *al*., 2020). Indeed, the species of this ubiquitous group show specific responses to the physico-chemical and biotic characteristics of their environment, such as temperature, salinity, food quantity and quality (Lindegren et *al*., 2020). Therefore, species composition of zooplankton communities will be highly dependent on the variation of abiotic and biotic environmental conditions (Laprise and Dodson, 1994), thus allowing to determine species distribution limits (Laprise and Dodson 1994; Helenius et *al*., 2017; Lindegren et *al*., 2020), and then ecological niche overlap and/or separation

(Hutchinson, 1957). Also, specific environmental parameters will induce differentiated ecophysiological responses in species, reflected by a combination of functional traits. The characterization of these combinations could help to understand how environmental factors contribute to structuring zooplankton communities and affecting their functioning (Lichtman et *al*., 2013). Therefore, the resulting distribution pattern of zooplankton will allow detection of changes in their environment (Russel, 1936).

Thus, studying zooplankton community dynamics is an important component for conservation and management of protected areas or areas of interest (Johnson et *al*., 2011). Especially within the context of the Canadian "Ocean Protection Plan", which defines the need for the evaluation of the ecological state of key coastal zones, the coastal area of the Lower St. Lawrence Estuary (LSLE) was chosen as an important ecological and economic area. Indeed, with its length of 200 km and width of 40 km, the LSLE shows a high spatio-temporal variation in biotic and abiotic factors (Plourde et *al*., 2002). Its hydrodynamics are influenced primarily by the St. Lawrence River runoff, tides and ice cover (Blais et *al*., 2018) which influence the physico-chemical factors, such as temperature and salinity throughout the seasons (Runge and Simard, 1990). The LSLE is a sanctuary for key taxa, such as krill and copepods, and for emblematic marine mammals, such as the beluga and the blue whale (Dufour et *al.,* 2010). In addition, commercial and recreational fisheries and touristic activities (*e.g.* whale watching) take place in this region. The coastal areas of the LSLE are highly productive and ecologically important ecosystems, due to their refuge and nursery functions (Archambault et *al*., 1998). Linking terrestrial and marine open water areas, coastal zones are subjected to numerous anthropogenic pressures (Dufour et *al*., 2010) and thus are sensitive to climate change impacts (Lu et *al*., 2018). However, the coastal zone of the LSLE has been scarcely studied so far, and no studies until now have been carried out on zooplankton communities.

Therefore, the aim of our study was to characterize spatio-temporal variations of coastal zooplankton community on the north shore of the LSLE. We described the structure, diversity and dynamics of zooplankton communities in relation to environmental parameters

focusing on two different seasons throughout three consecutive years from 2019 to 2021, using both taxonomic and functional approaches. These complementary approaches will help to understand the control of environmental conditions on zooplankton dynamics and to establish the first baseline on composition and biodiversity of zooplankton community in the coastal zone of the LSLE for future monitoring, in the context of climate change.

MATERIAL AND METHODS

2.1 Study area

The study region is situated between 48.51°N, 69.22°W - 49.31°N, 67.41°W on the northern coast of the Lower St. Lawrence Estuary (LSLE) (Fig. 5; Table 1). Due to the water mass fluxes, from tributary rivers, the St. Lawrence River or from the Gulf of St. Lawrence (Pinet et al., 2011b) and due to the geomorphological type differences, this area long of 170 km was separated in three sectors in this study, namely "Forestville", "Manicouagan" and "Baie-Comeau" (Fig. 5). Indeed, close to Forestville (QC, Canada), the substrate is characterized as fine sand and silt with large tabular seafloor and light slope, whereas around Baie-Comeau (QC, Canada), the coastal zone is characterized by sands with a rocky geomorphological signature and strong slope close to shoreline (Pinet et al., 2011a). Also, the Manicouagan zone (near Ragueneau, QC, Canada) is highly influenced by tributary rivers, as the Betsiamites River, Rivière-aux-Outardes and Manicouagan River (El Sabh 1979, Pinet et al., 2011b) and is characterized by submarine fan sand to silt, with gently sloping, low depth and large tabular seafloor.
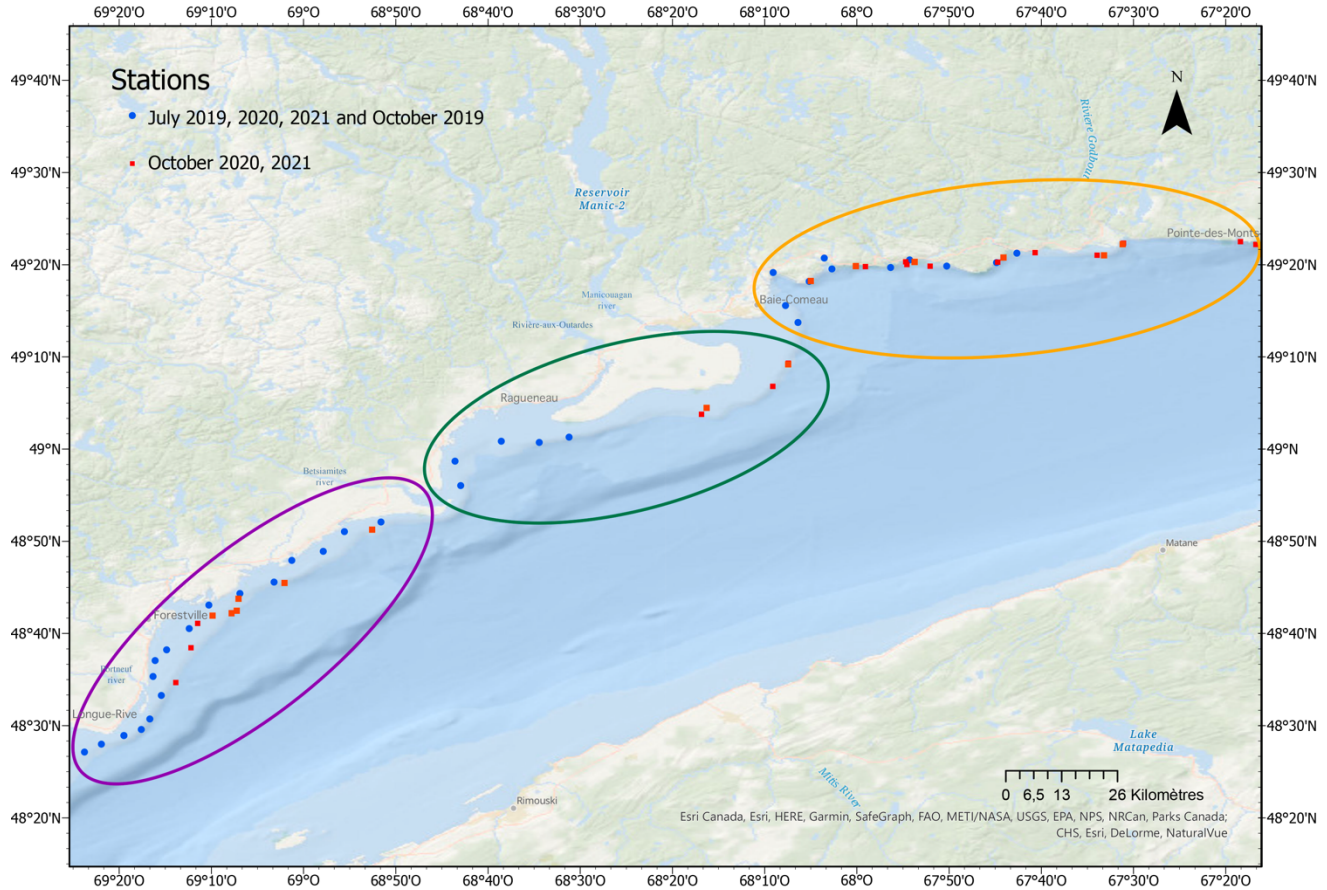
Fig. 5. Map of sampling stations along the north coast of LSLE. Stations in blue were sampled in July 2019, 2020 and 2021 and October 2019. Stations in red were sampled in October 2020 and 2021. Circles represented the different sectors: "Forestville" in purple, "Manicouagan" in green and "Baie-Comeau" in orange.

2.2 Sampling design, sampling protocols and laboratory procedure

2.2.1 Sampling design

Sampling campaigns were conducted in July and October 2019, 2020 and 2021. During each campaign between six and 37 stations were sampled in the coastal zone at depth less than 35 m and less than 1 km from the coast, between Longue-Rive and Pointe-des-Monts (QC, Canada) (Fig. 5; Table 1). Three research vessels have been used depending on their availability (ISMER-UQAR MACOMA 7 m, CCGS LEIM et CCGS PERLEY 22 m, Table

1), combining the sampling effort from campaigns by the Institut des Sciences de la Mer (ISMER-UQAR) and the Maurice Lamontagne Institut (DFO).

Table 1. Sampling campains characteristics with number of sampling stations, vessel used, and environemental data available (D: depth, T: temperature, S: salinity, F: fluorescence, Chla: chlorophyll a, pH: pH, Turb: turbidity, O2: oxygen, NO2+NO3: NO_2+NO_3, PO4: PO_4^{2-}).

Year	Month	Nb of station	Vessel	Environmental data
2019	Juillet	6	CCGS LEIM	D, T, S, F, Chla, O2
2019	Octobre	8	CCGS LEIM	D, T, S, F, Chla, pH, Turb, NO2+NO3, PO4
2019	Octobre	29	MACOMA	D, T, S, F, Chla, pH, Turb
2020	Juillet	32	MACOMA	D, T, S, F, Chla, pH, Turb, O2, NO2+NO3, PO4
2020	Octobre	10	CCGS LEIM	D, T, S, F, Chla, pH, Turb, O2, NO2+NO3, PO4
2021	Juillet	34	MACOMA	D, T, S, F, Chla, pH, Turb, O2, NO2+NO3, PO4
2021	Octobre	4	CCGS PERLEY	D, T, S, F, Chla, Turb, O2, NO2+NO3, PO4

2.2.2 Environmental parameters

At each sampling station, a vertical profile of environmental parameters (temperature, salinity, fluorescence, pH, dissolved oxygen and turbidity) was obtained by a CTD probe (SBE19plus, Sea-Bird Scientific, Bellevue, WA, US). Seawater samples have been collected with a 5L-Niskin bottle at 1 m depth for nutrients (NO_2+NO_3, PO_4^{2-}) and Chlorophyll *a* (chl *a*) concentrations analyses. For nutrient analyses, water samples were filtered over 0.2 µm cellulose acetate filters and stored at -20 °C. Then, nutrient measures were performed with an automated chemistry analyzer (AA500 Autoanalyzer, SEAL Analytical, Mequon, WI, US), according to the standard method of the JGOFS protocol (JGOFS, 1994). However, nutrient concentrations were not available for all months, depending on vessel and sampling campaigns (see Table 1).

For chl *a* analyses, water samples were filtered through a Whatman GF/F filter (25 mm diameter). Pigments were extracted with 90 % acetone during 20 h at 4 °C and chl *a* concentrations were measured with a fluorometer (10-AU-005-CE, Turner-Design, San Jose,

CA, US), according to the protocol by Mundy et *al*. (2011), in order to the calibrate the CTD fluorescence.

2.2.3 Zooplankton sampling

Mesozooplankton, the zooplankton organisms which their size is comprised between 0.2 and 20 mm, was collected with a 200 µm mesh standard plankton net (diameter 1 m) in vertical-oblique hauls throughout the entire water column. The volume filtered was determined with a flowmeter (2030R mechanical Flowmeter, General Oceanic, Miami, FL, US), later used for abundance calculations. Samples were conserved in 95 % ethanol.

2.2.4 Taxonomic biodiversity

Zooplankton taxa were identified to the lowest possible taxonomic level with a stereoscopic microscope (SZX2, Olympus, Tokyo, Japan) (max. 11x), staged and counted. For taxonomical analyses, a minimum 1/100 of sample was analysed with Hensen Stempel pipette of 5 mL to calculate abundance, or at least 400 copepodites and 30 *Calanus* spp. copepodites were counted to obtain a better representation of the species, for a precision obtained at 90 % confidence level according to Harris et *al*. (2000). Copepods specimens were determined at the species level when possible, and for other taxa at genus or species level, based on identification keys according to literature (Razouls et *al*., 2005-2022). Because we used a 200 µm mesh, nauplii of small copepods species were not retained, then all copepods nauplii were removed from further numerical analyses and only copepodites stages were considered here (CI to CVI). All taxa and stages identified are shown in Table S1. Biomass data were calculated based on sizes and specialized literature (Table S2).

2.2.5 Functional diversity

Four functional traits were chosen as they represent each functional trait typology (according to Martini et *al*., 2020): life history (life cycle), physiological (trophic type), behavioral (feeding strategy) and morphological (size), all with various levels (Table 2, Table S1).

Table 2. Description of functional traits. Life cycle: taxa which spend all their lifetime within the plankton (Holoplankton) or only part of their life cycle, such as larval stages (Meroplankton); Categories of trophic type and feeding strategy were determined according to Kiørboe, 2011 and Brun et *al*. 2016; Size: based on minimum and maximum of taxa adult size, CVI stage for copepod species and specific size of development for other taxa.

Life cycle	Holoplankton	
	Meroplankton	
Trophic type	Omnivore	
	Herbivore	
	Carnivore	
	Non-feeding	
	Detritivore	
Feeding strategy	Active ambush feeder	
	Passive ambush feeder	
	Cruise feeder	
	Current feeder	
	Mixed feeder	
Size	Class	(mm)
	1	[0.2; 0.5[
	2	[0.5; 1.0[
	3	[1.0; 1.5[
	4	[1.5; 2.5[
	5	[2.5; 5.0[
	6	[5.0; 10.0]
	7	>10.0

2.3 Numerical analyses

Taxa abundances were square-root transformed to reduce the dominant taxa effect (Clarke et *al*., 2014). Taxonomic diversity, Shannon-Wiener index (H'), Pielou evenness (J') and specific richness (S) were calculated with the 'vegan' R package (R Core Team, 2021, version 4.1.1). Three functional diversity indices were chosen: Functional richness (FRic) "measures the amount of niche space occupied by the species within a community"; functional divergence (FDiv) "measures the abundance-weighted functional differences among species within a community"; and functional evenness (FEve) describes "how evenly

spread the species (or abundance) of a community are in the niche space" (Mason et *al*., 2008). These indices were chosen because they describe independent aspects of species distribution in the niche space (Mason et *al*., 2008) and they can be compared with their analogous taxonomic diversity indices. The functional indices were calculated according to Villeger et *al*. (2008) with "mFD" R package, based on Gower distance.

Hotspot biodiversity maps (for both taxonomic and functional diversity indices) were compiled using Getis-Ord-Gi ® from ArcGIS® Pro software. Because only few stations were available for some months (Table 1), hotspot analyses were performed at the level of month ("July" and "October") with the three years (2019, 2020, 2021) pooled, to assure robustness of the analyses, by including a minimum of 30 sampling stations.

The SIMPER routine (Primer-e®+7 software) was used to determine which taxa contribute to dissimilarity among sectors, months and years. Non-parametric permutational multivariate analysis of variance (PERMANOVA), based on Euclidean distance, was used to test for differences of total zooplankton abundance and diversity indices among geographic sectors, months, and years, applying a Bonferroni correction to the post-hoc test results ('vegan' package, R Core Team, 2021). To test for the presence of differences in zooplankton assemblage composition among sectors, months and years, PERMANOVA based on Bray-Curtis similarity distance, were applied, followed by a Monte-Carlo post-hoc test (Primer-e®+7; Clarke et *al*., 2014).

Prior to perform correlation analyses of zooplankton composition, abundances and diversity indices with environmental parameters, collinearity among measured factors was investigated with Draftman plots ('Ggally' R package) and PCAs, and only one or two collinear environmental variables *per* collinear group were kept. Then, turbidity and pH were found to be collinear with chl *a* and temperature respectively and were removed from further analyses. Distance-based redundancy analysis (dbRDA) was used to characterize differences in the community among groups (year, month, sector) and to explore relationships with environmental parameters such as temperature, salinity and chl *a* (Primer-e®+7). Finally, generalized additive models (GAMs) were used to determine how environmental parameters

affect zooplankton abundance and diversity using the 'mgcv' R package (R version 4.1.1). The best model was determined depending on the lowest ΔAIC using the 'dredge' function from R package 'MuMIn' (Table S3), and the change points of each GAM model plot was determined with 'EnvCpt' R package (R version 4.1.1).

RESULTS

3.1 Environmental conditions

Environmental conditions of the coastal zone of the Lower St. Lawrence Estuary (LSLE) varied strongly with season and differed among sectors (Fig. 6, Table S4), and this pattern was stable over the three years ($p_{Year*Month*Sector} > 0.05$; Table S4). Highest mean temperatures (17.70 ± 0.72 °C) were found in Manicouagan in July 2020 and lowest (2.62 ± 0.47 °C) in the sector of Baie-Comeau in October 2020 (Fig. 6a). Mean temperature was higher in July than in October in 2019 and 2020 for all sectors ($p < 0.05$; Table S4, Table S5) but in 2021, all months were similar. Mean salinity ranging between 23.67 ± 1.16 PSU (Manicouagan, July 2020) and 31.20 ± 0.24 PSU (Baie-Comeau, October 2020) (Fig. 6b). Mean salinity was higher in October compared to July ($p < 0.001$; Table S4), except for 2021 when no significant difference was found between months. Similarly to salinity, mean Chl a conc. was higher in October (10.34 ± 1.12 mg m^{-3}, Manicouagan, 2019) compared to July (0.91 ± 0.18 mg.m^{-3}, Baie-Comeau, 2020) in 2019 and 2020 ($p < 0.004$, Table S5, Fig. 6c), whereas in 2021, higher concentrations (9.38 ± 10.63 mg m^{-3}, Forestville) were found in July compared to October (0.47 ± 0.12 mg m^{-3}, Manicouagan) ($p_{Year*Month} < 0.005$; Table S4, Fig. 6c). Oxygen conc. were similar between months of the same year ($p_{Month} > 0.05$, Table S4, Fig. 6d). Mean nutrients concentrations (NO_2+NO_3 and PO_4^{2-}) were significantly higher in October than in July ($p < 0.05$; Table S4). Indeed, NO_2+NO_3 concentrations were ranging between 0.60 ± 0.25 μM and 9.87 ± 0.96 μM in October and between 0.12 ± 0.05 μM and 1.11 ± 1.12 μM in July (Fig. 6e). PO_4^{2-} concentration were ranging between 0.35 ± 0.01 μM and 1.03 ± 0.04 μM in October and between 0.09 ± 0.06 μM and 0.34 ± 0.19 μM in July for PO_4^{2-} (Fig. 6f).
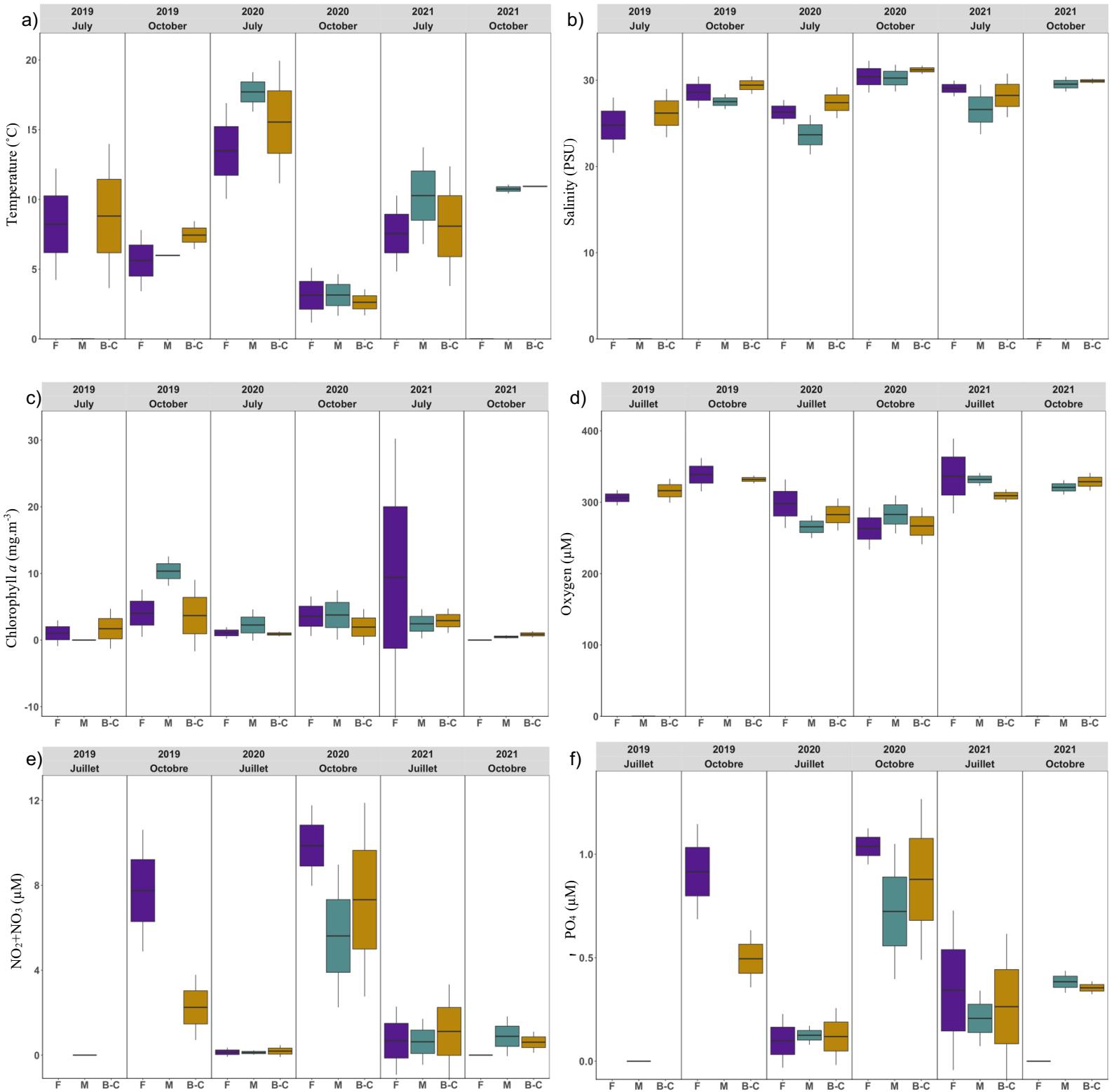
Fig. 6. Mean temperature (a), salinity (b), chlorophyl *a* (c), oxygen (d), NO₂+NO₃ (e) and PO₄ (f) *per* sectors, month and year. Forestville is given in purple, Manicouagan in green and Baie-Comeau in yellow.

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3.2 Meso-zooplankton community: taxonomic approach

3.2.1 Total zooplankton abundance and biomass

Mean total abundances ranged between 612.71 ± 298.99 ind m^{-3} in October 2020 (Forestville) and 14303.72 ± 9891.07 ind m^{-3} in July 2021 (Forestville) (Fig. 7a). Temporal variability in abundances were found in 2019 and 2020, showing higher mean total zooplankton abundances in July than October ($p_{Month} < 0.05$, Table S6), whereas comparable abundances were found for both months in 2021 ($p = 0.06$ Table S5). Strong spatial patterns in mean total abundances were found among sectors in July 2020, July 2021, with higher abundances in Baie-Comeau in 2020, whereas in July and October 2021 a decrease of total abundance was observed from Forestville to Baie-Comeau (Fig. 7a). Total biomass was in general higher in July compared to October, except in 2021 when the highest carbon concentration was found in October.

3.2.2 Zooplankton species diversity: distribution pattern

Hotspots in species richness were found in the Forestville sector in July. In contrast, in October, coldspots were detected in Forestville and hotspots were found in the sectors of Manicouagan and Baie-Comeau (Fig. 8a, b). For both months, Baie-Comeau contained hotspots of Shannon-Wiener diversity and the Pielou evenness, whereas Forestville showed coldspots for these diversity indices (Fig. 8c, d and 8e, f).
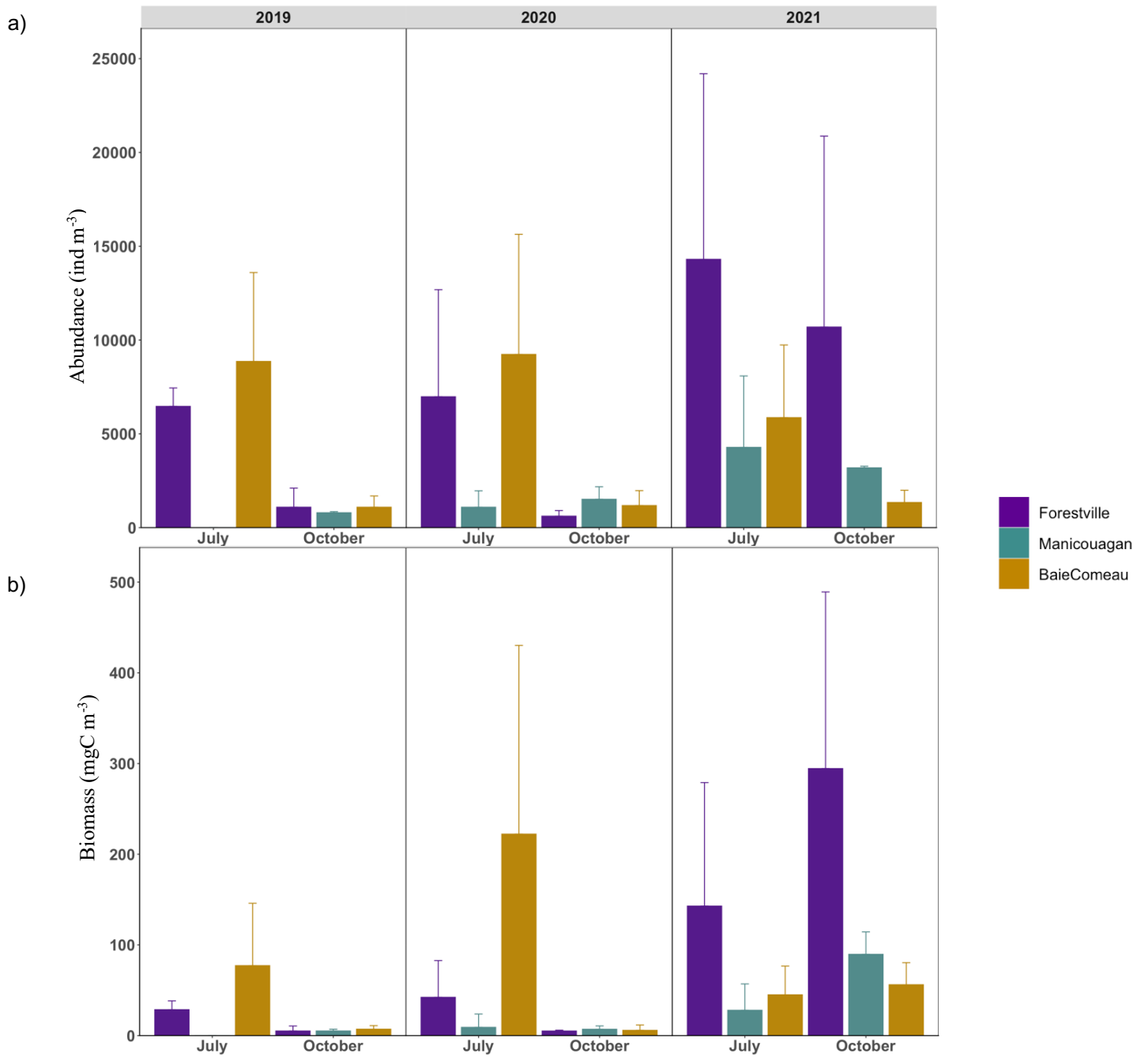
Fig. 7. Mean total abundance (ind m^{-3}) (a) and biomass (mgC m^{-3}) (b) *per* sector, month and year.
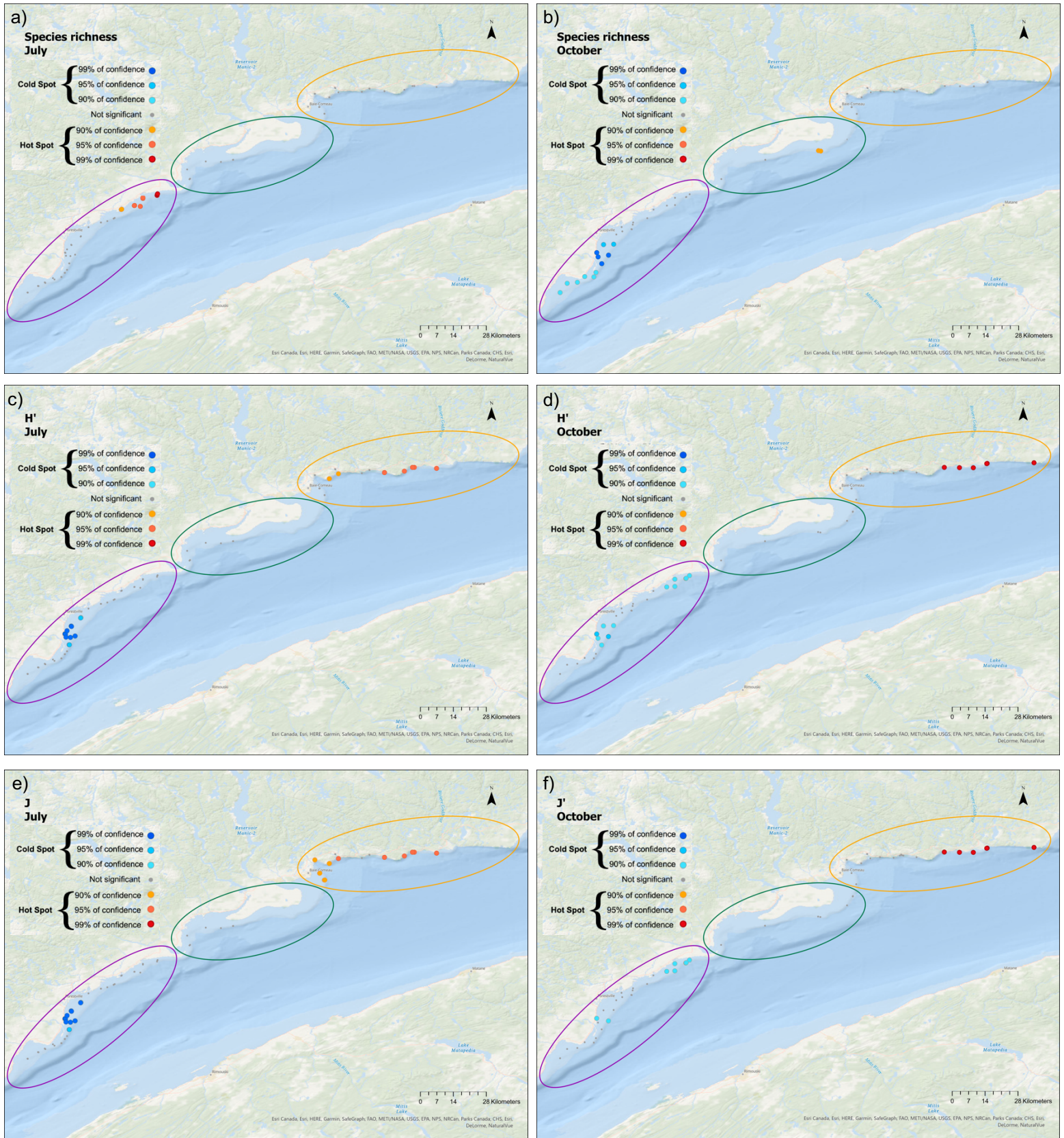
Fig. 8. Maps of hotspots and coldspots of species richness (a, b), Shannon-Wiener index (c, d) and Pielou index (e, f) in July and October, respectively.

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3.2.3 Taxonomic community structures

A total of 59 taxa were identified, including 15 genera (Table S1). Species composition was highly variable and differed among years, months and sectors ($p_{Year*Month*Sector} < 0.05$, Table S7). The zooplankton community was mostly composed of Copepoda (30.01-80.78 % throughout months and sectors) (Fig. 9a). In October, Appendicularia were dominant (40-43.8 %) in 2019 and 2020 but not in 2021 (12.5 %). July 2020 was characterized by a high proportion of Mollusca (49.7 % overall, but especially in Forestville 60.11%) compared to July in the other years (8.9-19.8 %). The contributions of Diplostraca were variable, ranging between 0.11 and 6.13 %, with higher percentages in July 2020 and 2021 as well as in October 2021. Echinodermata showed higher proportion in July than in October for all years (Fig. 9a). The zooplankton composition, based on carbon biomass, was characterized by a dominance of Appendicularia in October 2019 and 2020. Biomass composition was different in 2021 than the other years, with a dominance of Copepoda in October (Fig. 9b). However, similar zooplankton compositions were found in July 2019 and July 2021, likewise in October 2019 and October 2020, based on distance of centroid of Bray-Curtis dissimilarity (Fig. S1; $p > 0.05$; Table S8), indicating some degree of interannual seasonality. On the contrary, the zooplankton community in July 2020 and October 2021 were different from the ones in July and October of the other two years, respectively (Fig. S1; $p < 0.001$; Table S9). Spatial structure of communities among sectors was found in July 2020 and 2021 and in October 2019 ($p < 0.05$, Table S8). However, dissimilarities among sectors within the same month did not exceed 50 %, except in July 2020 (until 59.56% of dissimilarity) (Table S10).
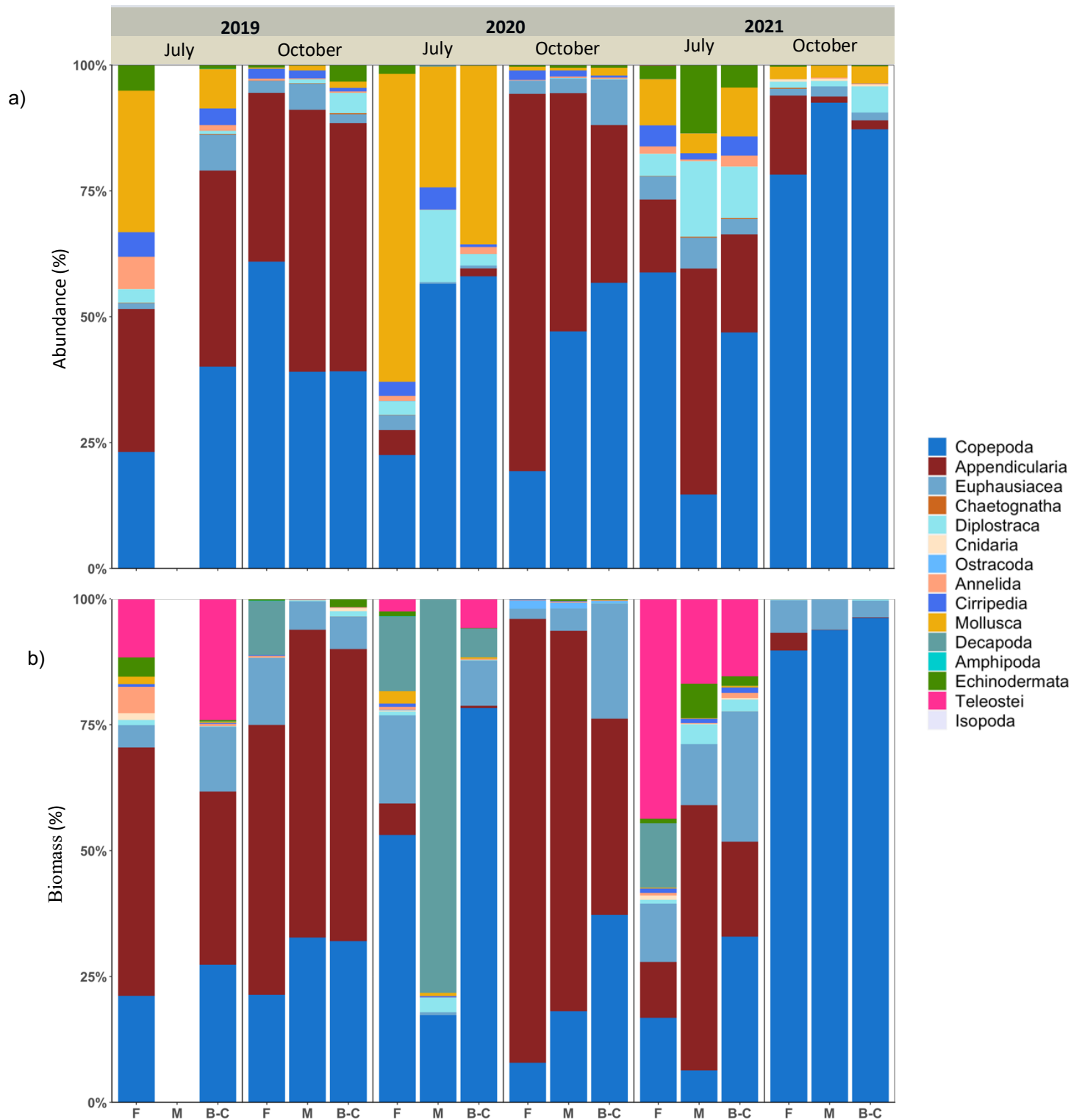
Fig. 9. Proportion of abundance (%) (a) and biomass (%) (b) of taxonomic groups *per* sector, month and year.

When considering specific taxa separately, the five taxa which mainly contributed to species composition (across the sectors) were Bivalvia, Cirripedia, *Fritillaria* sp., *Acartia longiremis*, and *Oithona similis* (Table S12). The first four taxa contributed to dissimilarity among months (all years and sectors) (data not shown). Their abundances were higher in July than in October ($p_{Month} < 0.001$, Table S6) and their repartition differed among the sectors. Indeed, in October, Bivalvia abundances were higher in Baie-Comeau and Manicouagan than Forestville (Fig. 10a, b). In July and October, Cirripedia abundances were higher in Forestville (Fig. 10c, d). *Fritillaria* spp. abundances did not show a clear pattern among sectors (Fig. 10e, f). *Acartia longiremis* abundances were higher in Forestville for both months (Fig. 10g, h). On the contrary, *O. similis* abundances were higher in Baie-Comeau in July and October (Fig. 10i, j) compared to the other two sectors.
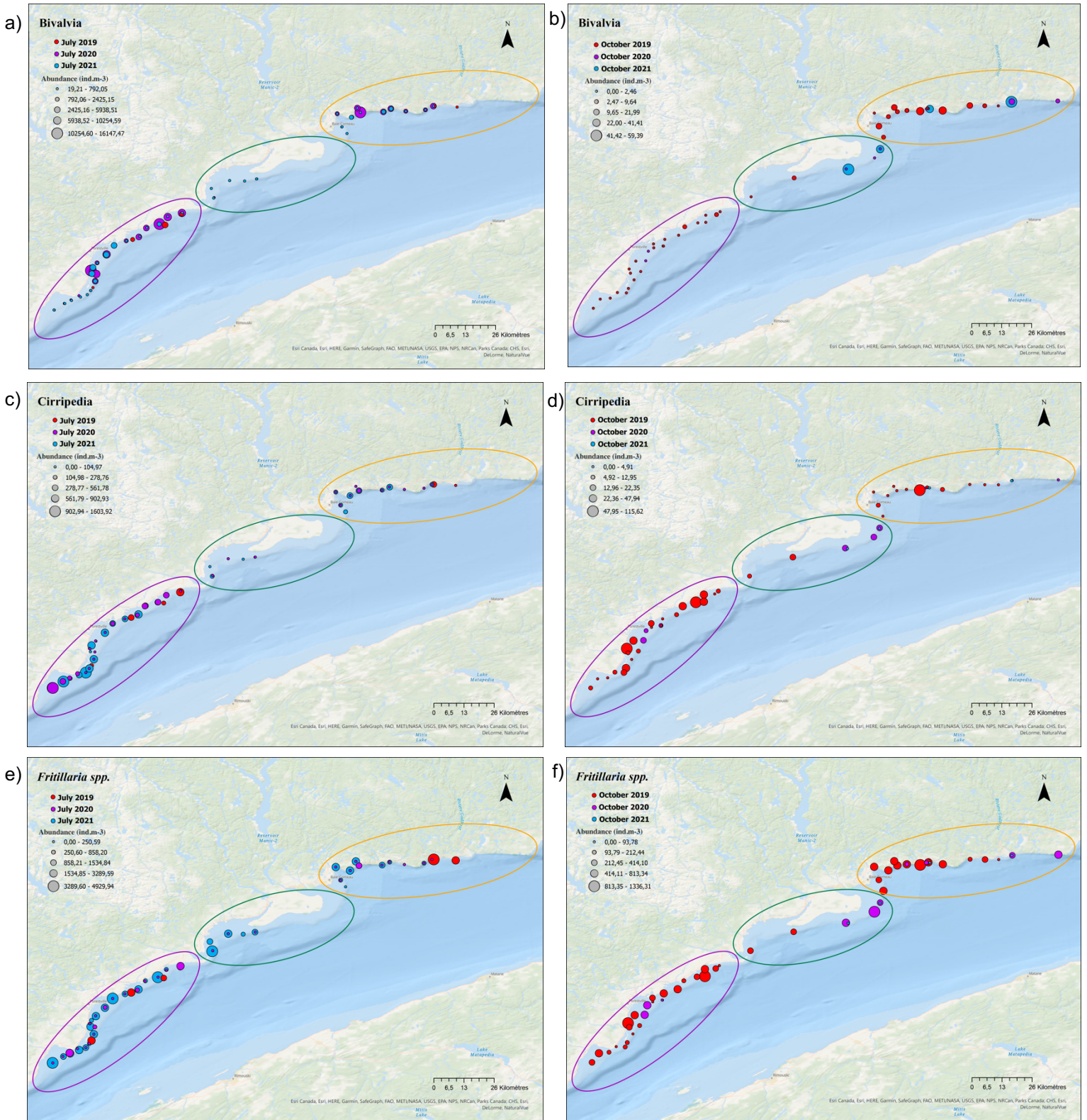
Fig. 10 (continued next page). Spatial representation of abundance (ind m⁻³) of the five majority taxa: Bivalvia (a, b), Cirripedia (c, d), *Fritillaria* spp. (e, f), *Acartia longiremis* (g, h) and *Oithona similis* (i, j) in July and October of the three years studied. Colors are represented the years sampled: red for 2019, purple for 2020 and blue for 2021.
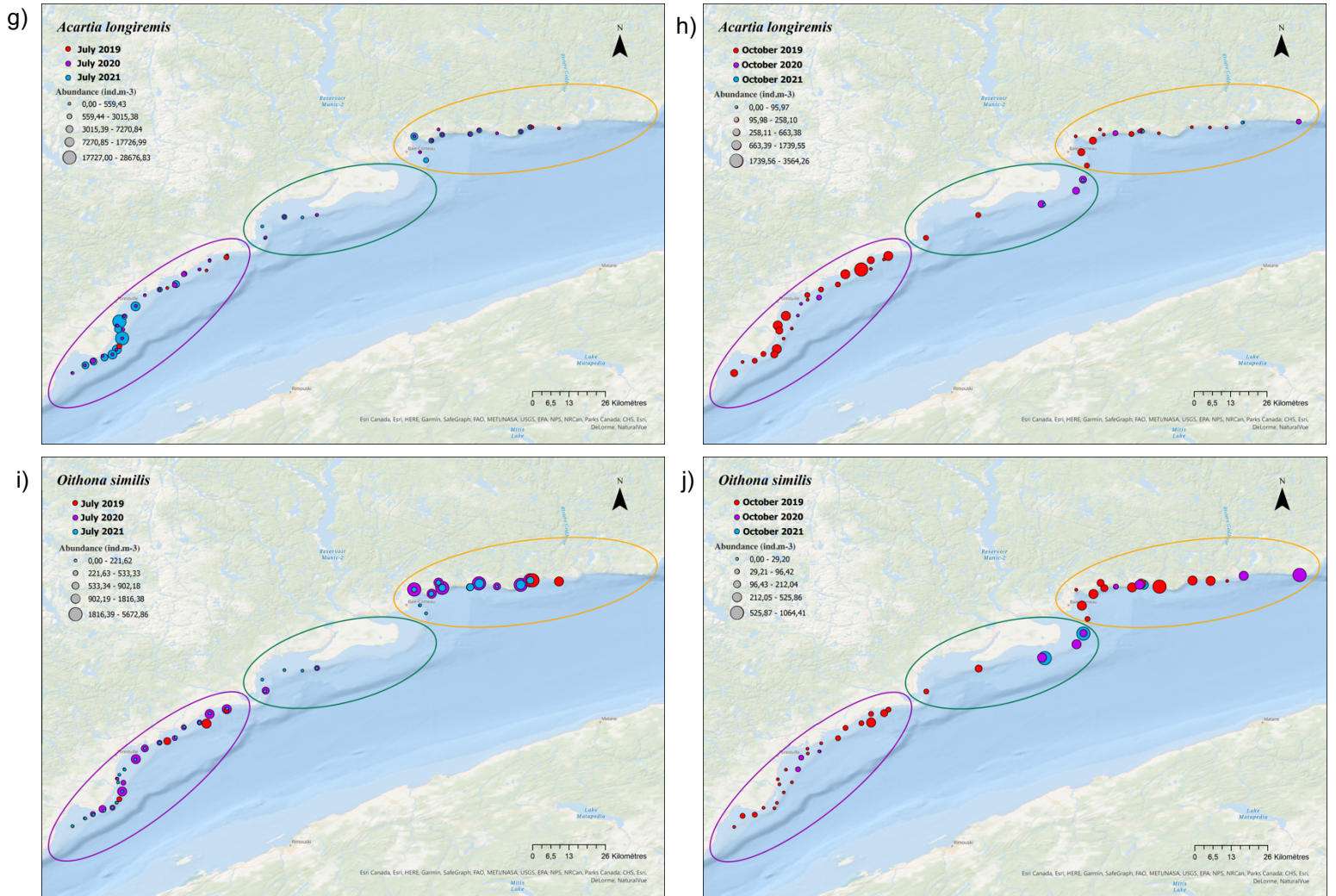
Fig. 10 (end). Spatial representation of abundance (ind m⁻³) of the five majority taxa: Bivalvia (a, b), Cirripedia (c, d), *Fritillaria* spp. (e, f), *Acartia longiremis* (g, h) and *Oithona similis* (i, j) in July and October of the three years studied. Colors are represented the years sampled: red for 2019, purple for 2020 and blue for 2021.

3.2.3 Species - environmental interaction

The zooplankton community composition, based on Bray Curtis dissimilarities, was influenced by different environmental parameters (Fig. 11). Temperature emerged as the main driver (dbRDA1: 75.5 % of fitted, 19.4 % of total variation) which mostly explained the variability found in zooplankton composition. Particularly, high temperatures in July 2020 were correlated to a distinct zooplankton community. Similarly, low temperatures were correlated to zooplankton communities in October. In July 2021, the zooplankton composition in Forestville was influenced by Chl *a* (secondary factor, dbRDA2 :15.1 % of fitted, 3.9 % of total variation). The communities in October were driven mostly by salinity (secondary factor, dbRDA2 :15.1 % of fitted, 3.9 % of total variation), excepted for October 2021, when the community was mainly influenced by relatively warmer temperatures. However, these results of October 2021 should be interpreted with caution because only environmental data of four stations were available. The threshold of a positive temperature effect on total abundance was at 7.5 °C, based on GAM analysis (Table 3; Fig. 12a). Also, temperature showed a positive effect on species richness within the range of 6.4 to 14.2 °C with an optimal temperature of 10.44 °C, and within the range of 6.1 to 13.6 °C for the Shannon-Wiener index (Fig. 12b, c). Before and over these ranges, abundance and diversity indices were negatively affected by temperature (Table 3; Fig. 12a, b, c). Total abundance was positively correlated with Chl *a* (Fig. 12a). Species richness was only influenced by temperature (Fig. 12b). The Shannon-Wiener and the Pielou evenness were negatively correlated with Chl *a* (Fig. 12c, d). Predictability of the relationship was low for all taxonomic diversity indices (deviance explained = 12.6-18.4 %), except for abundance (42.8 %) (Table 3).
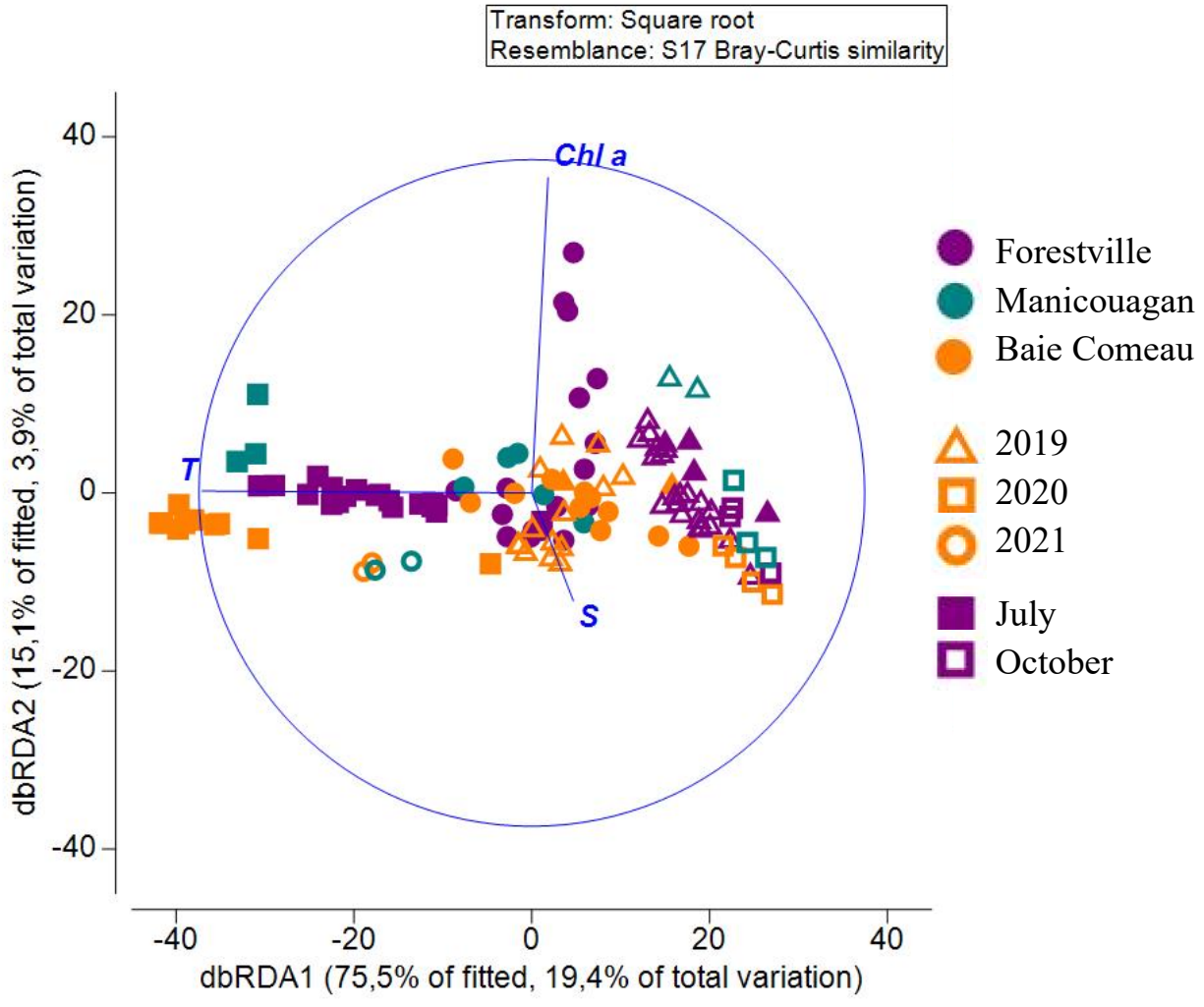
Fig. 11. Distance-based redundancy analysis, of zooplankton community composition based on Bray-Curtis dissimilarity, with three environmental parameters (temperature, salinity and chl *a*). Colors represented sectors, forms represented years, and full forms correspond to July and empty forms correspond to October.

Table 3. Summary of generalized additive models (GAM) results testing the effect of temperature, salinity and chl-*a* for abundance, species richness, Shannon-Wiener index, Pielou evenness, functional richness, functional divergence and functional evenness.

GAM		Estimate	Std. Error	t value	Pr(>|t|)	edf	Ref.df	F	p-value	R-sq.(adj)	Deviance expl.	REML	n
Abondance										0.401	42.80%	1227.6	123
	(Intercept)	5540.1	474.1	11.69	<2e-16								
	s(Temperature)					2.0159	9	1.315	0.000587				
	s(Salinity)					0.7652	9	0.14	0.161377				
	s(Chla)					2.7757	9	7.816	< 2e-16				
S										0.164	18.40%	295.81	123
Species richness	(Intercept)	18.0244	0.2336	77.17	<2e-16								
	s(Temperature)					3.017	9	2.655	2.57E-05				
H'										0.139	16.80%	64.673	123
Shannon-wiener indice	(Intercept)	1.56586	0.03505	44.67	<2e-16								
	s(Temperature)					2.1099	9	0.925	0.00711				
	s(Salinity)					0.5327	9	0.127	0.13282				
	s(Chla)					1.4798	9	0.957	0.00348				
J'										0.106	12.60%	-75.41	123
Pielou evenness indice	(Intercept)	0.54137	0.01129	47.97	<2e-16								
	s(Chla)					1.576	9	1.119	0.0018				
	s(Temperature)					1.165	9	0.215	0.175				
FRic										0.352	37.70%	-67.28	123
Functional richness	(Intercept)	0.56885	0.01175	48.4	<2e-16								
	s(Temperature)					2.981	9	6.882	< 2e-16				
	s(Chla)					1.679	9	0.847	0.00791				
F Div										0.325	34.90%	-69.26	123
Functional divergence	(Intercept)	0.76304	0.01164	65.53	<2e-16								
	s(Temperature)					2.361	9	4.421	<2e-16				
	s(Chla)					1.88	9	0.927	0.0083				
FEve										0.0886	10.00%	-138.3	123
Functional evenness	(Intercept)	0.366813	0.006795	53.98	<2e-16								
	s(Chla)					0.6226	9	0.111	0.19945				
	s(Salinity)					0.908	9	1.092	0.00122				

a)   Total abundance
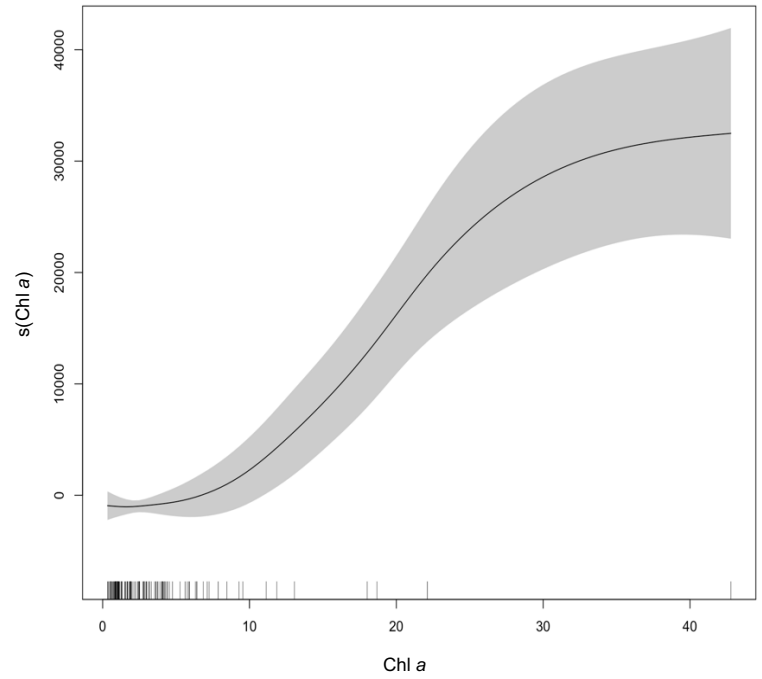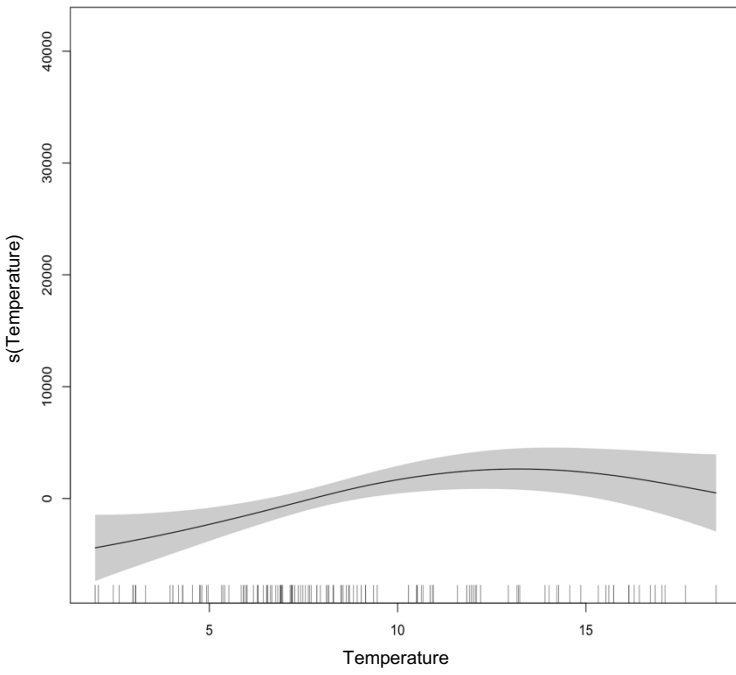
b) Species richness
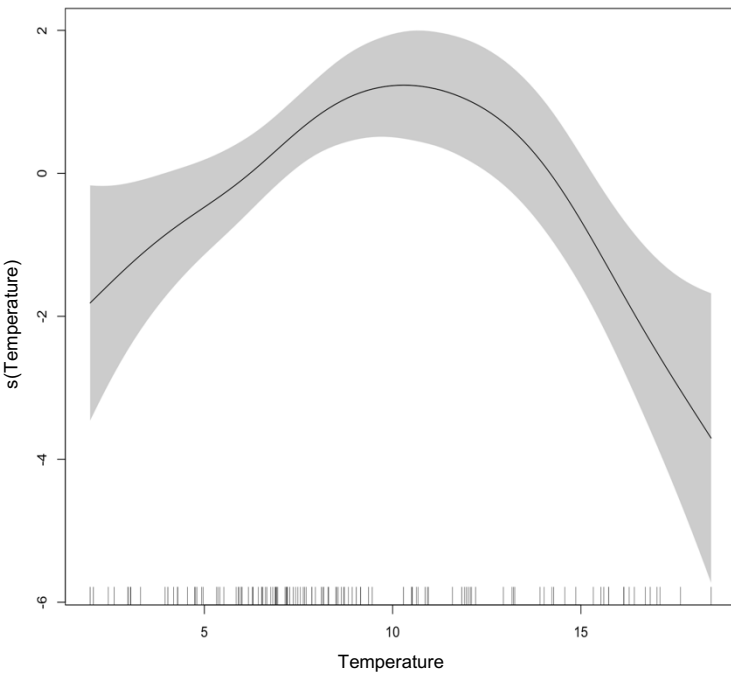
Fig. 12. (continued) Smoothed plot obtained with generalized additive models (GAM) of the effect of temperature, salinity and chl-*a* on total mean abundance (a), species richness (b), Shannon-Wiener index (c), Pielou evenness (d), functional richness (e), functional divergence (f) and functional evenness (g). Zone in grey represented the interval of confidence of 95%. Positive effect are zero of the contribution of the smoothed factor (vertical axe). Horizontal axe represented the environmental gradient.

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c) Shannon-Wiener index
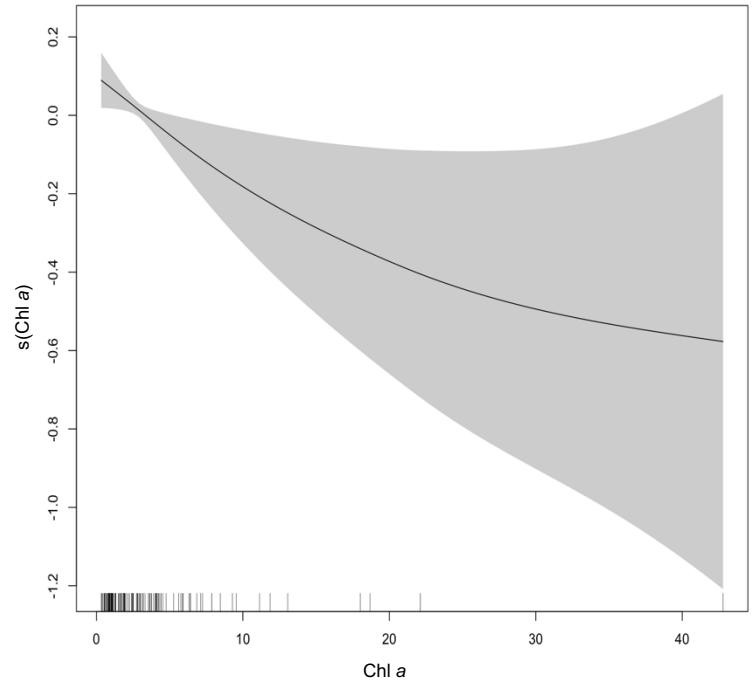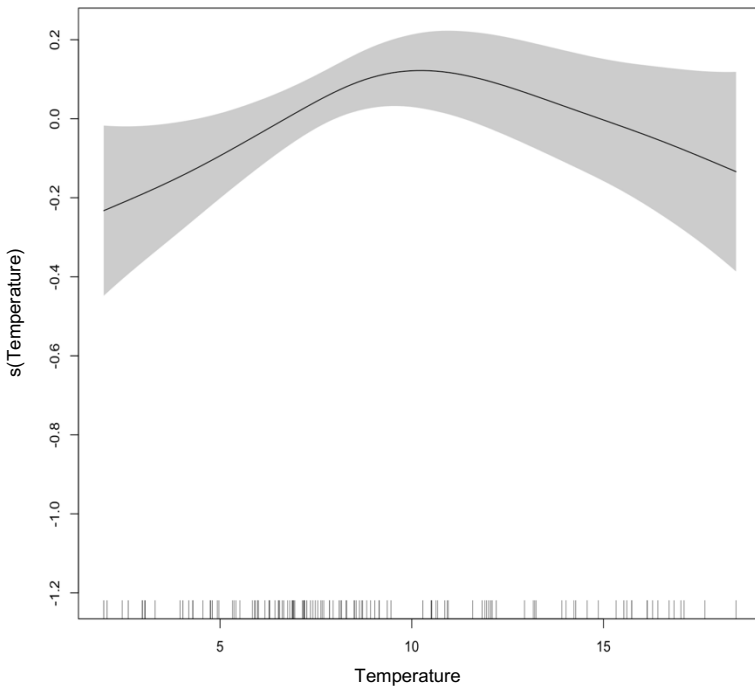
d) Pielou evenness index
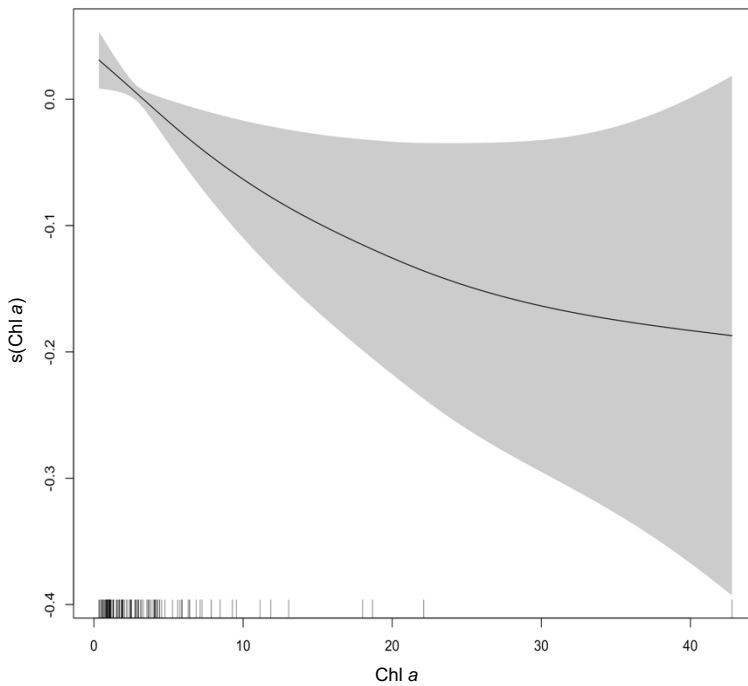
Fig. 12. (continued) Smoothed plot obtained with generalized additive models (GAM) of the effect of temperature, salinity and chl-*a* on total mean abundance (a), species richness (b), Shannon-Wiener index (c), Pielou evenness (d), functional richness (e), functional divergence (f) and functional evenness (g). Zone in grey represented the interval of confidence of 95%. Positive effect are above zero of the contribution of the smoothed factor (vertical axe). Horizontal axe represented the environmental gradient.

e) Functional richness
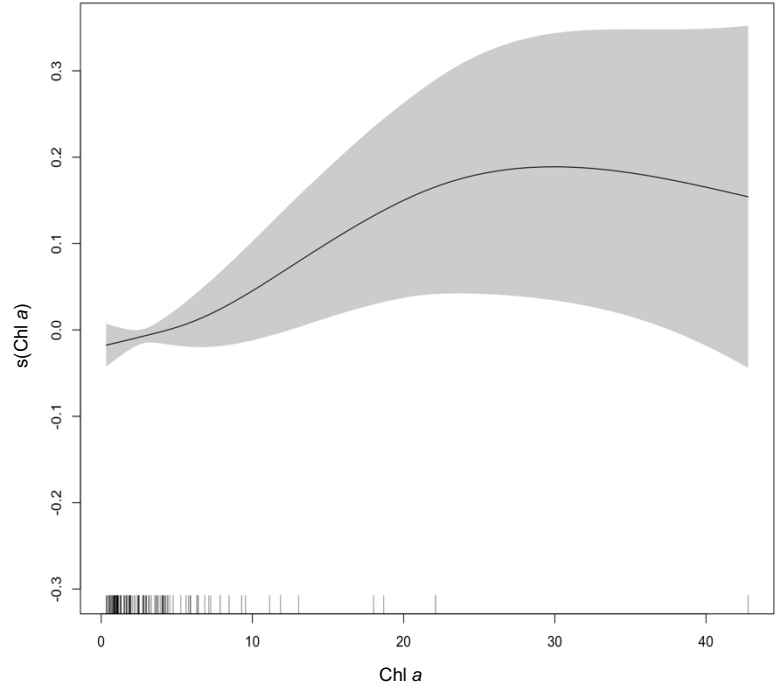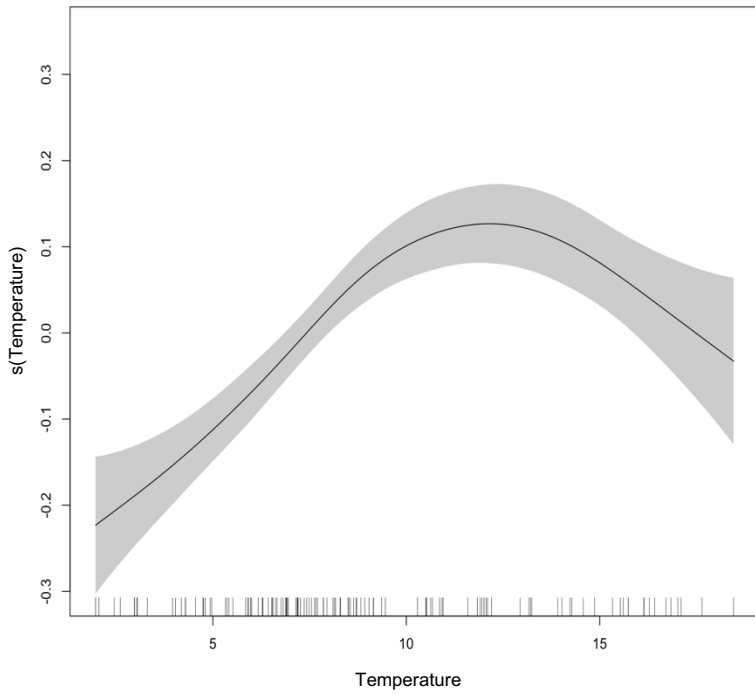
f) Functional divergence
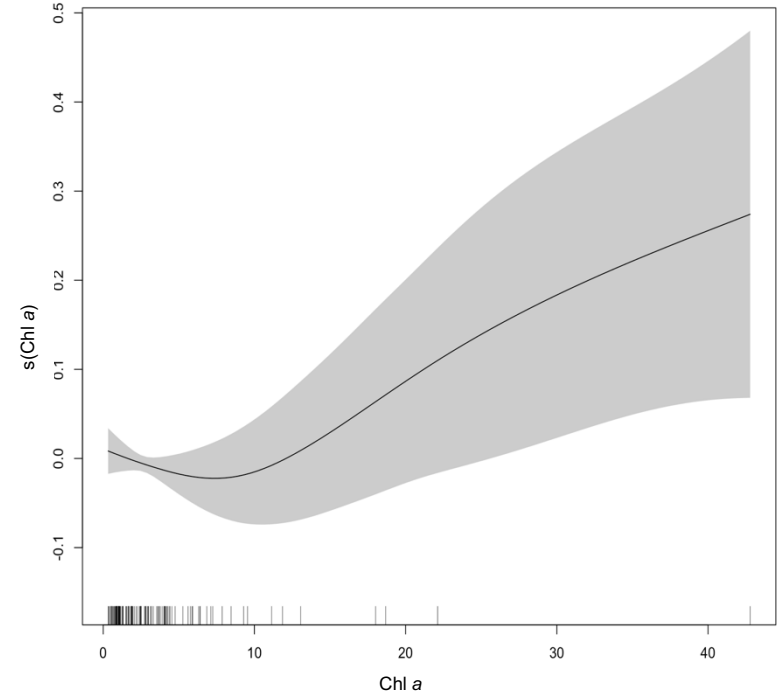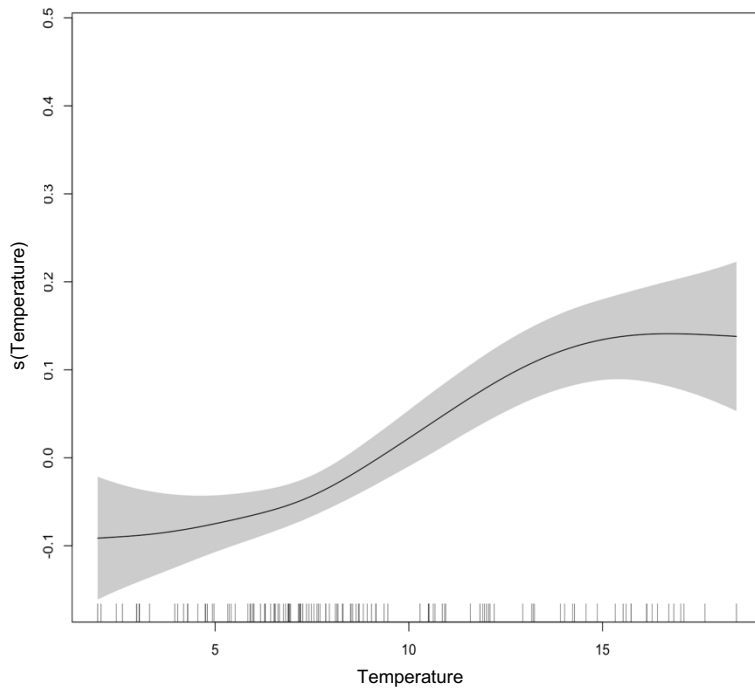
Fig. 12. (continued) Smoothed plot obtained with generalized additive models (GAM) of the effect of temperature, salinity and chl-*a* on total mean abundance (a), species richness (b), Shannon-Wiener index (c), Pielou evenness (d), functional richness (e), functional divergence (f) and functional evenness (g). Zone in grey represented the interval of confidence of 95%. Positive effect are above zero of the contribution of the smoothed factor (vertical axe). Horizontal axe represented the environmental gradient.

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g) Functional evenness
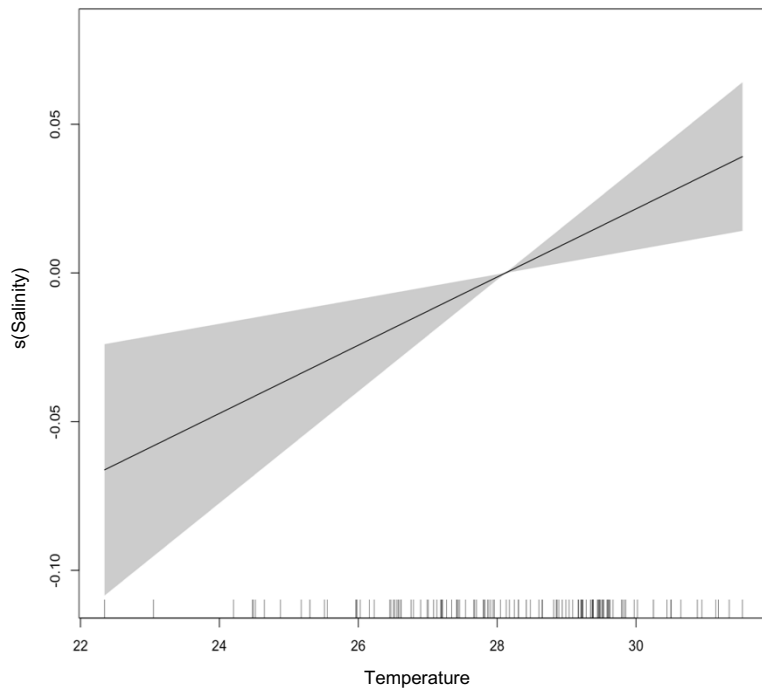
Fig. 12 (end) Smoothed plot obtained with generalized additive models (GAM) of the effect of temperature, salinity and chl-*a* on total mean abundance (a), species richness (b), Shannon-Wiener index (c), Pielou evenness (d), functional richness (e), functional divergence (f) and functional evenness (g). Zone in grey represented the interval of confidence of 95%. Positive effect are above zero of the contribution of the smoothed factor (vertical axe). Horizontal axe represented the environmental gradient.

3.3 Meso-zooplankton community: functional traits approach

3.3.1 Functional composition

The zooplankton community was mostly composed of holoplankton, independently of months or years. The proportion of meroplankton was higher in July, especially in July 2020, compared to October ($p < 0.05$, Table S13; Fig. 13a). In each month, omnivores largely composed the community. Herbivores were in higher proportion in July compared to October, except for October 2021 when they were in higher proportion than in all the other months. Carnivores were present in larger proportions in July (Fig. 13b). In July and October, the two feeding strategies, feeding current and active ambush, were proportionally more abundant than the four others. Mixed feeding was only present in July 2020 and October 2021 and was absent the other months. Cruise feeders were mostly present in July, except in October 2021 when they occurred in higher proportion than in all the other months (Fig. 13c). The small (Class 1: 0.2 to 0.5 mm) and medium (Class 5: 2.5 to 5.0 mm) zooplankton size classes occurred in higher proportion in July than in October. Class 2 to 4 (0.5 to 2.5 mm) were represented in equivalent proportion at each month (Fig. 13d).

3.3.2 Zooplankton functional diversity: distribution pattern

Hotspot analyses on functional diversity indices revealed that the functional richness (FRic) hotspots were located in Forestville and the coldspots in Baie-Comeau in July (Fig. 14a). In contrast, in October, Forestville showed coldspots and Baie-Comeau hotspots for FRic (Fig. 14b). In July, the hotspots of functional divergence (FDiv) were identified in Forestville and coldspots in Manicouagan, whereas hotspots of functional evenness (FEve) were detected in Baie-Comeau (Fig. 14c, e). Hotspots of FDiv and FEve occurred in Forestville in October (Fig. 14d, f).
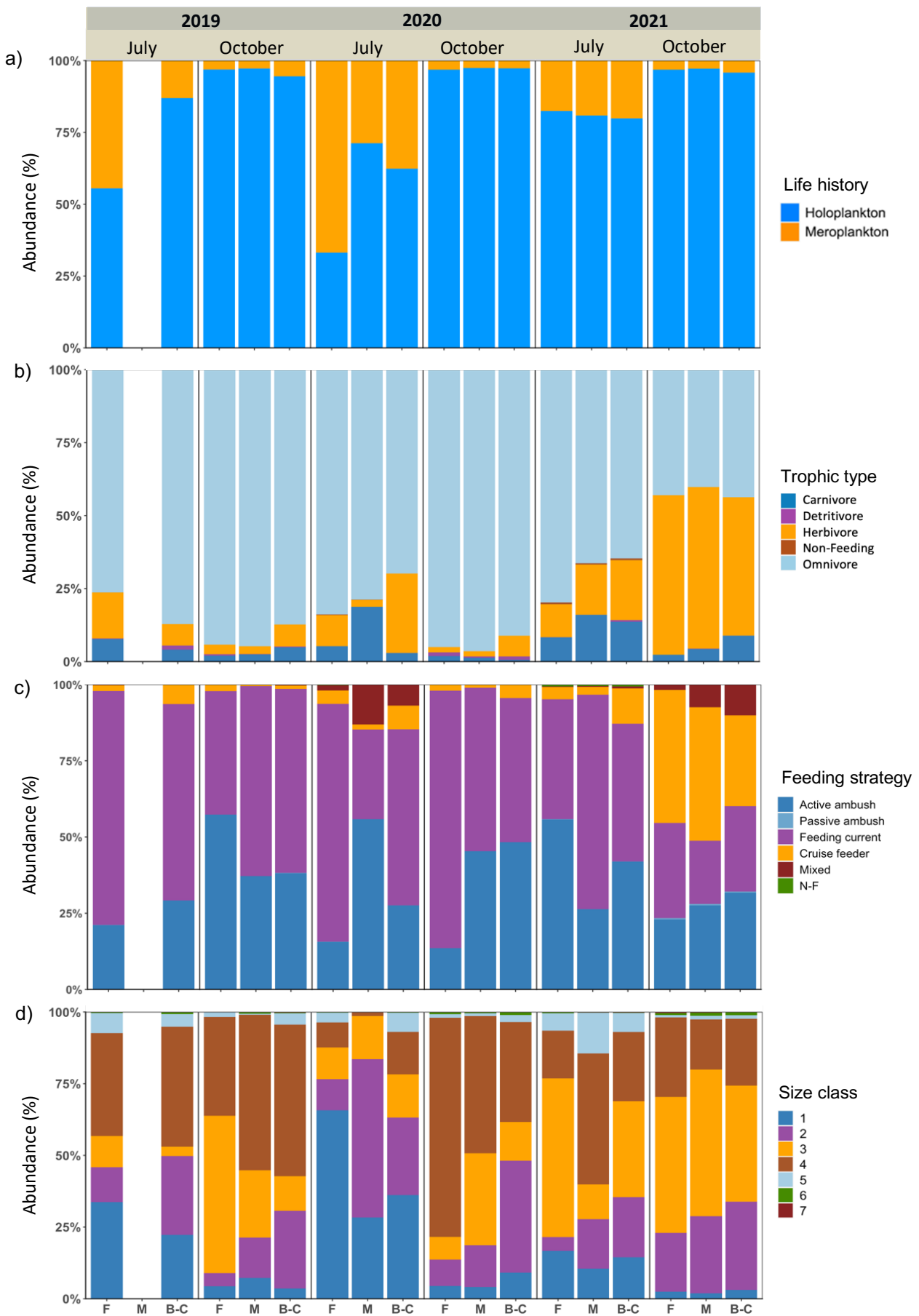
Fig. 13. Proportion of abundance (%) of the four functional traits: life history (a), trophic type (b), feeding strategy (c) and size class (d) of the zooplankton communities *per* sector, month and year.
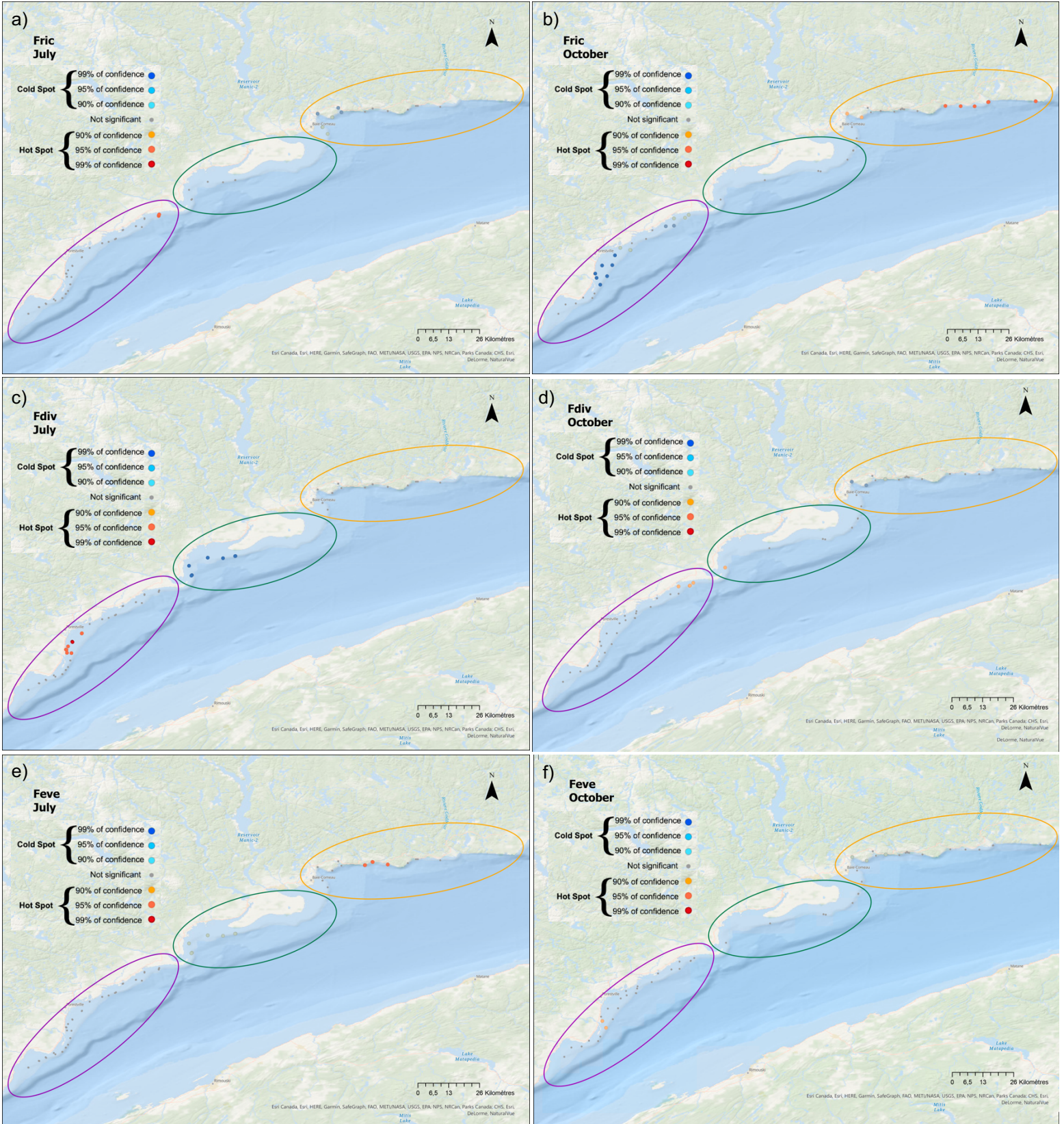
Fig. 14. Hotspot maps in July and October of functional richness (a, b), functional divergence (c, d) and functional evenness (e, f).

3.3.3 Trait-environment interaction

Functional diversity was influenced by different environmental factors in different ways (Fig. 12e, f, g). FRic was positively correlated with temperature within the range of 7.4 to 17.7 °C with an optimal point of 12.12 °C and then was negatively correlated below and over this range (Fig 12e). FRic was also positively correlated with chl *a* concentration up to a plateau of 29.9 mg.m^{-3} (Fig. 12e). FDiv was positively influenced by temperature and Chl *a* (Fig. 12f). Feve was positively influenced by salinity (Fig. 12g). Predictability of the correlations was reliable for Fric and Fdiv (deviance explained = 37.7 % and 34.9 % respectively), but not for Feve (deviance explained 10 %) (Table 3).

DISCUSSION

The zooplankton community of the coastal zone of the Lower St. Lawrence estuary (LSLE) is characterized by a strong spatio-temporal variation among the three sectors and across the three years investigated, showing varying zooplankton composition and taxonomic and functional diversities. Zooplankton abundance, composition and diversity are mostly driven by temperature and chl *a,* while salinity plays a minor role in structuring the communities. Spatial distribution of hotspots and coldspots differed between taxonomic and functional diversities. Thus, using functional traits adds complementary information to the characterization of zooplankton structure.

Environmental conditions

The present study is the first to document zooplankton communities in the coastal zone less than 35 m depth of the LSLE, as previous studies and the Atlantic Zone Monitoring Program concentrate their efforts on deeper pelagic areas (Laurentian Channel) of the LSLE (*e.g.* Runge and Simard, 1990; Plourde et *al*., 2002; Blais et *al*., 2021). Unlike the coastal zone, the deep zone of LSLE is characterized by three distinct layers in summer and autumn (Galbraith et *al*., 2019), inducing a stratification that can constitute a physical barrier for primary production and zooplankton vertical migration (Plourde et *al*., 2002). However, in the same way as the deep zone of LSLE, our coastal zone is characterized by strong seasonality of environmental conditions, which is highly dependent on the condition of ice-cover during winter but showing higher temperatures compared to the Laurentian Channel in summer (Blais et *al*., 2018; Galbraith et *al*., 2019). Water temperatures are higher in coastal environments, related to the shallow depth which is strongly dependent on air temperatures (Galbraith et *al*., 2019) and wind-related surface currents (El Sabh, 1979). Coastal waters were less salty in July than in October, due to the freshet, especially in Manicouagan and Forestville, where river runoffs bring more freshwater into the coastal zone in spring, as it has been also observed in the Romaine River in the northern coast of the gulf of the St. Lawrence (Senneville et *al*., 2018). Therefore, these rivers indirectly influence coastal

zooplankton communities and could help explaining differences between zooplankton composition, abundance and diversities among sectors.

Taxonomic and functional zooplankton diversities

Along the coastal zone, differences in spatial distribution patterns of hotspots and coldspots of taxonomic and functional diversities are revealed, depending on the sector and the month. Occurrences of hotspots of species richness, functional richness and functional evenness, varied spatially among the three sectors in the two different months, suggesting that this variability in diversity might be related to varying environmental conditions. Pomerleau et *al*. (2015) argue that abiotic factors could play a role in the expression of taxonomic and functional richness, either through direct effects on species or indirect effects *via* responses reflected in functional traits. As functional evenness (FEve), that measures the even spread of function in a community niche space (Mason et *al*., 2008), might be high, when for example species are using complementary resources (Becker et *al*., 2021), so that seasonal and spatial variations of resources would then modulate the location of FEve hotspots. In contrast, the hotspots of more complex diversity indices, the Shannon-Wiener, Pielou evenness and functional divergence (FDiv), occurred in the same sector in both months, therefore showing some seasonal stability. This could be related to a buffering effect to variability of environmental conditions, due to the calculation including the number of species and the relative abundance and for FDiv the abundance-weighted functional differences among species (Mason et *al*., 2008).

Comparative indices of taxonomic and functional diversities showed a difference in their distribution of hotspots and coldspots. In the two months investigated, hotspots of the Shannon-Wiener index occurred in Baie-Comeau while hotspots of functional divergence were found in Forestville. As functional divergence relates to how the species abundance are distributed in functional trait space (Villeger et *al*., 2008), hotspots in the sector of Forestville, indicate that few but highly abundant species showed a wide range of functional traits. Therefore, hotspots in the Forestville sector are likely to have a high degree of niche differentiation, and thus might show low resource competition with a more efficient use of

resources by zooplankton communities (Mason et *al*., 2005). Overall, despite the low Shannon-Wiener index, and due to high functional divergence, the Forestville sector would be expected to be resistant to disturbance or perturbation. Indeed, marine ecosystem stability could be promoted either by high biodiversity (taxonomic) as seen in benthic ecosystems (Beaugrand, 2014) and/or by a high number of different functions, as found in coral reef ecosystems (Monaco et Prouzet, 2015). Documenting functional diversity as a complement to taxonomic diversity provides additional information on the variation in ecosystem functions, that the regular studies which considering only taxonomic diversity indices alone could not. Then, using the complementarity of both types of diversities enable an integrative and comprehensive view of functionality/ecological perspective of the communities under study.

Zooplankton composition

Zooplankton species in the coastal zone of the LSLE are comparable to the ones found in deeper habitats of the LSLE in previous studies (Harvey and Devine, 2009, Blais et *al*., 2018, Plourde et *al*., 2002), but proportions, abundances and timing of occurrence of this species are different in the present study. Indeed, Copepoda is one of the most abundant groups found in our study and in the deeper zones of the LSLE, independent of the month. The small cyclopoid *Oithona similis* is one of the most abundant species in the LSLE in general, but in contrast to abundance peak in July in the present study, they occurred in higher numbers in fall in the deeper habitats (Plourde et *al*., 2002 and Savenkoff et *al*., 2017). Furthermore, large copepods, such as *Calanus finmarchicus* and *Calanus hyperboreus* are not highly represented in the coastal zone in contrast to the deeper habitats of the LSLE (Plourde et *al*., 2002; Harvey and Devine, 2009; Blais et *al*, 2018). Plourde et *al*. (2002) argue that small species as *Oithona* spp. and *Acartia* spp. are surface species*,* whereas bigger species such as *Calanus* spp. remain in deeper layers to avoid predators during the day, doing dial vertical migration. Then, small species are more susceptible to be advected with surface currents than *Calanus* spp. and might aggregate in coastal retention areas. (Savenkoff et *al*.,

2017). This might explain the lower abundance of *Calanus* spp. in the shallow coastal zone compared to the deeper LSLE.

The timing of meroplankton occurrence in the present study is in accordance with Harvey and Devine (2009) who found a higher abundance of meroplankton, and especially of Bivalvia, in June than in November in the middle of the LSLE. However, abundances of meroplankton are more than three times higher in the coastal zone than in the deeper habitats of the LSLE (mean 33 850 ind m^{-2} in July in the coastal zone versus 5 000 ind m^{-2} or 10 000 ind m^{-2} max. in June 2007 in deep LSLE). This might be explained by the hydrodynamics of the LSLE, including wind which is as an important factor on dispersion or aggregation of meroplankton in coastal areas. Indeed, zooplankton distribution is directly influenced by physical processes, such as wind and tides which is the major component in coastal area that influence the surface layer (Archambault et *al*., 1998; Campos et *al*., 2017; Senneville et *al*., 2018) in contrast to the deeper zone. However, wind direction and speed were not measured during our study, neither currents, which could be taken into consideration for future studies, in order to define the dispersal and origin of zooplankton communities. Furthermore, the benthic community characteristics such as adult abundance and density of recruits in the coastal area, could be a potential source of meroplankton organisms in our shallow study area (Archambault and Bourget, 1999; Titelman, 2004, Pineda-Metz et *al*., 2021).

Environmental influence on the variability of zooplankton communities

Temperature, salinity and Chl *a* are the most influencing factors, explaining the variability of the zooplankton communities in the coastal zone of LSLE. Zooplankton species are poikilotherms and thus highly dependent on the temperature of their environment (Castellani and Edwards, 2017) that modulate key biological processes, such as growth and reproduction. Meroplankton is more abundant in July when higher temperatures occurred than in October, matching with the reproduction timing of benthic species, as in the GSL, the Arctic and the Baltic Sea (Aucoin et *al*., 2004; Schulz et *al*., 2012; Deblois 2022; Soreide et *al*., 2022). Higher temperature in July 2020 induced a difference in zooplankton community composition and higher proportion of abundance of meroplankton, mainly composed of

Bivalvia veliger, compared to other years. Meroplankton is favored by rising surface temperatures, increasing larval survival (Strand et *al*., 2020) as seen for some bivalve species in the North Sea (Kirby et *al*., 2008). However, the positive effect of the temperature on *Mytilus edulis* was tangible up to a temperature threshold of 20 °C in Iles-de-la-Madeleine archipelago of the GSL (Guillou et *al*., 2023) which was not reached in the studied zone. Furthermore, it has been shown that the reproduction of bivalve species in Iles-de-la-Madeleine archipelago peaks in June and July (Aucoin et *al*., 2004). As we sampled only one week in July each year, we could have missed the reproduction peak in 2019 and 2021, potentially explaining why meroplankton was found in lower proportions than in 2020.

Chl *a* concentration is a proxy of phytoplankton biomass, the food source for herbivorous and omnivorous species (Dufour et *al.*, 2010). In the present study, Chl *a* concentrations in the coastal zone are higher in October than in July. These results differ from those obtained from observations of phytoplankton dynamics in the deeper zones of the LSLE, which are characterized by two typical blooms, with the first bloom of the year in late spring more important than the second one in autumn *(*Savenkoff et *al*., 2017). This difference could be explained by the concentration of nutrients, the principal variable of phytoplankton growth, which was found higher in autumn than in summer in the coastal zone. Upwelling induced by the frequency of storms, or by high amplitude of tides which are more frequent in autumn, can induced this difference in nutrient concentrations between months in the coastal area (Blais et *al*., 2018). Furthermore, phytoplankton growth is limited by environmental conditions induced by the freshet in spring (Sinclair et *al*., 1981). However, Chl *a* is positively correlated to total zooplankton abundance (GAMs), which seem in accordance with the assumption that a greater food availability promotes individual survival and hatching (Dudeck et *al*., 2021). Regarding the functional traits of trophic type, the proportion of herbivorous were higher in July than in October, despite generally low chl *a* concentrations in July. However, some omnivorous taxa consume phytoplankton as well, such as Appendicularia occuring in higher proportion of abundance in October than in July in 2019 and 2020, and thus may be linked to the phytoplankton bloom in October.

Low concentrations of chl *a* in July, might also be due to high grazing pressure by zooplankton in high abundance, and we might have sampled during the part of the plankton succession when phytoplankton concentration was consumed and zooplankton abundance is still high (Winder and Varpe, 2020). Differently, this might be due to the sampling time in July, missing the first bloom, so that Chl *a* concentrations in October were higher than in July, as similarly observed in the Mingan Channel by Deblois et *al*. (2022).

Nevertheless, in July 2021, the zooplankton composition was correlated with the high Chl *a* concentration in the sector of Forestville. However, the proportion of abundance of herbivorous in Forestville during July 2021 was not the highest found compared to other sectors and years. This might be explained by the fact that not all phytoplankton taxa are available for consumption and that some zooplankton species select a certain type of phytoplanktonic species and/or size (Braghin et *al*., 2019; Sodre and Bozelli 2019). As we did not determine the phytoplankton species composition, interpretation in this line of argumentation is limited in the present study. Alternatively, we might have sampled during the succession when phytoplankton is well proliferating but herbivorous species are not yet at their peak abundance.

Different studies in estuarine environments showed that salinity was the principal factor that influence the zooplankton communities (Helenius et *al*., 2017; Labuce et *al*., 2021), in particular in the St. Lawrence Estuary (Simard and Runge, 1990; Laprise and Dodson 1994; Winkler et *al*. 2003; Anderson, 2022). However, in the present study, placed in the north coast of the LSLE, covered a very restricted salinity range, between 23 and 31 PSU, salinity do not show to significantly affect total abundance and diversities in the coastal area. However, salinity influenced zooplankton species composition of different sectors, potentially through their osmotic tolerance (Laprise and Dodson, 1994). This is for example likely the case for two copepod species in particular, *Acartia longiremis* and *Oithona similis,* which are the most abundant species in the present study. These two species are in same taxonomic group (Copepoda), but from different orders (Calanoida and Cyclopoida) and

express the same functional traits (feeding type, feeding strategy, size class and life history), but they did not show the same spatial distribution patterns which might be related to differences in tolerance to abiotic factors. Indeed, *A. longiremis* is more abundant in Forestville and *O. similis* in Baie-Comeau for both seasons. In general, the Baie-Comeau sector was less influenced by freshwater rivers along the coast, so that salinity was less variable and mostly higher than in the sector Forestville. *Oithona similis* is an euryhaline and eurythermal species that favors high salinities (Schulz *et al.*, 2012), but have low tolerance to low salinities and low temperature (Ward and Hirst, 2007; Teodosio and Barbosa, 2021). On the contrary, *A. longiremis* is a true euryhaline species and can tolerate low salinities but is oligothermal and avoid warm surface layers (Schulz et *al.*, 2012). This suggests that the spatial distribution seen in the coastal zone might be linked to salinity for *O. similis* and to temperature for *A. longiremis*. Unfortunately, the lack of environmental tolerance data of the species found in the LSLE, does not allow us to test environmental tolerances as a functional trait. Indeed, these traits have been shown to be important for the understanding zooplankton distribution (Costello et *al.*, 2015; Martini et *al.*, 2020) and then might, for example, explain difference in distribution between these two copepod species.

CONCLUSION

Our study constitutes the first baseline of zooplankton coastal communities of the LSLE. The zooplankton dynamics showed to vary spatiotemporally among the three sectors studied, in abundance, composition and diversities between the two seasons, showing a higher abundance in July than in October. Using both types of diversity, taxonomic and functional, highlights that even if an area is not considered as "diverse" with taxonomic diversity indices, the functionality might be strong and therefore the area should be, for example, considered in protection and management plans.

Environmental factors, mainly temperature, were the main drivers that influence zooplankton abundance. These results highlight that in the context of climate change, and the expected

rising sea surface temperature, zooplankton composition and dynamic could be directly impacted. Thus, further long-term survey is needed for a better understanding the dynamics of the zooplankton communities, including more environmental parameters, seasons, trophic interactions and functional traits.

SUPPLEMENTARY MATERIAL

Table S1. Taxa identified with stages and their functional traits associated.

Subphyllum	ORDER/CLASS	Taxa	Stade	Life cycle	Size Class	Reference	TrophicType	Reference	Feeding stategy	Reference
ANNELIDA	ANNELIDA	Polychaeta	larva	MERO	4	[22]	Herbivore	[2]	Feeding current	[14]
CHAETOGNATHA	CHAETOGNATHA	Chaetognatha	unit	HOLO	7	[2]	Carnivore	[8]	Active ambush	[2]
CHORDATA	TELEOSTEI	Ichthyoplankton	larva	MERO	6	[22]	Carnivore	[2]	Active ambush	[2]
CNIDARIA	CNIDARIA	Cnidaria	unit	HOLO	7	[2]	Carnivore	[2]	Passive ambush	[16]
CNIDARIA	LEPTOTHECATA	*Obelia* sp.	unit	MERO	4	[2]	Carnivore	[2]	Passive ambush	[16]
CNIDARIA	SCYPHOZOA	*Aurelia aurita*	unit	HOLO	7	[2]	Omnivore	[4]	Passive ambush	[4]
CNIDARIA	TRACHYMEDUSAE	*Aglantha digitale*	unit	HOLO	7	[2]	Carnivore	[8]	Passive ambush	[16]
CRUSTACEA	AMPHIPODA	Amphipoda Caprellidae	unit	MERO	5	[2]	Omnivore	[10]	Mixed	[17]
CRUSTACEA	AMPHIPODA	Amphipoda Gammaridae	unit	MERO	7	[2]	Omnivore	[2]	Cruise feeder	[2]
CRUSTACEA	AMPHIPODA	Amphipoda Hyperiidae	unit	MERO	7	[2]	Omnivore	[2]	Active ambush	[2]
CRUSTACEA	CIRRIPEDIA	Cirripedia	nauplii	MERO	1	[2]	Carnivore	[2]	Feeding current	[2]
CRUSTACEA	CIRRIPEDIA	Cirripedia (cypris larva)	cyprid	MERO	3	[2]	Non-feeding	[2]	Non-feeding	[2]
CRUSTACEA	COPEPODA	*Acartia longiremis*	C1-C6	HOLO	3	[3]	Omnivore	[3]	Active ambush	[3]
CRUSTACEA	COPEPODA	Aetideidae	C1-C6	HOLO	5	[2]	Carnivore	[8]	Active ambush	[1]
CRUSTACEA	COPEPODA	*Anomalocera patersonii*	C1-C6	HOLO	5	[4]	Omnivore	[4]	Cruise feeder	[1]
CRUSTACEA	COPEPODA	*Calanus finmarchicus*	C1-C6	HOLO	5	[2]	Herbivore	[4]	Feeding current	[18]
CRUSTACEA	COPEPODA	*Calanus finmarchicus/glacialis*	C1-C6	HOLO	5	[5]	Herbivore	[4]	Feeding current	[19]
CRUSTACEA	COPEPODA	*Calanus glacialis*	C1-C6	HOLO	5	[2]	Herbivore	[4]	Feeding current	[19]
CRUSTACEA	COPEPODA	*Calanus glacialis/hyperboreus*	C1-C6	HOLO	5	[5]	Herbivore	[4]	Feeding current	[19]
CRUSTACEA	COPEPODA	*Calanus hyperboreus*	C1-C6	HOLO	6	[2]	Herbivore	[4]	Feeding current	[19]
CRUSTACEA	COPEPODA	*Calanus* spp.	C1-C6	HOLO	6	[2]	Herbivore	[8]	Feeding current	[19]
CRUSTACEA	COPEPODA	*Centropages hamatus*	C1-C6	HOLO	3	[2]	Omnivore	[1]	Mixed	[1]
CRUSTACEA	COPEPODA	*Eurytemora herdmani*	C1-C6	HOLO	3	[5]	Herbivore	[4]	Cruise feeder	[19]; [20]
CRUSTACEA	COPEPODA	*Metridia longa*	C1-C6	HOLO	5	[2]	Omnivore	[11]	Cruise feeder	[11]
CRUSTACEA	COPEPODA	*Metridia lucens*	C1-C6	HOLO	5	[2]	Omnivore	[2]	Cruise feeder	[11]
CRUSTACEA	COPEPODA	*Metridia* sp.	C1-C6	HOLO	5	[2]	Omnivore	[2]	Cruise feeder	[11]
CRUSTACEA	COPEPODA	*Microcalanus* spp.	C1-C6	HOLO	2	[2]	Omnivore	[1]	Feeding current	[1]
CRUSTACEA	COPEPODA	*Microsetella norvegica*	C1-C6	HOLO	1	[1]	Omnivore	[1]	Cruise feeder	[1]
CRUSTACEA	COPEPODA	*Microsetella* sp.	C1-C6	HOLO	2	[2]	Omnivore	[1]	Cruise feeder	[1]
CRUSTACEA	COPEPODA	*Oithona atlantica*	C1-C6	HOLO	3	[1]	Omnivore	[1]	Active ambush	[1]
CRUSTACEA	COPEPODA	*Oithona similis*	C1-C6	HOLO	2	[1]	Omnivore	[1]	Active ambush	[1]
CRUSTACEA	COPEPODA	*Paraeuchaeta norvegica*	C1-C6	HOLO	6	[2]	Carnivore	[2]	Active ambush	[3]
CRUSTACEA	COPEPODA	*Pseudocalanus* spp.	C1-C6	HOLO	4	[2]	Herbivore	[1]	Feeding current	[1]
CRUSTACEA	COPEPODA	*Scolecithricella minor*	C1-C6	HOLO	3	[2]	Omnivore	[12]	Feeding current	[12]
CRUSTACEA	COPEPODA	*Temora longicornis*	C1-C6	HOLO	3	[2]	Herbivore	[4]	Cruise feeder	[1]; [16]
CRUSTACEA	COPEPODA	*Tortanus discaudatus*	C1-C6	HOLO	3	[2]	Carnivore	[13]	Cruise feeder	[19]
CRUSTACEA	COPEPODA	*Triconia borealis*	C1-C6	HOLO	2	[2]	Omnivore	[1]	Cruise feeder	[16]
CRUSTACEA	COPEPODA	*Triconia* spp.	C1-C6	HOLO	2	[2]	Detritivore	[2]	Cruise feeder	[16]
CRUSTACEA	DECAPODA	Brachyura	larva	MERO	5	[2]	Omnivore	[2]	Active ambush	[21]
CRUSTACEA	DECAPODA	Decapoda	larva	MERO	4	[2]	Omnivore	[2]	Active ambush	[21]
CRUSTACEA	DIPLOSTRACA	*Bosmina* sp.	unit	HOLO	2	[2]	Omnivore	[2]	Active ambush	[2]
CRUSTACEA	DIPLOSTRACA	*Daphnia hyalina*	unit	HOLO	3	[23]	Herbivore	[15]	Active ambush	[2]
CRUSTACEA	DIPLOSTRACA	*Evadne* sp.	unit	HOLO	2	[2]	Carnivore	[2]	Active ambush	[2]
CRUSTACEA	DIPLOSTRACA	*Podon* sp.	unit	HOLO	2	[2]	Carnivore	[2]	Active ambush	[2]
CRUSTACEA	EUPHAUSIACEA	Euphausiidae	calyptopis	HOLO	4	[6]	Omnivore	[8]	Feeding current	[2]
CRUSTACEA	EUPHAUSIACEA	Euphausiidae	furcilia	HOLO	5	[22]	Omnivore	[8]	Feeding current	[2]
CRUSTACEA	EUPHAUSIACEA	Euphausiidae	metanauplius	HOLO	1	[6]; [7]	Omnivore	[8]	Feeding current	[2]
CRUSTACEA	EUPHAUSIACEA	Euphausiidae	nauplius	HOLO	1	[6]; [7]	Omnivore	[8]	Feeding current	[2]
CRUSTACEA	EUPHAUSIACEA	*Meganyctiphanes norvegica*	adult	HOLO	7	[6]; [7]	Omnivore	[2]	Cruise feeder	[2]
CRUSTACEA	EUPHAUSIACEA	*Thysanoessa raschii*	adult	HOLO	7	[2]	Omnivore	[2]	Cruise feeder	[2]

Table S1 (continued). All taxa, stages identified and their functional traits

CRUSTACEA	OSTRACODA	Ostracoda	unit	HOLO	5	[2]	Detritivore	[2]	Passive ambush	[2]
CRUSTACEA	THECOSTRACA	Facetotecta	unit	MERO	2	[2]	Carnivore	[2]	Feeding current	[2]
ECHINODERMATA	ECHINODERMATA	Echinodermata	larva	MERO	5	[2]	Herbivore	[2]	Feeding current	[14]
MOLLUSCA	GASTROPODA	Gastropoda	unit	MERO	5	[2]	Omnivore	[8]	Feeding current	[14]
MOLLUSCA	MOLLUSCA	Bivalvia	unit	MERO	1	[22]	Omnivore	[8]	Feeding current	[14]
MOLLUSCA	PTEROPODA	*Clione* sp.	unit	HOLO	6	[2]	Carnivore	[2]	Active ambush	[2]
TUNICATA	APPENDICULARIA	Appendicularia	unit	HOLO	6	[2]	Herbivore	[8]	Feeding current	[2]
TUNICATA	APPENDICULARIA	*Fritillaria* spp.	unit	HOLO	4	[2]	Omnivore	[3]	Feeding current	[3]
TUNICATA	APPENDICULARIA	*Oikopleura* spp.	unit	HOLO	4	[2]	Omnivore	[3]	Feeding current	[3]

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Table S2. Biomass data were calculated based on sizes and specialized literature. Copepod species formula are used for copepodite stages. Taxa with different specific stages are specified in bracket.

Taxon	Formule	Reference
Acartia longiremis	(1.023*10^(-8)*(LP*1000)^2.906)/1000	Hopcroft et *al.,* 2010
Acartia spp.	(1.11*10^-11)*(LP*1000)^2.92	Hopcroft et *al.,* 2010
Aglantha digitale	10^((LOG10(0.00194*(L)^3.05)-0.499)/0.991)	Hopcroft et *al.,* 2010; conversion Moriarty and O'Brien, 2013
Amphipoda Gammaridae	(10^((LOG10(1.592924*L^3.94344)-0.499)/0.991))	Martins et *al.*, 2002; conversion Moriarty and O'Brien, 2013
Amphipoda Hyperiidae	(10^((LOG10(0.049*(L^2.957)/1000)-0.499)/0.991))	Hopcroft et *al.,* 2005; conversion Moriarty and O'Brien, 2013
Appendicularia	10^(((3.21*LOG10(TL*1000)-9.11)-0.499)/0.991)/1000	Hopcroft et *al.,* 2005, conversion Moriarty and O'Brien, 2013
Aurelia aurita	10^((LOG10(0.00194*(D90)^3.05)-0.499)/0.991)	Hopcroft et *al* ., 2010; conversion Moriarty and O'Brien, 2013
Bivalvia	3.06*10^-8*(L*100)^2.88	Fotel et *al.,* 1999
Bosmina sp.	(10^((LOG10(2.7114+2.5294*(LOG10(D21))d)-0.499)/0.991))	Mason et *al.,* 1991
Brachyura (zoea larva)	(10^((LOG10(L)-0.499)/0.991))/1000	Uye 1982; conversion Moriarty and O'Brien, 2013
Calanus finmarchicus	0.0048*(PL^3.5687)	Senneville et *al.,* 2018
Calanus finmarchicus/glacialis	0.0048*(PL^3.5687)	Senneville et *al.,* 2018
Calanus glacialis	0.0048*(PL^3.5687)	Senneville et *al.,* 2018
Calanus glacialis/hyperboreus	0.0048*(PL^3.5687)	Senneville et *al.,* 2018
Calanus hyperboreus	0.0014*PL^3.3899	Senneville et *al.,* 2018
Centropages hamatus	(0.0281*PL^3)*0.447	Cohen and Lough, 1981
Centropages spp.	(0.0281*PL^3)*0.447	Cohen and Lough, 1981
Chaetognatha	10^((LOG10(0.000064*(L^3.3))-0.499)/0.991)	Hopcroft et *al.,* 2005, conversion Moriarty and O'Brien, 2013
Cirripedia (cypris larva)	0.011	Arendt et *al.,* 2013
Cirripedia (nauplius)	(10^((LOG10(L)-0.499)/0.991))/1000	Uye 1982; conversion Moriarty and O'Brien, 2013
Clione sp.	10^((LOG10(0.039*(L^3.5032))-0.41)/0.963)	Hopcroft et al., 2005 (*Limacina helicina*)
Cnidaria	10^((LOG10(0.00194*(L)^3.05)-0.499)/0.991)	Hopcroft et al., 2010; conversion Moriarty and O'Brien, 2013
Copepoda Harpacticoida	(EXP(1.15*LN(TL*1000)-7.79)/1000)	Satapoomin, 1999
Decapoda (larva)		Uye, 1982
Echinodermata	10^(((LOG10(L)-0.499)/0.991))	Wasson and Watts, 2001; conversion Moriarty and O'Brien, 2013
Euphausiidae (calyptopis larva)	10^(((LOG10(0.05)-0.499)/0.991))	Hopcroft et al., 2010; conversion Moriarty and O'Brien, 2013
Euphausiidae (furcilia larva)	10^(((LOG10(7.56)-0.499)/0.991))	Pond et *al* ., 2012; conversion Moriarty and O'Brien, 2013
Euphausiidae (metanauplius)	0.04	Teglhus et al, 2015
Euphausiidae (nauplius)	10^(((LOG10(0.003)-0.499)/0.991))	Hopcroft et al., 2010; conversion Moriarty and O'Brien, 2013
Eurytemora affinis	10^(2.088*(PL/1000)-0.859)*0.447	Hopcroft et al., 2010
Eurytemora herdmani	(10^(2.96*LOG10(PL)-7.6/1000))*0.447	Hopcroft et al., 2010
Eurytemora spp.	(10^(2.96*LOG10(PL)-7.6/1000))*0.447	Burkill and Kendall, 1982
Evadne sp.	0.0017	Walve and Larsson, 1999
Fritillaria spp.	10^(((3.21*LOG10(TL*1000)-9.11)-0.499)/0.991)/1000	Hopcroft 2005, conversion Moriarty and O'Brien 2013
Gastropoda	((6.07*((L*1000)*10^-6)^2.59)*10^8)*0.221)/1000	Robert et al., 2008
Ichtyoplancton (larva)	(10^((4.09*LOG10(O41*1000/1000)-1.114)/1000))*0.447	Laurence, 1979; Legendre and Michaud, 1998
Meganyctiphanes norvegica	2.415285711	Pond et *al.,* 2012; conversion Moriarty and O'Brien, 2013
Metridia longa	0.00605*PL^3.0167	Senneville et *al.,* 2018
Metridia lucens	0.00605*PL^3.0167	Senneville et *al.,* 2018
Metridia sp.	0.00605*PL^3.0167	Senneville et *al.,* 2018
Microcalanus spp.	9.47*10^-10*(PL*1000)^2.16	Thor et *al.,* 2005
Microsetella norvegica	(EXP(1.15*LN(TL*1000)-7.79)/1000)	Satapoomin, 1999
Microsetella spp.	(2.65*10^(-6)*TL^1.95)/1000	Uye et *al.,* 2002
Obelia sp.	10^((LOG10(0.025)-0.499)/0.991)	Hopcroft et al., 2010; conversion Moriarty and O'Brien, 2013
Oikopleura spp.	(10^(4.59*LOG10(D182)^3.2))/1000	Deibel, 1986
Oithona atlantica	0.016*PL^2.213	Cohen and Lough, 1981
Oithona similis	(9.4676*10^(-10)*(PL*1000)^2.16)	Thor et *al.,* 2005
Oncaea spp.	2.51*10^(-11)*(PL*1000)^2.9	Senneville et *al.,* 2018

Ostracoda	10^((LOG10((0.0228*TL^2.3698))-0.41)/0.963)	Hopcroft et *al.,* 2010; conversion Moriarty and O'Brien, 2013
Paraeuchaeta norvegica	10^((LOG10(0.0075 *LP^3.274)-0.41)/0.963)	Hopcroft et *al.,* 2010; conversion Moriarty and O'Brien, 2013
Podon sp.	0.0017	Walve et Larsson, 1999
Polychaeta	(10^((LOG10(11.3)-0.499)/0.991))/1000	Uye 1982, conversion Moriarty and O'Brien, 2013
Pseudocalanus spp.	6.12^(-11)*(PL*1000)^2.7302	Thor et *al.,* 2005
Scolecithricella minor	0.0077*TL^2.33	Dumont et *al.,* 1975
Temora longicornis	(((10^(2.2357*LOG10(PL*1000)-5.5458))/1000) +((10^(2.2357*LOG10(PL*1000)-5.5458))/1000)*0.07)*0.447	Hay et *al.,* 1991; Mauchline, 1998
Temora spp.	(((10^(2.2357*LOG10(PL*1000)-5.5458))/1000) +((10^(2.2357*LOG10(PL*1000)-5.5458))/1000)*0.07)*0.447	Hay et *al.,* 1991; Mauchline, 1998
Thysanoessa raschii	0.058704534	Pond et *al.,* 2012, conversion Moriarty and O'Brien, 2013
Tortanus discaudatus	((10^(2.61*(LOG10(TL*1000))-6.8))/1000)	Uye, 1982 (*Tortanus forcipatus*)
Triconia borealis	2.51*10^(-11)*(PL*1000)^2.9	Senneville et *al.,* 2018
Triconia spp.	2.51*10^(-11)*(PL*1000)^2.9	Senneville et *al.,* 2018

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Table S3. Summary of the model selection with ΔAIC for GAM analysis. The symbol "+" indicates the selection of the smoothed variable for the model.

Species richness	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	18.02			+	**5**	**-289.556**	**590.7**	**0**	**0.264**
	18.02	+		+	5	-289.556	590.7	0	0.264
	18.02	+	+	+	6	-289.466	591	0.23	0.236
	18.02		+	+	6	-289.465	591	0.23	0.236
	18.02				2	-302.097	608.2	17.47	0
	18.02	+			2	-302.097	608.2	17.47	0
	18.02	+	+		2	-302.097	608.2	17.47	0
	18.02		+		2	-302.097	608.2	17.47	0
Shannon-Wiener	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	1.566	+	+	+	**7**	**-55.697**	**126.1**	**0**	**0.431**
	1.566	+		+	6	-56.696	126.5	0.42	0.349
	1.566		+	+	6	-58.103	129.6	3.52	0.074
	1.566			+	5	-59.447	130.5	4.37	0.048
	1.566	+			3	-61.304	130.5	4.41	0.047
	1.566	+	+		3	-61.304	130.5	4.41	0.047
	1.566				2	-66.983	138	11.88	0.001
	1.566		+		2	-66.983	138	11.88	0.001
Pielou evenness	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	0.5414	+			**4**	**81.551**	**-154.8**	**0**	**0.217**
	0.5414	+	+		4	81.551	-154.8	0	0.217
	0.5414	+		+	5	82.982	-154.6	0.26	0.191
	0.5414	+	+	+	5	82.983	-154.6	0.26	0.191
	0.5414		+	+	7	83.835	-153.3	1.56	0.099
	0.5414			+	6	82.826	-152.8	1.99	0.08
	0.5414				2	74.682	-145.4	9.48	0.002
	0.5414		+		2	74.682	-145.4	9.48	0.002
FRic	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	0.5688	+		+	**7**	**78.994**	**-142.8**	**0**	**0.462**
	0.5688	+	+	+	7	78.994	-142.8	0	0.462
	0.5688			+	5	73.983	-137.8	4.98	0.038
	0.5688		+	+	5	73.983	-137.8	4.98	0.038
	0.5688	+	+		6	59.111	-105.7	37.1	0
	0.5688		+		4	57.056	-105.2	37.61	0
	0.5688				2	49.905	-95.8	47.01	0
	0.5688	+			2	50.246	-95.3	47.49	0
FDiv	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	0.763	+		+	**7**	**79.915**	**-145.2**	**0**	**0.462**
	0.763	+	+	+	7	79.915	-145.2	0	0.462
	0.763			+	4	74.878	-140.2	5.02	0.038
	0.763		+	+	4	74.878	-140.2	5.02	0.038
	0.763	+	+		8	75.596	-133.9	11.36	0.002
	0.763	+			5	65.487	-119.2	26.02	0
	0.763		+		4	63.488	-118.2	27.01	0
	0.763				2	53.528	-103.1	42.19	0
FEve	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	0.3668		+		**2**	**143.986**	**-282**	**0**	**0.273**
	0.3668		+	+	2	143.986	-282	0	0.272
	0.3668	+	+	+	4	144.762	-281.4	0.54	0.209
	0.3668	+	+		4	144.762	-281.4	0.54	0.209
	0.3668			+	2	141.257	-276.6	5.42	0.018
	0.3668	+		+	4	142.035	-276	6.01	0.013
	0.3668	+			3	140.315	-273.5	8.51	0.004
	0.3668				2	138.282	-272.6	9.42	0.002
Total Abundance	(Int)	s(Chla)	s(Salinity)	s(Temperature)	df	logLik	AIC	delta	weight
	5540	+		+	**7**	**-1226.167**	**2467.4**	**0**	**0.6**
	5540	+	+	+	9	-1224.965	2468.3	0.89	0.385
	5540	+	+		7	-1229.943	2475.3	7.9	0.012
	5540	+			4	-1233.883	2477.6	10.18	0.004
	5540			+	4	-1256.518	2521.1	53.73	0
	5540		+	+	5	-1255.473	2521.2	53.85	0
	5540				2	-1259.324	2522.6	55.27	0
	5540		+		2	-1259.323	2522.7	55.27	0

Table S4. Summary of permutational multivariate analysis of variance (PERMANOVA) results of environmental parameter, taxonomic indices, functional indices, abundance and biomass per Year*Month*Sector.

Temperature	Df	SumOfSqs	R²	F	Pr(>F)	
Year	2	611.41	0.31313	128.0289	0.001	***
Month	1	383.5	0.19641	160.6097	0.001	***
Sector	2	84.3	0.04318	17.6534	0.001	***
Year : Month	2	579.08	0.29657	121.2594	0.001	***
Year : Sector	4	14.97	0.00767	1.5672	0.19	
Month : Sector	2	16.16	0.00828	3.3844	0.032	*
Year : Month : Sector	2	10.04	0.00514	2.1031	0.125	
Residual	106	253.1	0.12963			
Total	121	1952.57	1			

Salinity	Df	SumOfSqs	R²	F	Pr(>F)	
Year	2	32.83	0.08539	21.4977	0.001	***
Month	1	173.79	0.45205	227.6162	0.001	***
Sector	2	49.81	0.12955	32.6155	0.001	***
Year : Month	2	15.69	0.04082	10.2771	0.001	***
Year : Sector	4	19.34	0.0503	6.3322	0.001	***
Month : Sector	2	10.47	0.02723	6.8551	0.004	**
Year : Month : Sector	2	1.59	0.00414	1.0422	0.379	
Residual	106	80.94	0.21052			
Total	121	384.46	1			

Chl a	Df	SumOfSqs	R²	F	Pr(>F)	
Year	2	196.54	0.12455	11.0339	0.001	***
Month	1	5.73	0.00363	0.643	0.429	
Sector	2	66.63	0.04223	3.741	0.024	*
Year : Month	2	148.1	0.09386	8.3147	0.004	**
Year : Sector	4	209.61	0.13284	5.8839	0.007	**
Month : Sector	2	6.55	0.00415	0.3676	0.646	
Year : Month : Sector	2	0.76	0.00048	0.0428	0.949	
Residual	106	944.03	0.59827			
Total	121	1577.95	1			

O₂	Df	SumOfSqs	R²	F	Pr(>F)	
Year	2	24905	0.15347	10.854	0.001	***
Month	1	5600	0.03451	4.881	0.041	*
Sector	2	9049	0.05576	3.9436	0.026	*
Year : Month	2	14078	0.08676	6.1355	0.01	**
Year : Sector	3	688	0.00424	0.1998	0.889	
Month : Sector	2	4270	0.02631	1.861	0.177	
Year : Month : Sector	2	14197	0.08749	6.1874	0.02	*
Residual	78	89486	0.55146			
Total	92	162272	1			

NO₃ / NO₂	Df	SumOfSqs	R²	F	Pr(>F)	
Year	2	101.21	0.1714	65.4908	0.001	***
Month	1	192.06	0.32525	248.5509	0.001	***
Sector	2	20.48	0.03468	13.2505	0.001	***
Year : Month	1	128.88	0.21826	166.7917	0.001	***
Year : Sector	3	70.02	0.11857	30.204	0.001	***
Month : Sector	2	20.5	0.03472	13.2677	0.001	***
Year : Month : Sector	1	0.93	0.00158	1.2086	0.271	
Residual	73	56.41	0.09553			
Total	85	590.5	1			

PO₄³⁻	Df	SumOfSqs	R²	F	Pr(>F)	
Year	2	1.1355	0.16256	28.7729	0.001	***
Month	1	2.2504	0.32215	114.0432	0.001	***
Sector	2	0.3379	0.04838	8.5627	0.002	**
Year : Month	1	1.339	0.19168	67.8552	0.001	***
Year : Sector	3	0.3671	0.05256	6.202	0.003	**
Month : Sector	2	0.1131	0.01619	2.8663	0.06	.
Year : Month : Sector	1	0.0019	0.00027	0.0959	0.757	
Residual	73	1.4405	0.20621			
Total	85	6.9855	1			

Table S5. Summary of permutational multivariate analysis of variance (PERMANOVA) result for significant differences between sector, month and year (*p<0.05*) of environmental data and abundance. The presence of variable abbreviation in a given part indicate a significant difference. Significative difference between month were represented above diagonal part of the table, and significant differences between Month*Sector in the below diagonal part of the table.

Year	Month	Sector	2019 Juillet Forestville	2019 Juillet Manicouagan	2019 Juillet BaieComeau	2019 Octobre Forestville	2019 Octobre Manicouagan	2019 Octobre BaieComeau	2020 Juillet Forestville	2020 Juillet Manicouagan	2020 Juillet BaieComeau
2019	Juillet	Forestville				Ab, Biomass, H, J, FRic t^*Sal, Chla			FDiv t^*		
2019	Juillet	Manicouagan									
2019	Juillet	BaieComeau									
2019	Octobre	Forestville	Ab, H, J / t^*, Sal, Chla		Ab				Ab, Biomass, H, J, FRic, FDiv, FEve t^*, Sal, Chla		
2019	Octobre	Manicouagan				Chla					
2019	Octobre	BaieComeau	Ab, FDiv			S, FRic/ Sal	Sal, Chla				
2020	Juillet	Forestville	FDiv / t^*, Sal		t^*	Ab, H, J, FRic, FEve	FDiv	Ab, FDiv			
2020	Juillet	Manicouagan	Ab /t^*			S		S	S, FRic, FDiv		
2020	Juillet	BaieComeau	Ab / t^*			Ab, H, FDiv, FRic		Ab, FDiv	Ab / Sal	Ab / Sal	
2020	Octobre	Forestville				t^*, Sal		FRic	FRic		J
2020	Octobre	Manicouagan						FDiv	FRic, FDiv		
2020	Octobre	BaieComeau						FRic / Sal	FRic, FDiv		Ab, FDiv
2021	Juillet	Forestville	Sal			Ab, S, J, FDiv, FRic	H	Ab, FRic, FDiv	Div, FEve/ t^*, Sal, Chla	Ab, S, FEve /t^*	Ab / t^*, Chla
2021	Juillet	Manicouagan				Ab, FRic		FRic, FDiv	FDiv/ t^*, Chla	H / t^*	Ab, FDiv / t^*, Chla
2021	Juillet	BaieComeau	FRic			Ab, S, H, J, FRic, FDiv	J	Ab, H, FRic, FDiv	H, FDiv / t^*	Ab, S / t^*	Ab, S / t^*, Chla
2021	Octobre	Forestville				Ab		Ab			
2021	Octobre	Manicouagan				Ab	Ab	Ab			
2021	Octobre	BaieComeau				J	H				

Table S5 (continued).

2020 Juillet			2020/2019 Octobre/Juillet			2021/2019 Octobre/Juillet			2020/2020 Octobre/Juillet		
			Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau
2019	Juillet	Forestville									
		Manicouagan	Ab, Biomass, H, J, FRic			FRic, FDiv			Sal		
		BaieComeau	t°, Sal, Chla			Sal					
2019	Octobre	Forestville									
		Manicouagan	t°, Sal			Ab, Biomass, H, J, FRic, Fdic			Ab, Biomass, H, J, FDiv		
		BaieComeau				t°			t°, Chla		
2020	Juillet	Forestville									
		Manicouagan	Ab, FRic, FDiv, Biomass			S, H, FRic, FDiv, FEve			FDiv		
		BaieComeau	t°, Sal, Chla, NO3, PO4			t°, Sal, Chla, NO3, PO4, O2			t°, Sal, O2, NO3, PO4		
2020	Octobre	Forestville									
		Manicouagan				Ab, S, H, J, FRic, FDiv			Ab, Biomass, H, J, FRic		
		BaieComeau				t°, Sal, PO4, O2			t°, Sal, Chla,		
2021	Juillet	Forestville	S, FRic	FRic, FDiv	FRic, FDiv						
		Manicouagan				Ab / t°			FRic		
		BaieComeau	S, H, J, FRic	H, FRic, FDiv	FRic, FDiv	Ab, H / Chla	FDiv		Sal		
2021	Octobre	Forestville									
		Manicouagan									
		BaieComeau						Chla			

Table S6. Summary of PERMANOVA results of abundance, biomass, taxa taxonomic indices, and functional indices *per* year, month and sector.

Abundance	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	853611101	0.18645	18.8028	0.001 ***
Month	1	663103393	0.14483	29.2128	0.001 ***
Sector	2	190238360	0.04155	4.1904	0.027 *
Year : Month	2	2997123	0.00065	0.066	0.935
Year : Sector	4	368886215	0.08057	4.0628	0.009 **
Month : Sector	2	80281227	0.01754	1.7684	0.168
Year : Month : Sector	2	13124037	0.00287	0.2891	0.725
Residual	106	2406100297	0.52554		
Total	121	4578341754	1		
Biomass	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	204662	0.12113	12.7867	0.001 ***
Month	1	17597	0.01041	2.1989	0.149
Sector	2	51112	0.03025	3.1933	0.037 *
Year : Month	2	70383	0.04166	4.3974	0.02 *
Year : Sector	4	329662	0.19511	10.2982	0.002 **
Month : Sector	2	71532	0.04234	4.4691	0.017 *
Year : Month : Sector	3	24336	0.0144	1.0136	0.391
Residual	115	920336	0.5447		
Total	131	1689621	1		
Bivalvia	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	158444521	0.16852	14.0644	0.001 ***
Month	1	89873879	0.09559	15.9553	0.001 ***
Sector	2	25116036	0.02671	2.2294	0.106
Year : Month	2	27212137	0.02894	2.4155	0.089 .
Year : Sector	4	12545210	0.01334	0.5568	0.672
Month : Sector	2	15672739	0.01667	1.3912	0.227
Year : Month : Sector	2	2980723	0.00317	0.2646	0.758
Residual	108	608346531	0.64705		
Total	123	940191776	1		
Cirripedia	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	2049865	0.18675	18.7067	0.001 ***
Month	1	945569	0.08614	17.2581	0.001 ***
Sector	2	960822	0.08753	8.7683	0.002 **
Year : Month	2	179109	0.01632	1.6345	0.169
Year : Sector	4	862513	0.07858	3.9356	0.018 *
Month : Sector	2	42534	0.00387	0.3882	0.663
Year : Month : Sector	2	19085	0.00174	0.1742	0.821
Residual	108	5917290	0.53907		
Total	123	10976788	1		
Fritillaria spp.	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	31664736	0.21617	23.3515	0.001 ***
Month	1	13117368	0.08955	19.3471	0.001 ***
Sector	2	780614	0.00533	0.5757	0.54
Year : Month	2	17497525	0.11945	12.9038	0.001 ***
Year : Sector	4	6904250	0.04713	2.5458	0.048 *
Month : Sector	2	487387	0.00333	0.3594	0.711
Year : Month : Sector	2	2803135	0.01914	2.0672	0.131
Residual	108	73224139	0.49989		
Total	123	146479155	1		
Acartia longiremis	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	328038909	0.15649	12.9687	0.001 ***
Month	1	15106498	0.00721	1.1944	0.26
Sector	2	142165683	0.06782	5.6204	0.009 **
Year : Month	2	34881584	0.01664	1.379	0.183
Year : Sector	4	208996276	0.0997	4.1312	0.029 *
Month : Sector	2	909772	0.00043	0.036	0.934
Year : Month : Sector	2	191237	0.00009	0.0076	0.988
Residual	108	1365908865	0.65161		
Total	123	2096198823	1		
Oithona similis	Df	SumOfSqs	R^2	F	Pr(>F)
Year	2	10931737	0.11737	15.0959	0.001 ***
Month	1	7098993	0.07622	19.6064	0.001 ***
Sector	2	17380766	0.1866	24.0016	0.001 ***
Year : Month	2	3197907	0.03433	4.4161	0.032 *
Year : Sector	4	7702763	0.0827	5.3185	0.011 *
Month : Sector	2	7558017	0.08114	10.4371	0.006 **
Year : Month : Sector	2	168096	0.0018	0.2321	0.755
Residual	108	39104149	0.41983		
Total	123	93142429	1		

Species richness	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	108.95	0.11113	10.6916	0.001	***
Month	1	15.94	0.01626	3.1287	0.075	
Sector	2	21.48	0.02191	2.1076	0.123	
Year : Month	2	3.75	0.00382	0.3678	0.714	
Year : Sector	4	179.6	0.1832	8.8127	0.001	***
Month : Sector	2	110.09	0.1123	10.8038	0.001	***
Year : Month : Sector	2	0.48	0.00049	0.047	0.955	
Residual	106	540.06	0.55089			
Total	121	980.34	1			

Shannon-Wiener index	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	3.6607	0.17466	14.7231	0.001	***
Month	1	0.7614	0.03633	6.1247	0.019	*
Sector	2	1.8511	0.08832	7.4452	0.002	**
Year : Month	2	0.8174	0.039	3.2876	0.047	*
Year : Sector	4	0.2785	0.01329	0.56	0.701	
Month : Sector	2	0.3996	0.01906	1.607	0.194	
Year : Month : Sector	2	0.0131	0.00062	0.0525	0.945	
Residual	106	13.1775	0.62872			
Total	121	20.9592	1			

Pielou eveness index	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	0.31492	0.15093	12.2994	0.001	***
Month	1	0.07026	0.03367	5.4885	0.023	*
Sector	2	0.18561	0.08896	7.2493	0.004	**
Year : Month	2	0.1044	0.05004	4.0775	0.023	*
Year : Sector	4	0.04114	0.01972	0.8034	0.555	
Month : Sector	2	0.01172	0.00562	0.4576	0.605	
Year : Month : Sector	2	0.00149	0.00072	0.0583	0.939	
Residual	106	1.35702	0.65036			
Total	121	2.08657	1			

Functional richness	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	0.03159	0.01837	1.1634	0.341	
Month	1	0.01733	0.01008	1.2767	0.268	
Sector	2	0.02434	0.01415	0.8964	0.407	
Year : Month	2	0.072	0.04186	2.6514	0.073	
Year : Sector	4	0.11293	0.06566	2.0794	0.087	
Month : Sector	2	0.01533	0.00891	0.5644	0.606	
Year : Month : Sector	2	0.00732	0.00426	0.2697	0.786	
Residual	106	1.43915	0.83672			
Total	121	1.71999	1			

Functional diversity	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	1.3468	0.46049	146.2644	0.001	***
Month	1	0.67829	0.23191	147.3252	0.001	***
Sector	2	0.00552	0.00189	0.5995	0.529	
Year : Month	2	0.31194	0.10665	33.8766	0.001	***
Year : Sector	4	0.03779	0.01292	2.0518	0.084	
Month : Sector	2	0.04838	0.01654	5.2541	0.005	**
Year : Month : Sector	2	0.008	0.00273	0.8684	0.428	
Residual	106	0.48802	0.16686			
Total	121	2.92473	1			

Functional eveness	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	0.03792	0.05375	4.3781	0.023	*
Month	1	0.00193	0.00273	0.4448	0.494	
Sector	2	0.04001	0.05672	4.6199	0.013	*
Year : Month	2	0.01158	0.01641	1.337	0.26	
Year : Sector	4	0.11773	0.1669	6.7971	0.001	***
Month : Sector	2	0.00861	0.01221	0.9941	0.368	
Year : Month : Sector	2	0.0286	0.04055	3.3029	0.051	
Residual	106	0.459	0.65072			
Total	121	0.70538	1			

Table S7. Summary of PERMANOVA results of species assemblage based on Bray Curtis dissimilarity *per* year, month and sector.

Zooplankton composition (BrayCurtis dissimilarity)						
	Df	SumOfSqs	R^2	F	Pr(>F)	
Year	2	4.9201	0.22967	31.3647	0.001	***
Month	1	2.7046	0.12625	34.483	0.001	***
Sector	2	1.5798	0.07375	10.0712	0.001	***
Year*Month	2	1.8401	0.08589	11.73	0.001	***
Year*Sector	4	0.9504	0.04437	3.0294	0.001	***
Month*Sector	2	0.6692	0.03124	4.2663	0.001	***
Year*Month*Sector	2	0.2872	0.01341	1.8308	0.041	*
Residual	108	8.4708	0.39542			
Total	123	21.4222	1			
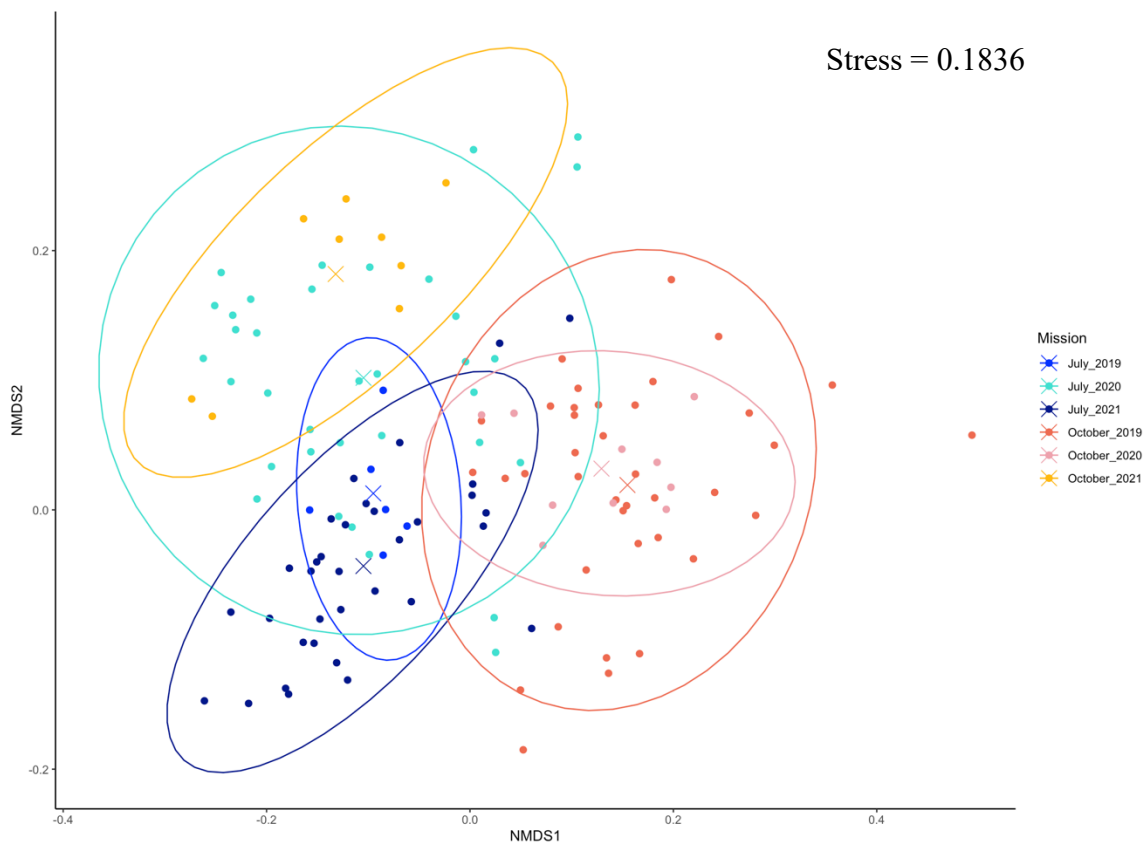
Fig S1. Non-metric multidimensional scaling based on species assemblage (Bray-Curtis dissimilarity) per month x year.

Table S8. Summary of pairwise results (Bonferroni adjustment) of PERMANOVA of species composition (based on Bray-Curtis dissimilarity). Each X represented significative interactions among sectors, month and year.

			2019			2019			2020		
			Juillet			Octobre			Juillet		
			Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau
2019	Juillet	Forestville									
		Manicouagan									
		BaieComeau									
2019	Octobre	Forestville	X		X						
		Manicouagan									
		BaieComeau	X		X	X					
2020	Juillet	Forestville	X		X	X	X	X			
		Manicouagan	X			X		X	X		
		BaieComeau	X		X	X	X	X	X	X	
2020	Octobre	Forestville	X					X	X		X
		Manicouagan	X					X	X		X
		BaieComeau	X			X		X	X	X	X
2021	Juillet	Forestville	X		X	X	X	X	X	X	X
		Manicouagan	X		X	X		X	X	X	X
		BaieComeau				X	X	X	X	X	X
2021	Octobre	Forestville	X			X		X	X	X	X
		Manicouagan				X		X	X		
		BaieComeau	X			X		X	X		X

			2020			2021			2021		
			Octobre			Juillet			Octobre		
			Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau
2019	Juillet	Forestville									
		Manicouagan									
		BaieComeau									
2019	Octobre	Forestville									
		Manicouagan									
		BaieComeau									
2020	Juillet	Forestville									
		Manicouagan									
		BaieComeau									
2020	Octobre	Forestville									
		Manicouagan									
		BaieComeau									
2021	Juillet	Forestville	X	X	X						
		Manicouagan	X	X	X	X					
		BaieComeau	X	X	X	X	X				
2021	Octobre	Forestville	X	X	X	X	X	X			
		Manicouagan				X	X	X			
		BaieComeau			X	X	X	X			

Table S9. Summary of pairwise results (Bonferroni adjustment) of PERMANOVA of species composition (based on Bray-Curtis dissimilarity) among month and years.

Pairs			F.Model	R^2	p.value	p.adjusted	
July 2019	vs.	July 2020	3.814527	0.09580742	0.06	0.09	
July 2019	vs.	July 2021	2.644484	0.06506378	0.027	0.405	
July 2019	vs.	October 2019	13.236009	0.23962646	0.001	0.015	*
July 2019	vs.	October 2020	14.540489	0.50946881	0.002	0.03	*
July 2019	vs.	October 2021	16.405549	0.67220569	0.006	0.09	
July 2020	vs.	July 2021	17.092748	0.21078023	0.001	0.015	*
July 2020	vs.	October 2019	41.51275	0.37906773	0.001	0.015	*
July 2020	vs.	October 2020	19.442163	0.32707698	0.001	0.015	*
July 2020	vs.	October 2021	5.991709	0.14982379	0.001	0.015	*
July 2021	vs.	October 2019	41.121635	0.37005967	0.001	0.015	*
July 2021	vs.	October 2020	22.439606	0.34822693	0.001	0.015	*
July 2021	vs.	October 2021	13.394931	0.27118027	0.001	0.015	*
October 2019	vs.	October 2020	1.649426	0.03461586	0.112	1	
October 2019	vs.	October 2021	14.393277	0.2646615	0.001	0.015	*
October 2020	vs.	October 2021	17.675908	0.59563158	0.002	0.03	*

Table S10. Summary of SIMPER dissimilarity matrix of species composition between sector, month and years.

Dissimilarity		Juillet_2019			Juillet_2020			Juillet_2021		
%		Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau
Juillet_2019	Forestville			35.51	38.83	63	50.87	38.66	40.44	34.55
	Manicouagan									
	BaieComeau				49.78	69.71	55.36	48.02	51.76	45.09
Juillet_2020	Forestville					58.12	58.51	51.12	52.39	46.14
	Manicouagan						59.56	74.51	64.97	62.2
	BaieComeau							62.41	68.01	54.02
Juillet_2021	Forestville								46.75	43.15
	Manicouagan									43.91
	BaieComeau									
Octobre_2019	Forestville	64.65								
	Manicouagan									
	BaieComeau			61.67						
Octobre_2020	Forestville				69.13					
	Manicouagan					69.55				
	BaieComeau						71.02			
Octobre_2021	Forestville							64.77		
	Manicouagan								70.48	
	BaieComeau									58.4

Dissimilarity		Octobre_2019			Octobre_2020			Octobre_2021		
%		Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau	Forestville	Manicouagan	BaieComeau
Juillet_2019	Forestville									
	Manicouagan									
	BaieComeau									
Juillet_2020	Forestville									
	Manicouagan									
	BaieComeau									
Juillet_2021	Forestville									
	Manicouagan									
	BaieComeau									
Octobre_2019	Forestville		38.13	50.07	41.29	38.13	45.6	74.42	81.24	78.32
	Manicouagan			33.76	36.16	29.52	34.13	66.76	71.02	64.66
	BaieComeau				48.71	40.1	40.61	61.81	65.11	58.37
Octobre_2020	Forestville					37.52	43.64	76.68	82.09	78.13
	Manicouagan						33.01	64.16	71.79	69.01
	BaieComeau							58.88	61.09	60.07
Octobre_2021	Forestville								41.23	48.52
	Manicouagan									30.33
	BaieComeau									

Table S11. Mean abundance (ind m^3) of each taxa, total abundance (ind m^3) per month and year and percentage of contribution of each Taxa (Order) per month and year (%).

Mission	Taxa Order	Abundance	Total Ab.	%
Juillet_2019	Appendicularia	14247.05	43583.46	32.69
Juillet_2019	Copepoda	13081.51	43583.46	30.01
Juillet_2019	Mollusca	8649.86	43583.46	19.85
Juillet_2019	Annelida	1865.81	43583.46	4.28
Juillet_2019	Cirripedia	1836.53	43583.46	4.21
Juillet_2019	Euphausiacea	1565.12	43583.46	3.59
Juillet_2019	Echinodermata	1448.89	43583.46	3.32
Juillet_2019	Diplostraca	797.53	43583.46	1.83
Juillet_2019	Chaetognatha	45.16	43583.46	0.10
Juillet_2019	Cnidaria	18.96	43583.46	0.04
Juillet_2019	Teleostei	15.58	43583.46	0.04

Mission	Taxa Order	Abundance	Total Ab.	%
Octobre_2019	Copepoda	21210.26	40842.72	51.93
Octobre_2019	Appendicularia	16395.16	40842.72	40.14
Octobre_2019	Euphausiacea	930.02	40842.72	2.28
Octobre_2019	Diplostraca	633.98	40842.72	1.55
Octobre_2019	Echinodermata	613.43	40842.72	1.50
Octobre_2019	Cirripedia	604.18	40842.72	1.48
Octobre_2019	Mollusca	266.3	40842.72	0.65
Octobre_2019	Annelida	127.24	40842.72	0.31
Octobre_2019	Chaetognatha	31.82	40842.72	0.08
Octobre_2019	Isopoda	9.9	40842.72	0.02
Octobre_2019	Cnidaria	9.09	40842.72	0.02

Mission	Taxa Order	Abundance	Total Ab.	%
Juillet_2020	Mollusca	125135.01	251384.08	49.78
Juillet_2020	Copepoda	95440.32	251384.08	37.97
Juillet_2020	Appendicularia	8670.87	251384.08	3.45
Juillet_2020	Diplostraca	6738.53	251384.08	2.68
Juillet_2020	Euphausiacea	4884.74	251384.08	1.94
Juillet_2020	Cirripedia	4671.04	251384.08	1.86
Juillet_2020	Annelida	2912.13	251384.08	1.16
Juillet_2020	Echinodermata	2562.23	251384.08	1.02
Juillet_2020	Decapoda	149.41	251384.08	0.06
Juillet_2020	Chaetognatha	97.41	251384.08	0.04
Juillet_2020	Teleostei	54.68	251384.08	0.02

Mission	Taxa Order	Abundance	Total Ab.	%
Octobre_2020	Copepoda	5287.2	11090.2	47.67
Octobre_2020	Appendicularia	4864.98	11090.2	43.87
Octobre_2020	Euphausiacea	620.1	11090.2	5.59
Octobre_2020	Mollusca	110.28	11090.2	0.99
Octobre_2020	Cirripedia	107.06	11090.2	0.97
Octobre_2020	Echinodermata	52.56	11090.2	0.47
Octobre_2020	Annelida	25.44	11090.2	0.23
Octobre_2020	Diplostraca	12.44	11090.2	0.11
Octobre_2020	Isopoda	4.91	11090.2	0.04
Octobre_2020	Ostracoda	4.46	11090.2	0.04
Octobre_2020	Amphipoda	0.77	11090.2	0.01

Mission	Taxa Order	Abundance	Total Ab.	%
Juillet_2021	Copepoda	184673.45	343383.54	53.78
Juillet_2021	Appendicularia	59460.34	343383.54	17.32
Juillet_2021	Mollusca	30650.47	343383.54	8.93
Juillet_2021	Diplostraca	21067.06	343383.54	6.14
Juillet_2021	Euphausiacea	15162.66	343383.54	4.42
Juillet_2021	Cirripedia	13564.75	343383.54	3.95
Juillet_2021	Echinodermata	12566.14	343383.54	3.66
Juillet_2021	Annelida	4913.64	343383.54	1.43
Juillet_2021	Teleostei	377.93	343383.54	0.11
Juillet_2021	Chaetognatha	346.1	343383.54	0.10
Juillet_2021	Cnidaria	343.5	343383.54	0.10

Mission	Taxa Order	Abundance	Total Ab.	%
Octobre_2021	Copepoda	42960.33	53179.37	80.78
Octobre_2021	Appendicularia	6664.03	53179.37	12.53
Octobre_2021	Mollusca	1432.19	53179.37	2.69
Octobre_2021	Diplostraca	846.84	53179.37	1.59
Octobre_2021	Euphausiacea	736.92	53179.37	1.39
Octobre_2021	Cnidaria	240.32	53179.37	0.45
Octobre_2021	Echinodermata	162.67	53179.37	0.31
Octobre_2021	Chaetognatha	97.11	53179.37	0.18
Octobre_2021	Annelida	29.21	53179.37	0.05
Octobre_2021	Cirripedia	6.57	53179.37	0.01
Octobre_2021	Decapoda	3.18	53179.37	0.01

Table S12. Taxa contribution (%) to species composition based on SIMPER (PRIMER®). The five taxa which mainly contributed to species composition are represented in dark orange.

Species	Juillet_2019	Juillet_2020	Juillet_2021	Octobre_2019	Octobre_2020	Octobre_2021
Acartia longiremis	10	7.1	16.7	20.1	19.4	
Bivalvia	15.8	24.9	9.1			18.6
Fritillaria sp.	19.7		16	31.3	24.1	
Oithona similis	11.9	14.4		8.8	18.8	
Cirripedia			7.8	4.2	4.7	
Pseudocalanus spp.		5.9				14.3
Evadne sp.			7.2			6.5
Euphausiidae				6.7	6.2	
Echinodermata	7.1					
Eurytemora herdmani		5.6				
Centropages hamatus						11
Temora longicornis						17.3

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Table S13. Summary of PERMANOVA (with Monte-Carlo adjustment) results for the four different functional traits: life history (a), trophic type (b), feeding strategy (c) and size class (d).

a)

Life history							
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perm	P(MC)
Year	2	847,35	423,68	2,6903	0,058	999	0,053
Month	1	4002,9	4002,9	25,418	0,001	997	0,001 *
Sector	2	866,59	433,29	2,7514	0,063	999	0,047 *
Year*Month	2	105,02	52,508	0,33342	0,79	999	0,792
Year*Sector	4	1877,5	469,38	2,9805	0,018	999	0,009 *
Month*Sector	2	1190,1	595,07	3,7786	0,012	998	0,016 *
Year*Month*Sector	2	98,003	49,002	0,31116	0,794	999	0,809
Res	111	17481	157,48				
Total	126	45401					

b)

Trophic type							
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perm	P(MC)
Year	2	1924,3	962,16	7,7406	0,001	999	0,001 *
Month	1	2239,4	2239,4	18,016	0,001	998	0,001 *
Sector	2	792,39	396,19	3,1874	0,009	999	0,009 *
Year*Month	2	1046,8	523,41	4,2108	0,002	998	0,004 *
Year*Sector	4	517,68	129,42	1,0412	0,43	999	0,421
Month*Sector	2	761,47	380,74	3,063	0,017	998	0,009 *
Year*Month*Sector	2	325	162,5	1,3073	0,251	997	0,263
Res	111	13797	124,3				
Total	126	37966					

c)

Feeding strategy							
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perm	P(MC)
Year	2	1543,5	771,76	6,6565	0,001	998	0,001 *
Month	1	1383,1	1383,1	11,93	0,001	999	0,001 *
Sector	2	607,61	303,81	2,6204	0,042	998	0,028 *
Year*Month	2	1225,8	612,9	5,2863	0,001	999	0,001 *
Year*Sector	4	773,42	193,36	1,6677	0,102	999	0,084
Month*Sector	2	962,79	481,39	4,1521	0,003	999	0,002 *
Year*Month*Sector	2	252,37	126,18	1,0884	0,391	998	0,369
Res	111	12869	115,94				
Total	126	30798					

d)

Size class							
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perm	P(MC)
Year	2	724,39	362,2	2,4983	0,043	999	0,036 *
Month	1	2732,6	2732,6	18,848	0,001	999	0,001 *
Sector	2	741,26	370,63	2,5564	0,031	999	0,036 *
Year*Month	2	875,72	437,86	3,0202	0,021	999	0,012 *
Year*Sector	4	1013	253,25	1,7468	0,083	998	0,055
Month*Sector	2	736,43	368,22	2,5398	0,046	999	0,04 *
Year*Month*Sector	2	190,31	95,154	0,65633	0,65	999	0,684
Res	111	16093	144,98				
Total	126	33318					

CONCLUSION GÉNÉRALE

Ce projet répond aux prérogatives du programme sur les données côtières de référence du MPO, permettant ainsi de créer le premier état de référence des communautés zooplanctoniques de la zone côtière de l'estuaire maritime du Saint-Laurent. Les communautés zooplanctoniques suivent une dynamique spatio-temporelle forte le long de la côte, avec des abondances plus élevées à l'été par rapport à l'automne. La composition des communautés est principalement influencée par la température, la chl *a* et la salinité. L'étude des diversités taxonomique et fonctionnelle, via l'analyses des hotspots, a ainsi permis de mettre en évidence les zones à "haute diversité" variant entre les secteurs et les saisons. Les zones de haute diversité différaient entre les indices de diversité taxonomique et de diversité fonctionnelle soulignant ainsi la complémentarité des deux approches. Une zone considérée comme faiblement diversifié au niveau taxonomique serait peu considérée dans des plans de protection et/ou gestion et notre étude a montré que ces mêmes zones peuvent être fonctionnellement hautement diversifiées et devrait alors être plus sérieusement considérées dans ces plans.

Limites de l'étude

Deux différentes entités de recherche, ISMER-UQAR et MPO, ont été impliquées dans le projet, la parfaite collaboration des équipes a permis de pourvoir réaliser dans les temps et avec rigueur les échantillonnages et les analyses de l'étude. Les difficultés ont cependant été retrouvées dans l'uniformisation des données récoltés par les deux types de bateaux différents. En effet, les bateaux de l'IML-MPO, ayant un tirant d'eau plus important que le bateau de l'ISMER-UQAR, ne permettaient pas d'échantillonner à faible profondeur. Certaines stations considérées comme trop profondes ont alors été retirées de l'analyse limitant le nombre de stations totales pour certains mois. Aussi, par le manque de disponibilité de certaines données environnementales, les analyses des relations de la composition spécifique avec les facteurs environnementaux n'ont pu qu'être partiellement

effectuées. En effet, de nombreuses données de nutriments et certains facteurs environnementaux (enregistrés avec la CTD) étaient manquants dépendamment de la mission (problème technique ou mise en place tardive des protocoles expérimentaux, notamment pour la première année d'échantillonnage). Une uniformisation du protocole pour de futurs suivis permettra de dresser une analyse complète incluant tous les facteurs environnementaux.

Les difficultés d'échantillonnage ont été rencontrées notamment à l'automne, dû à une période de temps d'échantillonnage restreinte pendant une saison où les conditions météorologiques sont très limitantes, réduisant aussi le nombre de stations exploitables pour cette saison.

Très peu de traits fonctionnels sont disponibles pour les taxa retrouvés dans la présente étude, notamment pour les organismes autres que les copépodes, limitant le nombre de traits intégrés dans l'analyse. De plus, comme le zooplancton est considéré comme un groupe sentinelle et donc fortement dépendant des caractéristiques abiotiques de son environnement, l'intégration de traits sur les tolérances environnementales des taxa (notamment la salinité ou la température) auraient, par exemple, permis de mieux comprendre la dynamique de ces communautés zooplanctonique et serait alors un point à développer et intégrer pour de futures études sur ce groupe.

Perspectives

L'aspect des différents stades des copépodes n'a pas été abordé dans la présente étude, même s'ils ont été analysés lors des identifications taxonomiques et intégrés notamment pour le calcul des biomasses, ils seraient intéressants à analyser plus en détails dans une autre étude afin de souligner les successions des différents stades en relation avec les conditions environnementales.

Le zooplancton est un maillon clé dans le réseau trophique, les interactions avec les niveaux inférieurs et supérieurs seraient importantes à étudier car nous avons notamment pu

montrer que la chl *a* était un facteur contrôlant les communautés zooplanctoniques. Les successions entre le phytoplancton et le zooplancton seraient un point à examiner plus en détails, pour permettre d'expliquer notamment les différences dans les abondances des communautés du zooplancton. Du fait de restrictions logistiques, les échantillonnages de notre étude s'étalaient seulement sur une semaine à deux saisons différentes, ce qui s'est avéré être trop court pour expliquer ces successions et donc précisément la dynamique des communautés zooplanctonique en lien avec la chl *a*.

De plus, l'étude de la dispersion du zooplancton dans les zones côtières permettrait de déterminer si les communautés retrouvées en zone côtière sont une source ou une agrégation des communautés retrouvées en milieu plus profonds de l'EMSL. Archambault et Bourget (1999) ont montrés que le recrutement des larves des organismes benthiques sur la côte sud de l'EMSL était lié à la configuration côtière et aux conditions hydrodynamiques, qui pouvaient ainsi favoriser leur rétention. Cependant, aucune étude au niveau de l'EMSL n'a encore intégré cette variable aux communautés zooplanctoniques au complet (holoplancton et méroplancton). Si les zones côtières de la côte nord de l'EMSL s'avéraient être une source (comme la définition de la zone côtière, dans le sens où elles constituent des refuges et nurseries pour de nombreuses espèces de zooplancton, holoplancton et méroplancton inclus), une modification des conditions environnementales côtières aurait alors des impacts non seulement sur la dynamique de la zone côtière mais également sur la dynamique de l'EMSL au complet.

L'utilisation des traits fonctionnels séparés et non de groupes fonctionnels a montré que les traits indépendamment considérés apportent de plus amples informations même s'ils peuvent être considéré comme « redondants ». En effet, l'approche par groupe fonctionnel aurait conduit à considérer les deux espèces de copépodes *Oithona similis* et *Acartia longiremis,* qui possèdent de nombreux traits fonctionnels en commun, dans le même groupe alors que leur répartition spatio-temporelle est différente et semblerait être fortement dépendante de leur environnement. Dans ce cas et même si nous avions eu accès aux traits des tolérances environnementales, en utilisant la méthode des groupes fonctionnels, la seule

différence entre ces deux taxa, liée aux traits des tolérances environnementales, aurait eu moins de poids que les autres traits cumulés et ce type d'analyse aurait alors placé ces deux taxa dans le même groupe. Cependant, considérés et analysés à part, les traits des tolérances environnementales auraient considéré ces deux taxa indépendamment et auraient permis de mieux comprendre leur dynamique et répartition. Afin de comparer ces deux types d'analyses, par traits indépendants ou par groupe fonctionnel, il serait intéressant de développer de nouvelles études, notamment sur les communautés zooplanctoniques marines, pour déterminer quel type est le mieux adapté aux différents questionnements et besoins, et ainsi de développer un protocole d'étude précis pour l'utilisation des traits fonctionnels et des diversités fonctionnelles. L'utilisation des traits fonctionnels dans le cadre de la caractérisation des écosystèmes est une méthode assez récente en plein essor et l'application d'une méthode standardisée pour l'évaluation des écosystèmes permettrait de pouvoir plus facilement comparer les différents milieux et dans le temps.

Ce projet a donc permis de dresser le premier état de référence des communautés zooplanctoniques côtière de l'EMSL, qui n'avait jusqu'alors jamais été réalisé. Cette étude a permis de créer un point de comparaison avec des données futures, pour des zones soumises à de nombreuses pressions anthropiques et liées au changement climatique. Un suivi sur le plus long terme serait alors nécessaire pour une meilleure compréhension de la dynamique des communautés zooplanctoniques. En incluant plus de paramètres environnementaux, différentes saisons pour un cycle annuel complet, les interactions trophiques et plus de traits fonctionnels dont notamment les tolérances environnementales, ceci permettrait alors de mieux comprendre la dynamique des communautés zooplanctoniques côtières de l'EMSL dans un climat global à tendance au rapide changement.

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