UQAR
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à Rimouski

Dynamique spatio-temporelle des communautés zooplanctoniques de l'estuaire moyen du Saint-Laurent face aux influences environnementales

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PAR

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"Life breaks free. Life expands to new territories. Painfully, perhaps even dangerously. But life finds a way."

Jurrassic Park

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RÉSUMÉ

Parmi les écosystèmes aquatiques dont le suivi de l'état est d'une grande importance écologique et sociale se retrouvent les estuaires, particulièrement dynamiques et productifs. Le zooplancton est un groupe animal occupant une position centrale dans les réseaux trophiques estuariens et qui représente donc un groupe clé dont les variations sont étudiées dans l'optique de mieux comprendre le fonctionnement de ces écosystèmes. L'estuaire du Saint-Laurent, au Québec, est l'un des plus grands au monde, mais pour lequel il existe un manque de données sur les communautés zooplanctoniques depuis les années 1990. Ce manque de données touche plus particulièrement la zone de transition estuarienne (ZTE), aussi appelée estuaire moyen, où les eaux limnétiques et marines se rencontrent. En réponse à ce manque de données et aux incertitudes soulevés par les changements anthropiques affectant l'estuaire, un suivi annuel des communautés zooplanctoniques et des conditions environnementales de la ZTE a été effectué en août de 2019 à 2023. Le but de la présente étude était d'analyser ces données pour déterminer les variations spatio-temporelles du zooplancton de la ZTE sous l'angle de la diversité taxonomique et fonctionnelle, tout en déterminant les influences des facteurs environnementaux sur ces variations. Le zooplancton a été identifié au binoculaire et des traits fonctionnels ont été sélectionnés (taille, cycle de vie, groupe(s) trophique(s), mode(s) d'alimentation) pour calculer des indices de biodiversité. Les copépodes dominaient la majorité des communautés échantillonnées, avec des densités qui variaient annuellement. Ces communautés étaient fortement structurées par la salinité et avaient une diversité taxonomique et fonctionnelle élevée en zone limnétique et polyhaline, et faible en zone oligohaline et mésohaline. Les facteurs environnementaux les plus structurant variaient selon l'année et la zone de salinité. Ce projet est le premier à faire un relevé complet de la composition et des variations des communautés zooplanctoniques de la ZTE du Saint-Laurent depuis les années 1990, tout en incluant un angle fonctionnel. Les résultats renforcent l'importance d'effectuer un suivi écologique à long terme de ces communautés, dont les principales influences environnementales varient de façon importante dans le temps et l'espace.

Mots clés : zooplancton, zone de transition estuarienne, structure spatio-temporelle, biodiversité, diversité fonctionnelle, influences environnementales, fleuve Saint-Laurent

ABSTRACT

Among the aquatic ecosystems for which monitoring is of a great ecological and social importance are estuaries, which are especially dynamic and productive. Zooplankton occupies a central position in estuarian food webs and that represents a key component with variations that are studied to better understand the functioning of these ecosystems. The St. Lawrence Estuary, in Québec, is one of the biggest in the world, but for which there has been a lack of data on zooplankton communities since the 1990s. This lack of data is especially important in the estuarine transition zone (ETZ), also called middle estuary, where freshwater meets marine water. In response to this absence of data and the uncertainties surrounding anthropic changes observed in the Estuary, an annual survey of the zooplankton communities and environmental conditions of the ETZ has been carried out in August 2019 to 2023. The goal of the present study was to determine the spatio-temporal variations of the zooplankton of the ZTE from a taxonomic and functional diversity angle, while also describe the influences from environmental factors on these variations. Zooplankton was identified using a stereomicroscope and functional traits were selected (body size, life cycle, trophic groups, feeding method(s)) to calculate biodiversity indices. Copepods dominated the majority of sampled communities, with densities that varied annually. These communities were highly structured by salinity and showed a taxonomic and functional diversity that was high in freshwater and polyhalines zones, and low in oligohaline and mesohaline zones. Environmental factors that were the most structuring varied among years and salinity zones. This project is the first one to do a complete monitoring of the composition and variations of zooplanctonic communities of the ETZ of the St. Lawrence since the 1990s, while including a functional angle. Results reinforce the importance of a long-term ecological monitoring of the communities, for which principal environmental influences vary in time and space.

Keywords: zooplankton, estuarian transition zone, spatio-temporal variations, biodiversity, functional diversity, environmental influences, St. Lawrence River

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ETZ / ZTE	Estuarine Transition Zone / Zone de transition estuarienne
Fric	Functional richness / Richesse fonctionnelle
Fdiv	Functional divergence / Divergence fonctionnelle
Feve	Functional evenness / Équitabilité fonctionnelle
MTZ / ZTM	Maximum Turbidity Zone / Zone de turbidité maximale
PIM / MIP	Particulate inorganic matter / Matière inorganique particulaire
POM / MOP	Particulate organic matter / Matière organique particulaire
SPM / MPS	Suspended particulate matter / Matière particulaire suspendue

INTRODUCTION GÉNÉRALE

La santé des écosystèmes

L'étude de l'impact humain sur les écosystèmes est un thème récurrent dans les médias et le monde scientifique depuis la fin du 20e siècle, particulièrement depuis la tenue de la Conférence des Nations Unies sur l'environnement de Stockholm en 1972 et la publication du rapport Meadows la même année. En réponse aux préoccupations par rapport aux impacts anthropiques sur l'état des écosystèmes est né le concept de santé des écosystèmes. C'est à partir des travaux du psychologue Hans Selye (1973, 1974) sur la réponse des organismes aux stress qu'a été créée une adaptation de ce concept pour l'impact du stress au niveau écosystémique (Rapport et al., 1985). La santé d'un écosystème réfère à la capacité de celui-ci à maintenir son fonctionnement, son organisation et son autonomie face à différents stress. La santé d'un écosystème est alors déterminée par trois critères (Giraudoux, 2022) :

1) Sa vigueur : l'activité d'un écosystème en fonction de sa production primaire
2) Son organisation : la biodiversité et les interactions entre les organismes
3) Sa résilience : la capacité d'un écosystème à maintenir sa structure et ses processus à un niveau spatial et temporel face à des stress

La destruction d'habitat, l'exploitation de territoire et l'introduction d'espèces envahissantes ne sont que quelques exemples de phénomènes anthropiques qui affectent la santé des écosystèmes (Lu et al., 2015). Malgré les critiques sur la subjectivité du concept de santé des écosystèmes en lien avec sa dépendance intrinsèque à des critères sociaux variables définissant ce qui est attendu des écosystèmes, une constatation a toutefois été mise en lumière : l'importance d'être capable de mesurer et assurer le « bon fonctionnement » des écosystèmes (Giraudoux, 2022). Les indicateurs utilisés à cette fin peuvent être classifiées en plusieurs catégories, soit biologiques, physicochimiques et socioéconomiques (Lu et al., 2015). Parmi les indicateurs biologiques essentiels pour établir l'état d'un écosystème se retrouve la biodiversité. On la distingue en trois volets, soit (Gaston and Spicer, 2004) :

1) Diversité génétique : basée sur les gènes qui composent et distinguent les organismes
2) Diversité taxonomique : basé sur les la classification taxonomique des organismes
3) Diversité fonctionnelle : traits et groupes fonctionnelles des organismes en lien avec leurs rôles dans l'écosystème

Diversité taxonomique : une approche traditionnelle

La diversité taxonomique, parfois appelée diversité spécifique ou diversité des organismes, est généralement la mesure de diversité la plus utilisée dans l'étude du fonctionnement des écosystèmes (Balvanera et al., 2006). Les mesures de ce type de diversité sont basées sur des systèmes de classification taxonomique créés dans l'optique de distinguer et de regrouper certains organismes partageant des caractéristiques similaires (Hey, 2001). Différents niveaux de classification des taxons vont du plus large au plus spécifique, soit, en ordre : règne, embranchement, classe, ordre, famille, genre, espèce. Peu importe les mesures de diversité utilisé, l'identification des espèces, ou taxons, demeure essentielle (Steele et Pires, 2011).

Les espèces peuvent être identifiées avec différentes méthodes adaptées en fonction du type d'organismes. Généralement, une combinaison d'informations morphologiques, géographiques et écologiques sont utilisées. L'analyse génétique ou moléculaire est parfois la seule à pouvoir distinguer certaines espèces d'apparence très similaires, mais est plus longue et couteuse (Steele et Pires, 2011). Les espèces identifiées dans un milieu et leurs abondances ou densités peuvent par la suite être utilisées dans le calcul de divers indices de diversité qui mesurent leur richesse, uniformité et disparité. La richesse spécifique équivaut généralement au nombre absolu d'espèces dans un habitat donné. L'indice de diversité de Shannon, ou Shannon-Wiener, mesure la diversité à travers l'incertitude liée au processus d'échantillonnage, qui est plus élevée lorsque la diversité d'organismes est plus grande. L'indice d'équitabilité de Piélou, aussi répandu, est calculé à partir de l'indice de Shannon et mesure l'équitabilité entre les abondances des espèces (Daly et al., 2018).

Toutefois, le fait que la diversité taxonomique dépende des espèces et de la classification de ces dernières en fait une mesure qui découle directement de la conception humaine de ce qui distingue les espèces. La définition du concept d'espèce comporte certains défauts qui se transmettent également dans les indices qui en dépendent. L'évolution est un processus extrêmement long et graduel à travers lequel il est difficile de regrouper les organismes en catégories strictes, surtout prenant en compte la subjectivé inévitablement impliquée dans cette classification (Hey, 2001).

Un tel problème récurrent est souligné chez plusieurs groupes zooplanctoniques avec la détection moléculaire de complexes cryptiques, des espèces génétiquement distinctes mais morphologiquement trop similaires pour être différenciées sur la simple base de leur apparence. L'inaptitude à différencier ces espèces par observation entraîne une incertitude dans le suivi d'espèces et de diversité dans plusieurs milieux (Peters et al., 2025). Le complexe estuarien *Eurytemora affinis* témoigne de certains de ces enjeux entourant la diversité spécifique. Les opinions scientifiques sur la nature des espèces cryptiques sont nombreuses et il demeure que les études basées sur la morphologie ne pourront détecter ces différentes espèces, ce qui induit un biais et des sous-estimations dans les mesures de diversité (Lajus et al., 2015; Peters et al., 2025).

Approche de la diversité fonctionnelle : pourquoi est-elle importante?

En complément aux autres types de diversité se retrouve la diversité fonctionnelle, dont l'usage dans la littérature scientifique a grandement augmenté depuis les années 1990 (Schleuter et al., 2010) en raison de son importance dans la compréhension du fonctionnement des écosystèmes (Balvanera et al., 2006). Le fonctionnement des écosystèmes, qui réfère à leurs processus, peut être décrit par les stocks d'énergie et de biomasse, les cycles de transformation de ces derniers ainsi que la variation de ces stocks et de ces cycles (Hébert et al., 2017). De la même façon que les espèces constituent la base de la diversité taxonomique, ce sont les traits fonctionnels qui sont à la base de la diversité fonctionnelle, qui se mesurent au niveau des organismes et permettent de les classifier dans des groupes fonctionnels reflétant leurs rôles dans l'écosystème (Benedetti et al., 2016). Les traits sont qualitatifs ou quantitatifs et peuvent être de plusieurs natures : comportementale, morphologique, physiologique, etc. (Violle et al., 2007). Des traits plus complexes à mesurer, souvent de nature physiologique, sont généralement représentés par des traits équivalents appelé 'proxy', qui sont plus facilement accessibles et mesurables dans un cadre de recherche avec de nombreux organismes. Au niveau quantitatif, la taille et la masse des organismes sont des traits proxy fréquemment utilisés pour mesurer la croissance, le taux d'alimentation, le taux d'excrétion, etc. en raison de relations allométriques existantes (Hébert et al., 2017). Les traits fonctionnels, qui sont plutôt qualitatifs, possèdent plusieurs valeurs possibles. L'alimentation des organismes, par exemple, est étudiée à travers des traits comme le niveau trophique et le mode d'alimentation (Kiørboe, 2011; Hébert et al., 2017).

Pour mesurer la diversité fonctionnelle, il est important de prendre en compte l'échelle continuelle de plusieurs des mesures et du fait que plusieurs traits sont souvent utilisés pour représenter une seule fonction (Schleuter et al., 2010). Les indices de diversité fonctionnelle généralement utilisés sont la richesse fonctionnelle (*functional richness*), mesurant l'espace fonctionnel occupé dans une communauté, l'« uniformité » fonctionnelle (*functional eveness*), mesurant la régularité de la distribution des traits, ainsi que la divergence fonctionnelle (*functional divergence*), mesurant l'hérérogénéité dans la distribution des traits

(Villéger et al., 2008). La richesse fonctionnelle décrit ainsi le niveau d'occupation de l'espace de niches écologiques dans un milieu donné, tandis que l'« uniformité » fonctionnelle et la divergence fonctionnelle décrivent comment cet espace est utilisé. L'utilisation de ces 3 indices est essentielle pour avoir toutes les facettes de la diversité fonctionnelle d'une communauté (Villéger et al., 2008; Schleuter et al., 2010). Mesurer la diversité fonctionnelle des communautés biologiques et les variations de celle-ci peut notamment aider à comprendre les pressions de sélection que subissent les organismes en lien avec les influences environnementales et les changements dans les fonctions des écosystèmes (Litchman et al., 2013). Ces changements ne sont pas toujours détectables à travers les groupes taxonomiques uniquement. Par exemple, il a été trouvé que plusieurs espèces cryptiques peuvent occuper des fonctions distinctes dans l'écosystèmes, ce qui peut être pris en compte à travers l'approche de la diversité fonctionnelle (De Meester et al., 2016; Fišer et al., 2018).

Le zooplancton : indicateur biologique de la santé des écosystèmes aquatiques

Différents types d'écosystèmes possèdent différentes taxons clés qui sont étudiées dans l'optique d'évaluer la biodiversité en raison de leur dominance dans l'écosystème ou leur sensibilité à certains stress. Dans les écosystèmes aquatiques tel les rivières, lacs, estuaires et écosystèmes marin, ces organismes sont le plancton, les invertébrés benthiques et les poissons à haut niveau trophique (Lu et al., 2015). Le zooplancton est un groupe particulièrement important dans l'étude des systèmes aquatiques puisqu'il relie le phytoplancton au reste des organismes constituant les niveaux supérieurs du réseau trophique. Leur petite taille ainsi que leurs cycles de vie généralement courts en font également des indicateurs des changements dans l'écosystème en raison de leur sensibilité aux variations environnementales et influences anthropiques (Chiba et al., 2018). De plus, la position centrale du zooplancton dans les réseaux trophiques aquatiques en fait un maillon important dont les variations auront une influence sur les niveaux trophiques inférieurs et supérieurs à travers les relations proies prédateurs (Fig. 1) (Vanni, 2002).

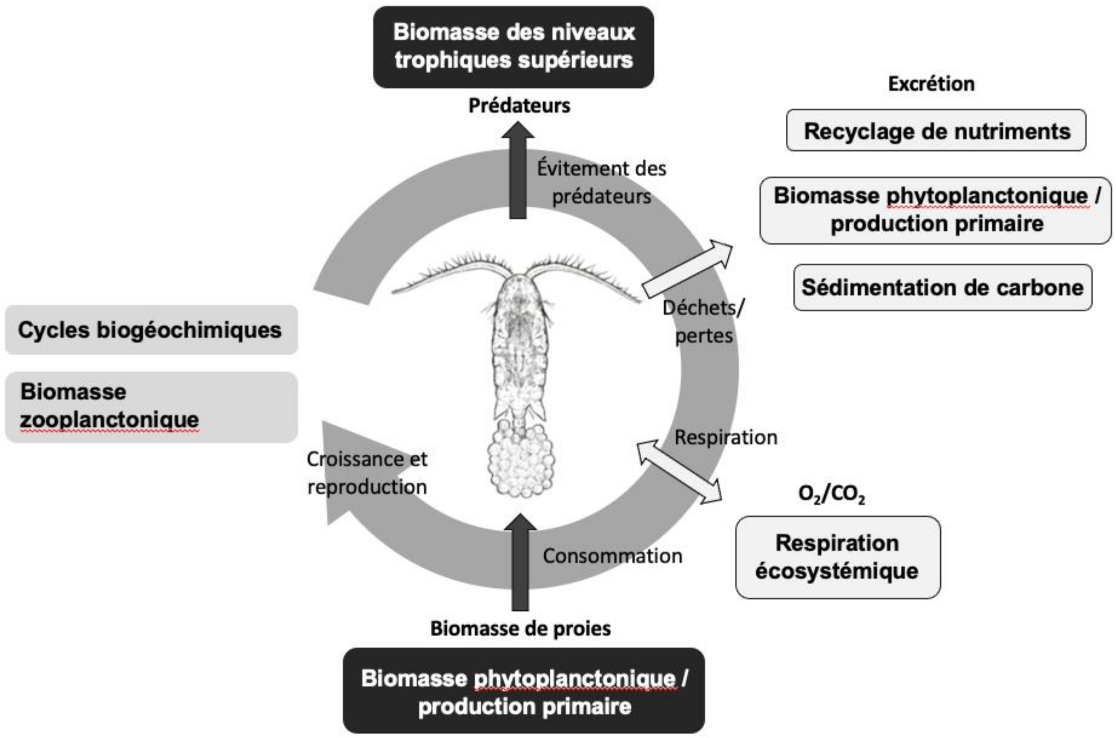


Figure 1. Schéma des interactions et échanges typiques d'un copépode dans son écosystème d'un point de vue de transferts énergétiques (Traduit et modifié de Hébert et al., 2017). Les boîtes représentent des exemples de processus écosystémiques influencés par le zooplancton. Le texte sur la flèche circulaire indiques les fonctions des organismes qui régulent les échanges : l'évitement des prédateurs, la respiration, la consommation et les déchets/pertes. Toutes ces fonctions affectent la croissance et la reproduction, qui affecte la biomasse zooplanctonique et les cycles biogéochimiques.

Le potentiel d'utilisation du zooplancton en tant que bioindicateur a été déterminé comme étant élevé, entre autres puisque la taille des populations est corrélée à plusieurs paramètres biotiques et abiotiques et que la présence ou l'absence de certaines espèces peut être indicatrice de la pollution d'un milieu (Ferdous et Muktadir, 2009).

Les fonctions de base de tout organisme se résument à l'alimentation, la reproduction et la croissance ainsi que la survie. Chez le zooplancton, des traits telle la production de matière fécales et la fréquence de reproduction sont utilisés afin d'étudier la croissance et la reproduction, tandis que la longévité et le rythme métabolique de base peuvent être utilisés en lien avec la survie. Certains traits sont toutefois particulièrement utiles puisqu'ils sont des indicateurs de plusieurs fonctions, notamment le ratio volume/biomasse et la taille des individus (Litchman et al., 2013). La taille des organismes est reliée à de multiples processus écologiques du zooplancton et au rythme de la plupart des processus physiologiques (Litchman et al., 2013; Heneghan et al., 2020). Les groupes trophiques sont entre autres fortement reliés à la taille du zooplancton, avec un taux de carnivorie positivement relié à la taille des individus et un taux d'herbivorie qui y est négativement relié (McLaskey et al., 2024).

Particularités et importance des communautés zooplanctoniques estuariennes

Les estuaires forment des écosystèmes aquatiques d'une grande importance écologique, sociale et économique. On retrouve plusieurs estuaires dans le monde dont les tailles sont variables, et dans lesquels il est possible de distinguer plusieurs sections avec des caractéristiques très distinctes les unes des autres et formant ainsi une succession d'habitats (Runge et Simard, 1990; David et al., 2016; Sun et al., 2023).

L'aspect central définissant les estuaires est la zone de mélange entre les eaux douces d'un fleuve et les eaux salées de la mer. Ce mélange donne lieu à l'une des caractéristiques principales de ces milieux, soit le très important gradient de salinité qu'on y retrouve et qui contraint la présence de certaines espèces aux caractéristiques physiologiques leur permettant de tolérer ces conditions. La salinité est un des gradients les plus évidents des estuaires, mais ceux-ci sont en réalité affectés par de nombreux gradients agissant sur différentes échelles, formant ainsi un milieu d'une grande complexité. On pense tout d'abord à la distinction entre les gradients spatiaux et temporels, ainsi qu'à la distinction entre les gradients chimiques et physiques, qui ont tous des effets sur la biologie de ces écosystèmes. Au niveau temporel, différents phénomènes peuvent avoir des effets sur des échelles de temps très différentes, tel l'influence des marées à court terme, par rapport à des changements dans le système dont les effets ne seraient distinguables que sur le long terme, par exemple sur plusieurs années (McLusky, 1993).

Une des difficultés majeures reliées à l'étude de l'écologie des estuaires est de distinguer les variations environnementales naturelles des modifications anthropiques ainsi que leurs impacts respectifs sur les espèces du milieu (Telesh et Khlebovich, 2010 ; Dafforn et al., 2012). La complexité due au dynamisme de ces systèmes rend d'autant plus difficile de faire des suivis de leur état en lien avec les influences anthropiques des dernières décennies (Dafforn et al., 2012).

Les conditions estuariennes créent des environnements propices à de fortes abondances de zooplancton (Benfield, 2012), mais où les populations de zooplancton sont également structurées par les gradients abiotiques préalablement décrits à travers les tolérances physiologiques des espèces (Runge et Simard, 1990; Laprise et Dodson, 1994). La rétention hydrodynamique ainsi que la resuspension par les marées entrainent des concentrations élevées de matières en suspension et de nutriments (d'Anglejan et Smith, 1973), permettant en retour une croissance importante de phytoplancton et ainsi de zooplancton qui s'en alimente (Benfield, 2012). Ces fortes abondances zooplanctoniques ont des répercussions sur tout le réseau trophique, donnant lieu à des pouponnières propices aux populations de poissons (Dodson et al., 1989; Ross, 2003; Macário et al., 2021 ; Humphreys et Little, 2022). Le suivi et la compréhension des communautés zooplanctonique des estuaires sont donc cruciaux dans la perspective où ce sont des écosystèmes particulièrement productifs aux conditions uniques en comparaison aux systèmes marins et limnétiques. Toutefois, les nombreux processus dynamiques à l'échelle spatiale et temporelle des estuaires en font des écosystèmes particulièrement complexes à étudier, demandant notamment une grande quantité d'échantillonnage pour atteindre une certaine représentativité en raison de la variation très élevée des communautés. Peu d'études à large échelle sur le sujet ont donc été réalisées (Benfield, 2012).

L'estuaire moyen du Saint-Laurent

L'estuaire du Saint-Laurent, situé dans le nord-est de l'Amérique du Nord et reliant les Grands Lacs laurentiens au golfe du Saint-Laurent, est l'un des plus grands estuaires au monde avec un bassin versant où habitent approximativement 30 millions de personnes (Fig. 2), lui procurant une importance indéniable d'un point de vue social et écologique (El-Sabh et Silverberg, 1990). On y retrouve en effet des pouponnières propices à des quantités importantes de larves d'espèces comme l'éperlan arc-en-ciel, le hareng et le bar rayé (Dodson et al., 1989; Sirois et Dodson, 2000; Vanalderweireldt et al., 2019). Les différentes caractéristiques abiotiques et topographiques sont utilisées pour distinguer l'estuaire en plusieurs zones, les principales étant l'estuaire fluvial, l'estuaire moyen et l'estuaire maritime. L'estuaire moyen est également nommé la zone de transition estuarienne (ZTE) du Saint-Laurent, et est située entre l'Île d'Orléans et l'embouchure du Fjord du Saguenay (El-Sabh et. Silverberg, 1990). Cette zone est constituée d'eaux saumâtres résultant du mélange des eaux douces et marines, où la rétention hydrodynamique et la resuspension engendrent une grande productivité primaire qui procure à la ZTE une grande importance écologique (d'Anglejan et Smith, 1973; Dodson et al., 1989). À l'intérieur de cette dernière se trouve la zone de turbidité maximum (ZTM), qui est définie comme étant la zone avec la concentration la plus élevée de matière en suspension, généralement reliée à la *null zone*, endroit auquel les courants en amont et en aval s'annulent (McLusky, 1993). Cette étude s'attardera plus spécifiquement sur la ZTE, constituée en grande partie d'eaux saumâtres et située de l'Île d'Orléans à l'embouchure de la rivière du Saguenay (El-Sabh et Silverberg, 1990).

Nos connaissances actuelles sur les communautés zooplanctoniques de la ZTE du Saint-Laurent proviennent d'un nombre relativement faible d'études et de travaux universitaires (El-Sabh et Silverberg, 1990). Ces communautés se distinguent par quelques taxons dominants qui forment des communautés distinctes dans différentes zones de l'estuaire et sont structurées par les conditions environnementales (Runge et Simard, 1990; Laprise et Dodson, 1994; Vincent et Dodson, 1999; Winkler et al., 2003). Bousfield et al. (1975) ont réalisé une des études les plus complètes du zooplancton de l'estuaire moyen, identifiant environ 25 taxons distincts. L'estuaire moyen est caractérisé par une forte présence des copépodes *Acartia* spp. et *Eurytemora* spp. (Bousfield et al. 1975; Laprise et Dodson, 1994), *Eurytemora affinis* étant une espèce euryhaline répandue dans plusieurs estuaires du monde

(Devreker et al., 2004). Dans l'estuaire marin, on retrouve davantage d'espèces du genre *Calanus*, alors que de nombreux taxons distincts autres que des copépodes tels que le diplostraca *Bosmina* sont présents dans la zone limnétique de l'estuaire (Bousfield et al. 1975; Laprise et Dodson, 1994).

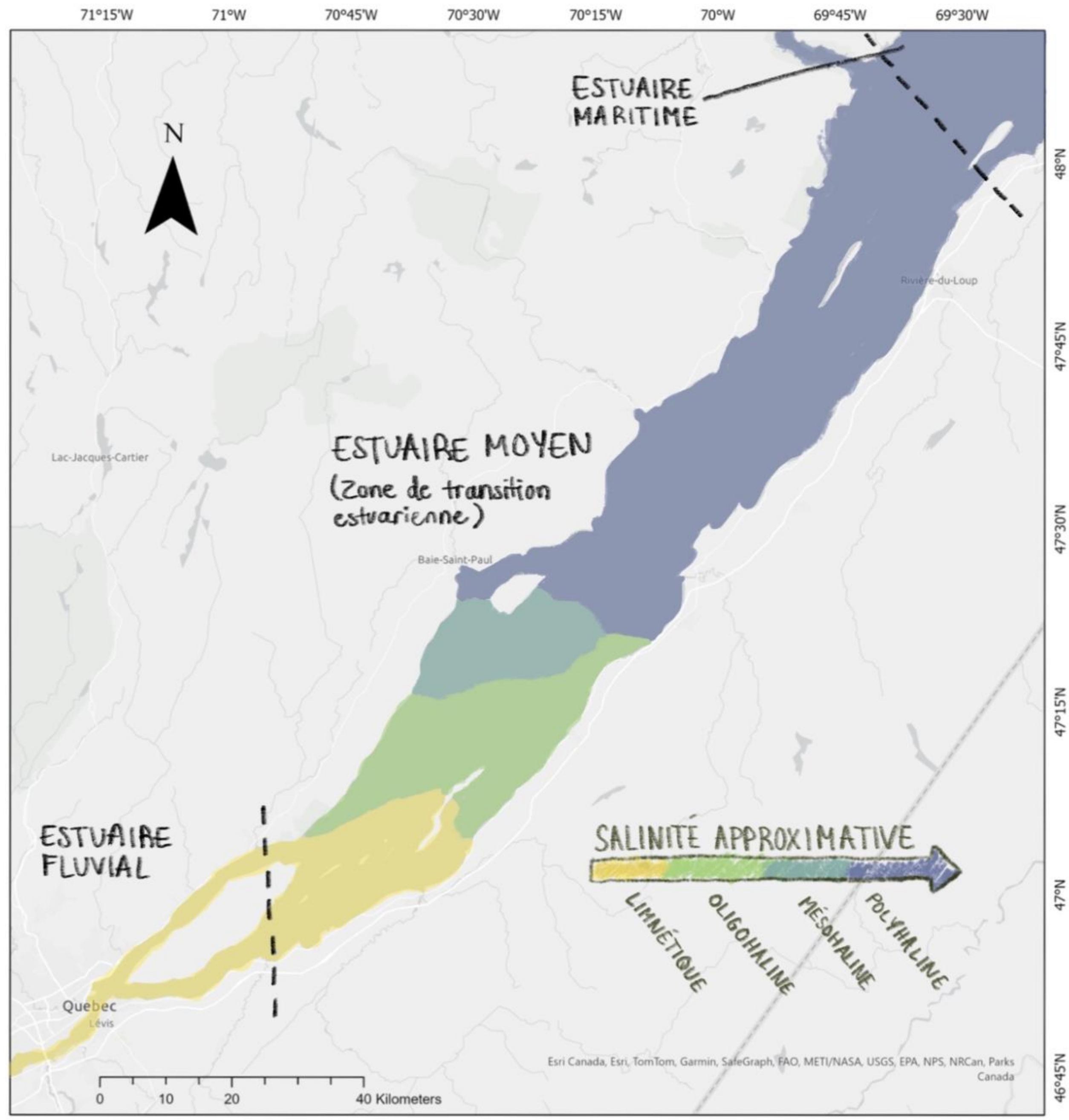


Figure 2. Carte de l'estuaire moyen du Saint-Laurent et des zones approximatives de salinité entre 2019 et 2022 selon la classification de Venise.

Problématique

Manque de données récentes et pressions anthropiques croissantes sur les communautés zooplanctoniques de l'estuaire moyen du Saint-Laurent

Tel que discuté précédemment, les dernières études à grande échelle du zooplancton de la ZTE du Saint-Laurent sur lesquelles se basent nos connaissances de ces communautés datent des années 1990 (Runge et Simard, 1990; Laprise et Dodson, 1993; Laprise et Dodson, 1994). Il est ainsi difficile d'avoir un portrait des communautés zooplanctoniques actuelles de l'estuaire et des changements qu'elles ont potentiellement subis depuis les dernières décennies. Cette lacune scientifique est problématique considérant la sensibilité accrue de la ZTE du Saint-Laurent aux influences anthropiques croissantes (Vincent et Dodson, 1999). Plusieurs études suggèrent que la structure des communautés zooplanctoniques est affectée par des changements environnementaux tels que les augmentations de température (Laprise et Dodson, 1994; Winkler et al., 2005, Blais et al. 2023b), ce qui risque d'avoir des implications pour tout le réseau trophique et l'écosystème en raison de la place centrale qu'occupe le zooplancton dans l'estuaire. On observe depuis plusieurs années des changements environnementaux importants dans le fleuve Saint-Laurent, tels des anomalies de température (Galbraith et al. 2022), l'établissement d'espèces invasives (Winkler et al., 2005), une augmentation de certains polluants (Desrosiers et al., 2019), ou encore une acidification et une augmentation de l'hypoxie reliée aux activités anthropiques (Schloss et al., 2018). Des impacts au niveau des groupes fonctionnels ont entre autres été observés chez certains groupes taxonomiques du Saint-Laurent comme les macroinvertébrés benthiques (Schloss et al., 2018). Compte tenu du faible nombre d'études sur les impacts touchant le zooplancton de la zone de transition estuairienne, la présente étude pourrait servir de base de référence pour analyser les effets des changements climatiques.

Il demeure difficile de prédire les impacts de ces influences en raison de la complexité du fonctionnement de l'estuaire, comme démontré par l'absence d'impact détecté sur le zooplancton de la ZTE à la suite de l'arrivée de l'espèce invasive *Dreissena polymorpha*

(Winkler et al., 2005). La moule zébrée (*Dreissena polymorpha*) fut introduite en Amérique du Nord vers la fin des années 1980 et s'est depuis établit dans les Grands Lacs et le fleuve Saint-Laurent (Kingsbury et al., 2025). Dans des systèmes aussi dynamiques que les estuaires, l'une des difficultés principales est la distinction du rôle que viennent jouer les impacts anthropiques par rapport aux variations environnementales qui n'y sont pas reliées (Sun et al., 2020), soulignant l'importance d'un plus grand effort d'étude dans ces milieux.

Objectif

En lumière des enjeux soulevés, l'objectif central de ce projet de recherche est d'établir l'état actuel et le niveau de variabilité interrannuelle des communautés zooplanctoniques de l'estuaire moyen du Saint-Laurent entre 2019 et 2022 afin d'avoir une compréhension plus complète de ces écosystèmes et ainsi d'anticiper les changements futurs en lien avec les facteurs environnementaux (Fig. 3). Plus précisément, ce projet a comme sous-objectifs de déterminer la composition et les variations de la biodiversité des communautés zooplanctoniques d'un point de vue taxonomique et fonctionnel le long du gradient de salinité de la ZTE, ainsi que de déterminer les facteurs environnementaux qui influencent ces assemblages. Ceci sera réalisé à travers l'analyses de la composition et de la diversité taxonomique et fonctionnelle des communautés zooplanctoniques de l'estuaire moyen de 2019 à 2022 durant le mois d'août, permettant de décrire leur structure geographique et leurs variations. L'utilisation de facteurs environnementaux permettra également, le cas échéant, de relier ces assemblages et ces variations potentielles à des conditions environnementales afin d'établir un portrait complet des interactions du zooplancton et de son écosystème.

Le projet actuel est le premier à analyser en profondeur les données de ces communautés de zooplancton depuis les dernières études sur le sujet datant du début des années 2000. Ces nouvelles données proviennent d'un suivi annuel avec le potentiel de se poursuivre dans les prochaines années.

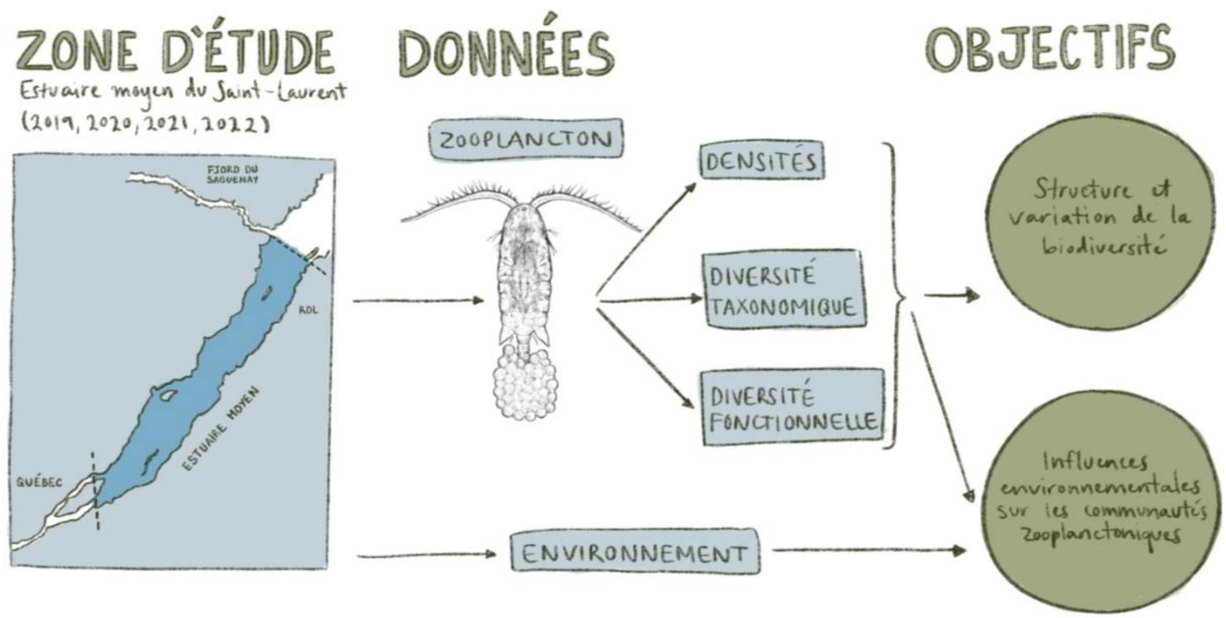


Figure 3. Schéma récapitulatif de la zone d'étude, des données et des objectifs de la présente étude.

CHAPITRE 1: DYNAMIQUE SPATIO-TEMPORELLE DES COMMUNAUTES ZOOPLANCTONIQUES DE L'ESTUAIRE MOYEN DU SAINT-LAURENT FACE AUX INFLUENCES ENVIRONNEMENTALES

SPATIO-TEMPORAL DYNAMICS OF ZOOPLANKTON COMMUNITIES IN THE MIDDLE ESTUARY OF THE ST. LAWRENCE IN RESPONSE TO ENVIRONMENTAL INFLUENCES

INTRODUCTION

The health of an ecosystem is defined by multiple factors, mainly its productivity, its biological composition as well as the interactions among organisms, and its capacity to maintain its structure and function in the event of stress, both spatially and temporally (Giraudoux, 2022). One way to study the composition of an ecosystem is through its biodiversity, which traditionally considers the proportions and densities of different taxonomic groups present in each community, and is also used to calculate different diversity indices (Daly et al., 2018). Our understanding of biodiversity has however recently been shifting to the inclusion of functional diversity to improve our understanding of ecosystems (Schleuter et al., 2010). This approach is based on functional traits, which can refer to morphological, physiological or behavioral characteristics instead of taxonomical groups (Violle et al., 2007). Using functional groups can provide a complementary understanding of the structure and variation of the multiple process in an ecosystem, which would otherwise not necessarily be detected using only taxonomic groups (Balvanera et al., 2006; Violle et al., 2007; Hébert et al., 2017).

In aquatic habitats, zooplankton occupy a key position in the food web by linking phytoplankton with higher trophic levels (Vanni, 2002). Their small size, short lifespan, and sensitivity to environmental changes make them highly suitable as bioindicators of pollution and indicators of global ecosystem health (Ferdous et Muktadir, 2009; Chiba et al., 2018). Dynamic environments such as estuaries create habitats with high nutrient availability through the mixing between saltwater and freshwater, hydrodynamic retention and resuspension by tides (Bousfield et al. 1975; Day et al., 2013). This entrapment and rapid recycling of nutrients from freshwater inputs, combined with the couplings of heterotrophic and autotrophic processes, support high productivity levels (Dodson et al., 1989) and therefore abundant zooplankton concentrations (Winkler et al., 2003; Benfield, 2012; Day et al., 2013). A good understanding of these communities through zooplankton monitoring is therefore crucial for our understanding and conservation of these ecosystems while also representing a challenge because of the high spatio-temporal variations (Chiba et al., 2018).

In North America, the St. Lawrence estuary is one of the largest waterways, linking the Great Lakes to the Atlantic Ocean. The freshwater discharge mixes with the saltwater from upstream in the estuarine transition zone (ETZ), located between Ile d'Orléans, (Québec City) and Tadoussac, creating major currents that lead to both spatial and temporal variations of the environmental factors such as the temperature and salinity (d'Anglejan et Smith, 1973). Between Ile d'Orléans and Île-aux-Coudres is the Maximum Turbidity Zone (MTZ), an ecologically significant zone for its very high concentrations of suspended matters due to the tidal circulation (d'Anglejan et Smith, 1973). The resulting ecosystem consists of fluctuating environmental conditions that structure the community composition depending on organisms' tolerance to these conditions (Runge et Simard, 1990; Laprise et Dodson, 1994; Winkler et al., 2003). The estuarine nutrient-dense zone provides an ideal environment for the nurseries of multiple fish species (Dodson et al., 1989; Vanalderweireldt et al., 2019).

The ETZ is an area with major ecological, economic and social implications with complex zooplankton communities but where a survey of these communities over the entire ETZ has been lacking since the 1990s. This is especially problematic considering the major changes in the estuary since the last large-scale surveys, such as the reintroduction of the striped bass in 2002 (Vanalderweireldt et al., 2019) or the invasion by zebra mussels

(*Dreissena polymorpha*) veligers (Winkler et., 2005). Environmental factors as well as biological aspects of zooplankton have been found to be the main drivers of intraannual variations in the communities (Laprise et Dodson, 1994; Winkler et al., 2003). Distinct communities are present in different zones of the Estuary and are strongly structured by the salinity gradient (Runge et Simard, 1990; Laprise et Dodson, 1994). Specific taxas characterize each habitat, such as *Bosmina longirostris* in the limnetic zone upstream, *Eurytemora affinis* in brackish waters and *Acartia* spp. and *Calanus* spp. downstream (Bousfield et al. 1975; Laprise et Dodson, 1994). Zooplankton occupies a key role in estuarian ecosystems (Vanni, 2002). Because the St. Lawrence ETZ is particularly sensitive to anthropogenic disturbances, that can interact with environmental parameters, it is essential to understand factors driving zooplankton variations (Vincent et Dodson, 1999; Kneitel et Chase, 2004; Veríssimo et al., 2017).

The aim of this study is to improve our understanding of the environmental factors structuring the zooplankton communities of the ETZ of the St. Lawrence using zooplankton and environmental data collected annually in August or September from 2019 to 2022. The functional diversity of these communities will also be analysed to create a complete picture of spatio-temporal taxonomic and functional variations along the salinity gradient. The first specific objective is to describe the structure and variations of the zooplankton communities of the ETZ between 2019 and 2022, both taxonomically and functionally. The second objective is to find the main environmental factors structuring the communities during those years and their respective influences. The monitoring and understanding of the zooplankton of the St. Lawrence Estuary is essential to assess the multiple anthropogenic pressures that could affect the functioning of the ecosystem and to insure successful management (Vincent et Dodson, 1999; Desrosiers et al., 2019).

MATERIAL AND METHODS

STUDY AREA

The estuarine transition zone, the St. Lawrence Middle Estuary, between Québec City and Cacouna was sampled for four year 2019-2022, mainly in August (Fig. 4). The sampling stations varied each year, due to weather conditions and logistical issues (Fig. 4). The locations of the sampling sites were chosen to achieve a broad range in community types and environmental conditions, enabling us to examine both spatial and temporal variations. Stations can be divided into two sectors, respectively from Québec to Isle-aux-Coudres, characterized by mean depths of less than 10 m, and from Isle-aux-Coudres to Cacouna, with station depths that can reach around 50 m.

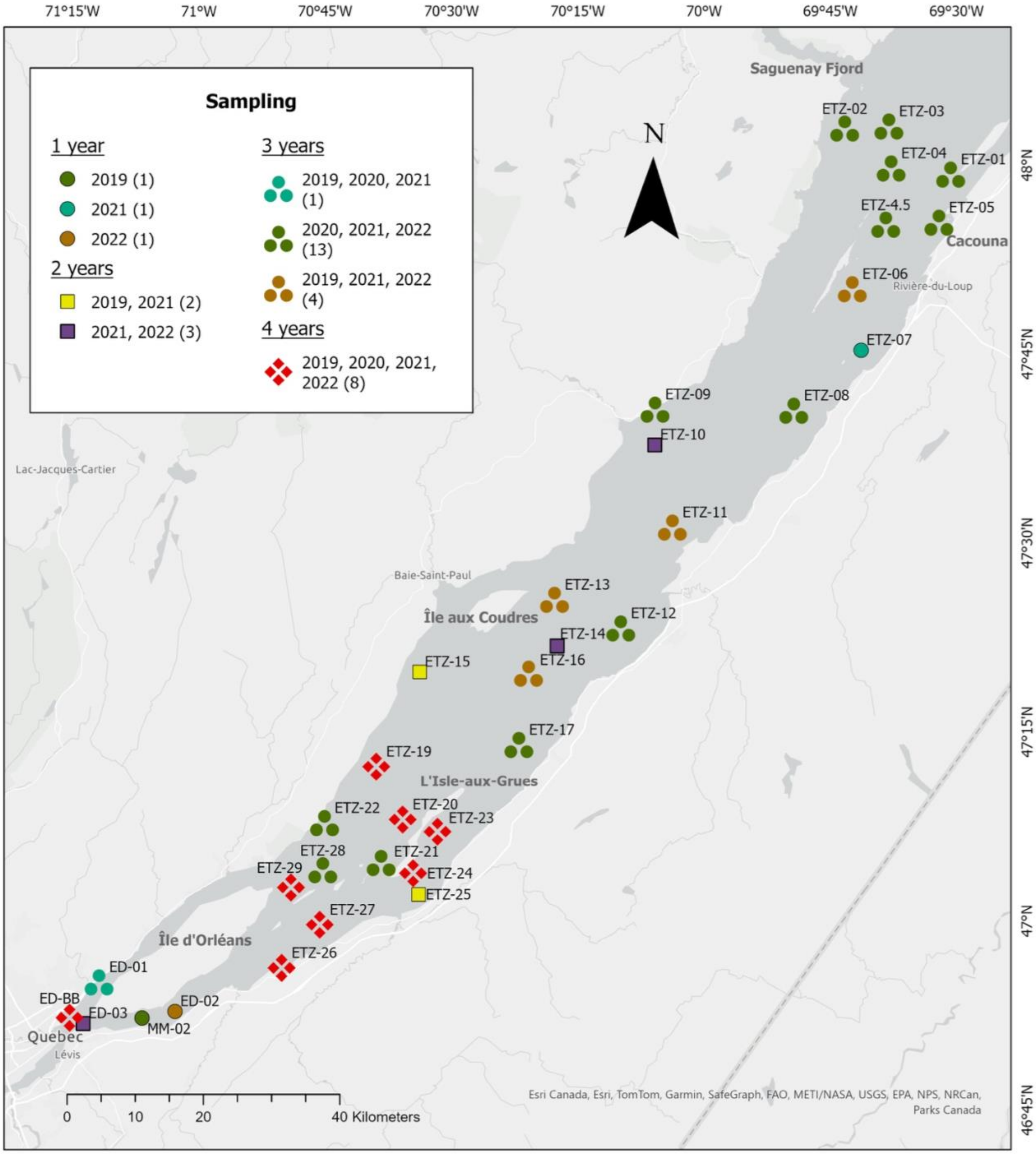


Figure 4. Location of the sampling stations in the Estuarian Transition Zone (ETZ) of the St. Lawrence where zooplankton was collected each year from 2019 to 2022. Samples were collected in August except in September of 2019.

SAMPLING

All the data used in this study were sampled on the Lampsilis, the research catamaran of the Université du Québec à Trois-Rivières (UQTR) during early to mid-August in 2020, 2021 and 2022 and in early September in 2019. Between 25 and 51 stations were sampled for zooplankton in the St Lawrence Estuary each year (Table 1, Table A1), while a total of 34 stations were analysed (Fig. 4). The number of sampling stations that could be analysed was restrained by limited time and resources, and a priority classification was used to ensure that the stations analysed captured a broad spectrum of communities and environmental conditions, as well as locations of particular ecological or geographical importance within the estuary.

Zooplankton samples were collected using plankton nets at each station. Verticals hauls were conducted with a 63 µm plankton net (diameter 1 m) to collect microzooplankton, while oblique hauls were done with a 200 µm plankton net (diameter 1 m) to collect mesozooplankton (Table 1; Table A1). The hauls were taken throughout the entire water column for both nets, except when suspended matter clogged the 63µm net, in which case we sampled surface layer of the first 5 m only (at 36 stations out of a total of 70 stations during the 4 years). Out of these stations, 48 stations were very shallow with a depth of 10 m or less. The resulting samples of both nets were then filtered through corresponding mesh size sieves and conserved in 95 % ethanol at 4 °C. Ethanol changes were done 24 h after each sampling to assure stable pH and ethanol concentration. To calculate the water volume filtered through each oblique haul, flowmeters (Model 2030R mechanical Flowmeter, General Oceanic) were attached to the openings of the 200 µm nets to later calculate the volume filtered since these were oblique hauls.

Table 1. *Sampling dates of each mission and number of stations sampled and analysed with the 63µm and 200µm plankton nets.*

Mission	Sampling dates	Stations sampled		Samples analysed	
		63 µm	200 µm	63 µm	200 µm
MAL 2019	2019/08/30 - 2019/09/08	26	27	12	17
MAL 2020	2020/08/03 - 2020/08/12	25	25	19	25
MAL 2021	2021/08/04 - 2021/08/13	34	51	24	30
MAL 2022	2022/08/11 - 2022/08/17	29	29	17	29

To characterize physico-chemical water properties (temperature, pH, fluorescence, turbidity and salinity), a CTD probe (Model SBE19plus, Sea-Bird Scientific) a profile of the water column was taken at the beginning and end of the sampling at each station. Niskin bottles of 5-L were used to collect water samples at a depth of 1 m for every station and at 1 m above the bottom for stations with a depth of >10 m. Water was used to measure Chlorophyll *a* (chl *a*), nutrients (PO_4^{3-}, NO_2^-+NO_3^-), pico- and nanoeucaroytes, pico- and nanocyanobacteria, bacteria and suspended matter (SPM, POM, PIM). Since environmental conditions can vary with tides, each station in each year was classified into a salinity group according to the Venice classification by calculating the median of the salinity values measured through the entire water column (Table 2) (Anon, 1959). The same station can therefore be part of different salinity zone depending on the year.

LABORATORY ANALYSIS

Onboard filtration of water samples for the analysis of environmental factors were done directly after sampling. Two replicates were filtered for chl *a* concentration at each depth by filtering water over 0.7 µm (diameter 25 mm) Whatman GF/F filters and adding acetone to extract the pigment for 20 h at 4 °C. Different types of suspended matters (SPM, POM, PIM) were also measured by filtering water over the same type of previously weighed Whatman GF/F filters and storing them at -20 °C. For nutrients, three replicates were filtered over 0.2 µm cellulose acetate filters and stored at -20 °C before further analysis. Three replicates were also taken for bacterio-, pico- and nanoplankton, for which water was filtered over 40 µm and fixed with 1 % glutaraldehyde at room temperature and left in the dark for 10 minutes before being stored at -80 °C.

The following analysis were done at Institut des Sciences de la Mer de Rimouski (ISMER, Rimouski, Qc) in the weeks after the sampling. Chl *a* concentrations were measured by fluorometry (10-AU-005-CE, Turner-Design) according to the methods described by Mundy et al. (2011). Suspended matters were measured by lyophilizing the filters before weighing them. Two out of the three replicates for each station were then place at 450 °C for 5 hours to burn the organic matter, leaving only the particulate inorganic matter to be measured. Nutrient concentrations were determined using an automated analyzer (AA500 Autoanalyzer, SEAL Analytical) following the JGOFS protocol (JGOFS, 1994). The water samples fixed with glutaraldehyde were also analysed by flow cytometry according to methods described by Belzile et al. (2008) to measure pico-, nano- eukaryotes, cyanobacteria and bacteria.

Table 2. *Salinity classes from the Venice classification system (Anon, 1959) and number of stations (samples) analysed in each category based on the year and plankton net.*

Venice classification	Salinity range (%)	Number of stations for which zooplankton samples were analysed for each year and plankton net							
		2019		2020		2021		2022	
		63 µm	200 µm	63 µm	200 µm	63 µm	200 µm	63 µm	200 µm
Freshwater	< 0.5	4	7	6	12	3	5	4	9
Oligohaline	0.5 - 5	2	3	3	3	4	6	4	4
Mesohaline	5 - 18	3	3	2	2	5	6	2	2
Polyhaline	18 - 30	3	4	7	8	6	13	7	13

After sampling, zooplankton samples were transferred to a - 20 °C freezer until further analysis. Each sample was first filtered over 63 µm or 200 µm sieves and diluted in a volume of water at which the organism density was appropriate for visual identification. A Hensen Stemple pipette of 5 ml or 10 ml was then used to sub-sample the zooplankton samples the number of times necessary to reach a count of 400 individuals of all zooplankton taxa. Organisms were counted and identified with a stereoscopic microscope (Model SZX2, Olympus) to the lowest possible taxonomic level according to morphological characteristics from the literature. When possible, the sex, development stage and number of eggs for females were also noted. The identification and enumeration were considered representative once a count of 400 individuals (excluding bivalves) per sample was reached, which equals to a precision of ±10 % of individuals counted (Lund et al., 1958). To calculate zooplankton density, the formula for calculating a cylinder's volume was used for vertical hauls by multiplying the area of the opening of the net with the length of the cable. For oblique hauls, the number of rotations from the flowmeter could be multiplied with the area of the opening of the net and the constant 26873/999999. The number of individuals identified was then adjusted according to the dilution volume in laboratories and divided by the volume filtered by the plankton nets to determine the density in ind. m^{-3}.

LITERATURE REVIEW FOR FUNCTIONAL TRAITS

A total of 4 functional traits were selected for this study based on their relevance for zooplankton species (Martini et al., 2020 ; Santo, 2023) : body size, life cycle, trophic group(s) and feeding method(s) (Table 3). An extensive literature review was done to create a database with the selected functional traits values for each identified taxon. When a taxon was described to fit in multiple categories of the same functional trait, all were included unless one was predominant. Some taxa were identified at a lower taxonomic level and therefore contained multiple species: the functional groups the most present among the taxa were considered according to the literature.

Table 3. *Description of each functional traits used in this study and possible values for non-numeric variables.*

Functional traits	Values	Description
Body size	Continuous numerical value	Mean total size, specific to each developmental stage when relevant (Benedetti et al., 2016).
Life cycle	Holoplankton	Taxa, which are considered parts of the plankton throughout their whole life, cycle (Allen et al., 2014).
	Meroplankton	Taxa that are only part of the plankton during certain phases of their life cycle (Allen et al., 2014).
	Bentho-plankton	Not genuinely planktonic, will swim among the plankton during certain phases of their life cycle. Ex: Isopoda (Poore and Bruce, 2012).
Trophic group(s)	Omnivore	Typically refers to organisms that consume food from multiple trophic groups, but can includes a wide range of diets that do not fit other trophic groups (Benedetti et al., 2016).
	Herbivore	Taxa that primary consume plants (Benedetti et al., 2016).
	Carnivore	Taxa that mainly feed off animals (Benedetti et al., 2016).
	Detritivore	Organisms that feed off particulate organic matters (Benedetti et al., 2016).
	Coprophage	Refers to taxa that exclusively or mainly eat another individual's faeces. The only species considered coprophagous is this project is *Microsetella norvegica* (Priou, 2015).
	Non-feeding	Typically includes early stages of some taxa where feeding has not yet started, or the necessary appendage has not developed yet (Allen et al., 2014).
Feeding method(s)	Active ambush feeding	Taxa that find their prey by passively encountering them but capture them with active attacks (Kiørboe, 2011).
	Passive ambush feeding	These taxa are referred to as passive since they do not remotely detect their prey, but rather consume it as it encounters them. Here, the grazer is therefore non-motile (Kiørboe, 2011).
	Current feeder	Often referred to as suspension feeder or filter feeder, current feeders create a current through which they filter particulate matter that they eat (Kiørboe, 2011).
	Cruise feeder	Cruise feeder actively encounter their prey by swimming towards them before attacking (Kiørboe, 2011).
	Parasite	Taxa whose feeding method is exclusively or primarily parasite by extracting nutrients from another organism. Only the rotifera taxa *Proales* sp. and some *Isopoda* species were found to be of this category (Kumar, 2005 Gilbert, 2022).
	Mixed strategies	Taxa in which different species use different feeding methods.

NUMERICAL ANALYSIS

Since this study aimed to look specifically at zooplankton communities, taxa present in the samples but classified with a life cycle other than planktonic were not considered in the abundance and diversity analysis. To ensure only representative data was used, eggs, egg sacs, embryos and broken individuals were removed. Additionally, taxa identified to order or higher were not considered in the taxonomic and functional diversity analysis since different species can be part of different functional groups and need to be considered separately to remain relevant (Table 4).

Table 4. *List of taxa excluded from different numerical analysis and corresponding exclusion criteria.*

Analysis from which the taxa were excluded	Exclusion criteria	Taxa excluded for the analysis
Abundance Taxonomic diversity Functional diversity	1. Taxa that are not part of the zooplankton;	Ascidiacea (benthos) Gadidae (ichtyoplankton) Gammaridae (benthos or plankton) Hydrozoa polyp (benthos) Ichtyoplankton Isopoda (benthos) *Microgadus tomcod* (ichtyoplankton) *Osmerus mordax* (ichtyoplankton) Tardigrada (benthos)
	2. Unicellular organisms;	Foraminiferida Radiolaria Tintinnina
Functional diversity	3. Taxa which were identified as an order or a higher classification category, sometimes identified at larval life stages such as nauplius or copepodites;	Acantharea Amphipoda Appendicularia Bivalvia Brachyura Calanoida Chaetognatha Cirripedia Diplostraca Cnidaria Copepoda Echinodermata Ctenophora Cumacea Cyclopoida Decapoda Ectoprocta Facetotecta Gastropoda Harpacticoida Hyperiidae Mollusca Mysidacea Oligochaeta Ostracoda Polychaeta Rotifera

Taxa (St) and species (S) richness, Shannon-Wiener index (H') and Pielou evenness (J'), accounting for taxonomic diversity, were calculated using the 'vegan' R package (R, version 4.1.1). In all analysis and calculations except for species richness, taxa were considered instead of species due to the varying identification level. Similar functional diversity indices were chosen and calculated with the 'mFD' R package based on Gower's distance, including the four functional traits described above (R, version 4.1.1). Functional richness (Fric) corresponds to the 'volume of the functional space occupied by the community', while functional divergence (Fdiv) is the 'divergence in the distribution of abundance in this volume' and functional evenness (Feve) measures the 'regularity of the distribution of abundance in this volume' (Villéger et al., 2008).

The community data was composed of densities of the taxa found at each sampling station. Prior to multivariate analysis of zooplankton communities, a square-root transformation was applied to the community data to reduce the contribution of high-density taxa. Density and diversity indices were compared using Euclidian distance, while Bray-Curtis distance was used for community data. Non-metric multidimensional scalings (nMDS) were performed to visualise similarities or dissimilarities of communities in different salinity zones and years (PRIMER-E 7). Zooplankton communities were compared by performing two-way PERMANOVA (permutational MANOVA) (PRIMER-E 7) with the two factors being year and salinity zone for three sets of response variables: community data, mean total density station and taxonomic and functional diversity indices. A One-Way Similary Percentage analysis (SIMPER) (PRIMER-E 7) was performed on the square-root transformed community data to distinguish which taxa were mainly responsible for the differences in zooplankton communities between years and salinity zones (Table A9).

As for environmental data, surface values were calculated for each station using mean values measured at a depth of 1 m (0.992 m) from the two of three CTD casts. All environmental data were then normalised prior to all analyses. Collinearity among environmental factors was examined prior to analysis with a correlation plot from a correlation matrix created with the 'corrplot' R package (R, version 4.1.1). BEST analysis with the BIOENV method (PRIMER-E 7) were used to find the subset of environmental variables with the best correlation to community data (Hossain, 2013). Variables with a Spearman correlation coefficient of 0.70 or higher were considered to have a strong correlation and were not used simultaneously in the redundancy analyses (Schober et al., 2018). The set of environmental variables that best explained community variation, while excluding strongly correlated variables, was used in redundancy analyses (dbRDA) to examine the relationships between environmental predictors and community response data.

RESULTS

Environmental conditions

From 2019 to 2022, environmental conditions of the St Lawrence Estuary varied strongly among salinity zones, but less so among years, for both abiotic and biotic variables. While 2019 data were not included in the PERMANOVA due to multiple missing values, environmental conditions were similar between 2020 and 2021 ($p_{Year} > 0.05$; Table A4). For most variables, two groups of salinity zones appeared: freshwater and oligohaline zones were different from mesohaline and polyhaline zones. Salinity values corresponded to the Venice Classification, resulting in greater variability in the mesohaline and polyhaline ranges (Fig. 5A). Temperature was negatively correlated with salinity, varying from 9.07 °C in polyhaline waters in 2022 to 23.6 °C in freshwater in 2020, as was nitrogen (NO_2NO_3) (Fig. 5B & C). On the other hand, phosphorus (PO_4^{3-}) values were positively correlated with salinity (Fig. 5D). Fluorescence and turbidity followed similar patterns, with freshwater having lower values than oligohaline waters in 2019 and 2020 but higher values in 2021 and 2022. Fluorescence and turbidity amplitude and variance were lower and decreasing between mesohaline and polyhaline waters (Fig. 5E & F). Bacteria concentrations were consistently higher in oligohaline waters with the exception of 2022, again (Fig. 5H). The mean concentration varied from 7.72×10^5 cells ml^{-1} for polyhaline waters in 2019 to 2.85×10^6 cells ml^{-1} for freshwater in 2022.

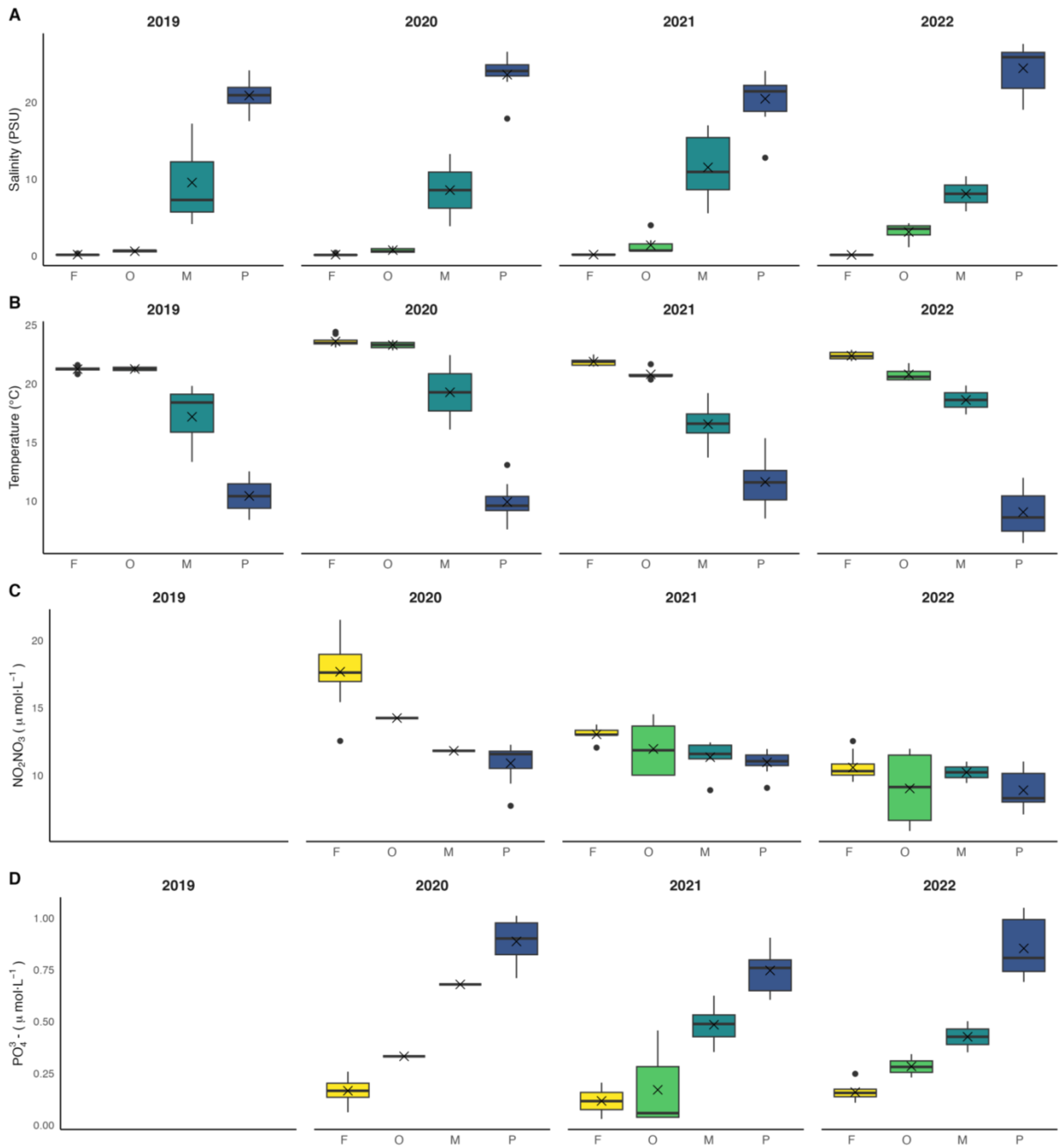


Figure 5. Medians of abiotic environmental variables from 2019 to 2022 for each salinity zone: freshwater (F, yellow), oligohaline (O, green), mesohaline (M, turquoise) and polyhaline (P, blue). Measured environmental variables are: salinity (A), temperature (B), NO_2NO_3 (C), PO_4^{3-} (D), fluorescence (E), turbidity (F), POM (G) and bacteria (H). Nitrogen (NO_2NO_3) and phosphorus (PO_4^{3-}) were not measured in 2019. The box represents the interquartile range (25th percentile to 75th percentile) while the median is the thick line inside it and the black cross is the mean. The whiskers extend to the most extreme data points and black dots indicate outliers.

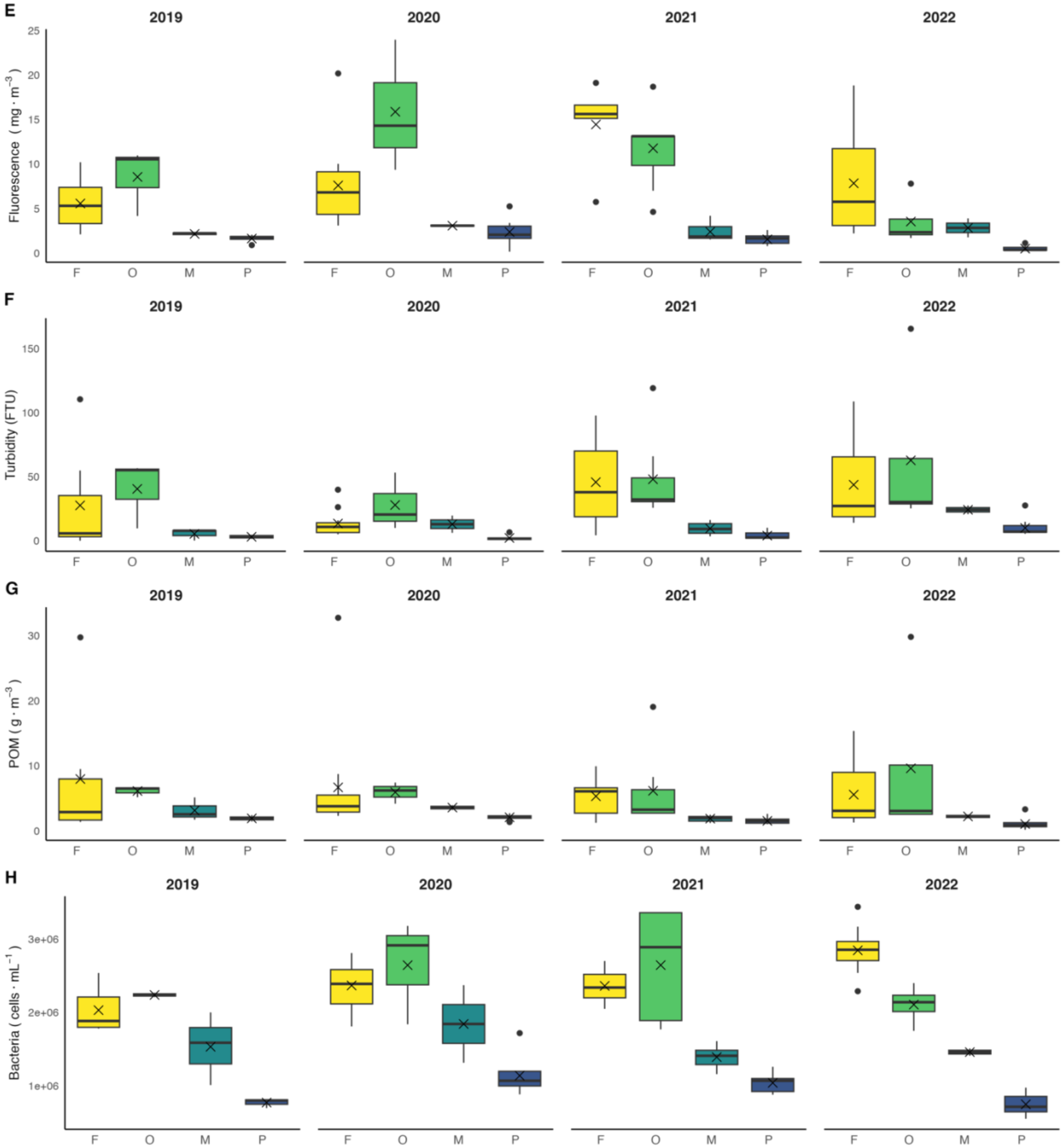


Figure 5 (continued).

Density and distribution of zooplankton

Mean total zooplankton density varied between 2,372 ind. m^{-3} (oligohaline, 2021) and 170,719 ind. m^{-3} (mesohaline, 2022) for 63 µm (Fig. 6). Overall, high densities were found in 2019 and 2021 compared to 2020 and 2022. Significant variations among years ($p_{Year} <$ 0.05 ; Table A4) were found (in 63 µm) between 2019 and 2022, 2021 and 2022 and between 2020 and 2021. In 2020, lowest mean density was found in the mesohaline zone, while in 2021, the mean density was higher in oligohaline and mesohaline zones compared to the polyhaline zone.

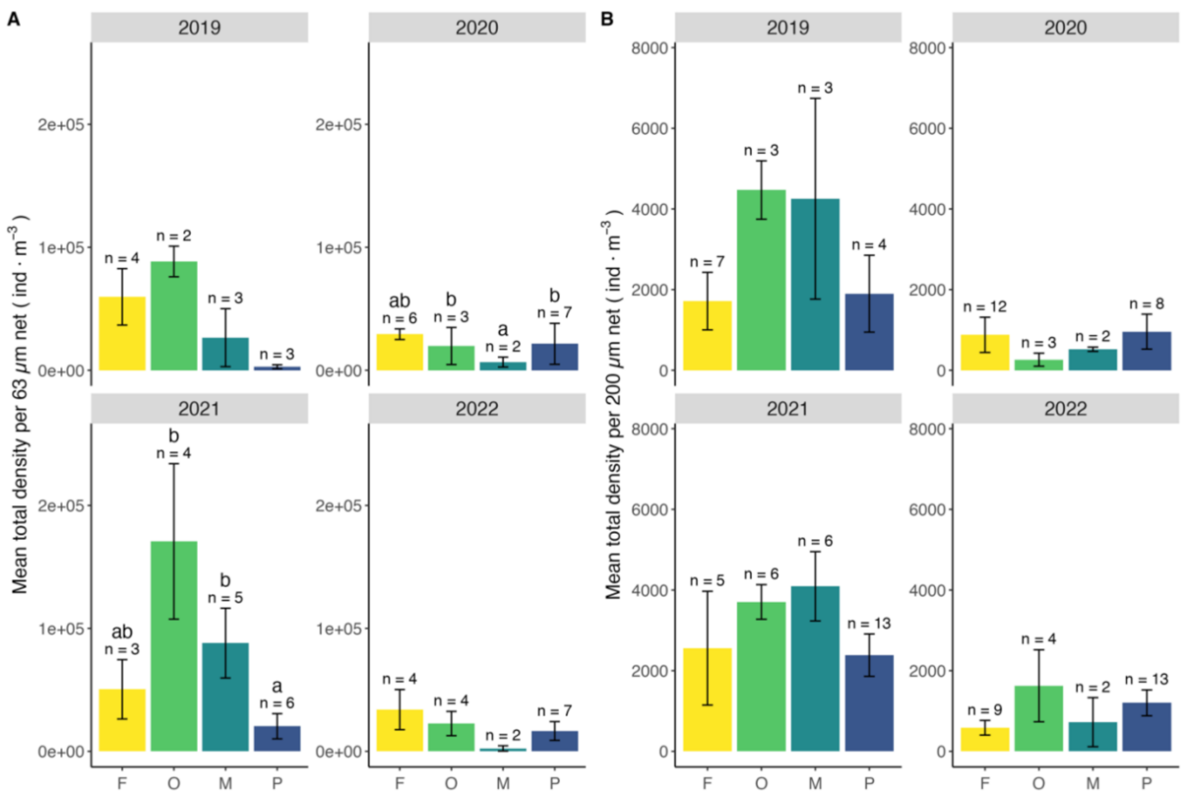


Figure 6. Mean total zooplankton density per station by year and salinity zone for 63 µm nets (A) and 200 µm nets (B) for freshwater (F, yellow), oligohaline (O, green), mesohaline (M, turquoise) and polyhaline (P, blue). Error bars represent the standard error of the mean of the total density, and the number of stations per category is equal to *n*. Different letters indicate significant differences according to PERMANOVAs ($p_{Year*salinity\ zone} < 0.05$; Table A8).

Total densities in 200 µm nets were much lower than in 63 µm nets, with the minimum value being 262 ind. m^{-3} (oligohaline, 2020) and the maximum one being 4,468 ind. m^{-3} (oligohaline, 2019). General patterns were similar to 63 µm as oligohaline and mesohaline densities varied more than freshwater and polyhaline. However, unlike 63 µm, only significant differences between years were found: between 2019 and 2020, 2019 and 2022, 2020 and 2021 as well as 2021 and 2022 ($p_{Year} < 0.05$; Table 4).

According to the SIMPER analysis (Table A9), the taxa that contributed the most to the dissimilarity in both 63 µm and 200 µm zooplankton communities were *E. affinis, E. herdmani*, and *Halicyclops,* while *Acartia* spp. and Bivalvia also contributed in 63 µm and *Acartia longiremis* and *Bosmina longirostris* also contributed in 200 µm. The distribution of taxa common to both 63 µm and 200 µm is similar for both nets. Bivalvia are mainly present in freshwater, and in lesser portions in polyhaline waters, and therefore contribute for an important part of the dissimilarity when comparing freshwater to other salinity zones in all years. When comparing the three other salinity zones, the taxa accounting the most for dissimilarity is *Eurytemora* spp., with the exception of polyhaline and mesohaline zones in 2022 being mostly differentiated by *Acartia* spp. Throughout the 4 years, a similar pattern was observed in the distributions of these taxa, where distinct communities are observed in different zones of the estuary: Bivalvia and *Halicyclops* dominated between Québec and Cap Saint-Ignace, while *E. affinis* dominated between the east tip of Ile d'Orléans to Anse Ste.-Anne, where *E. herdmani* and *Acartia* spp. dominate the community further downstream, all the way to the Saguenay Fjord (Fig. 7).

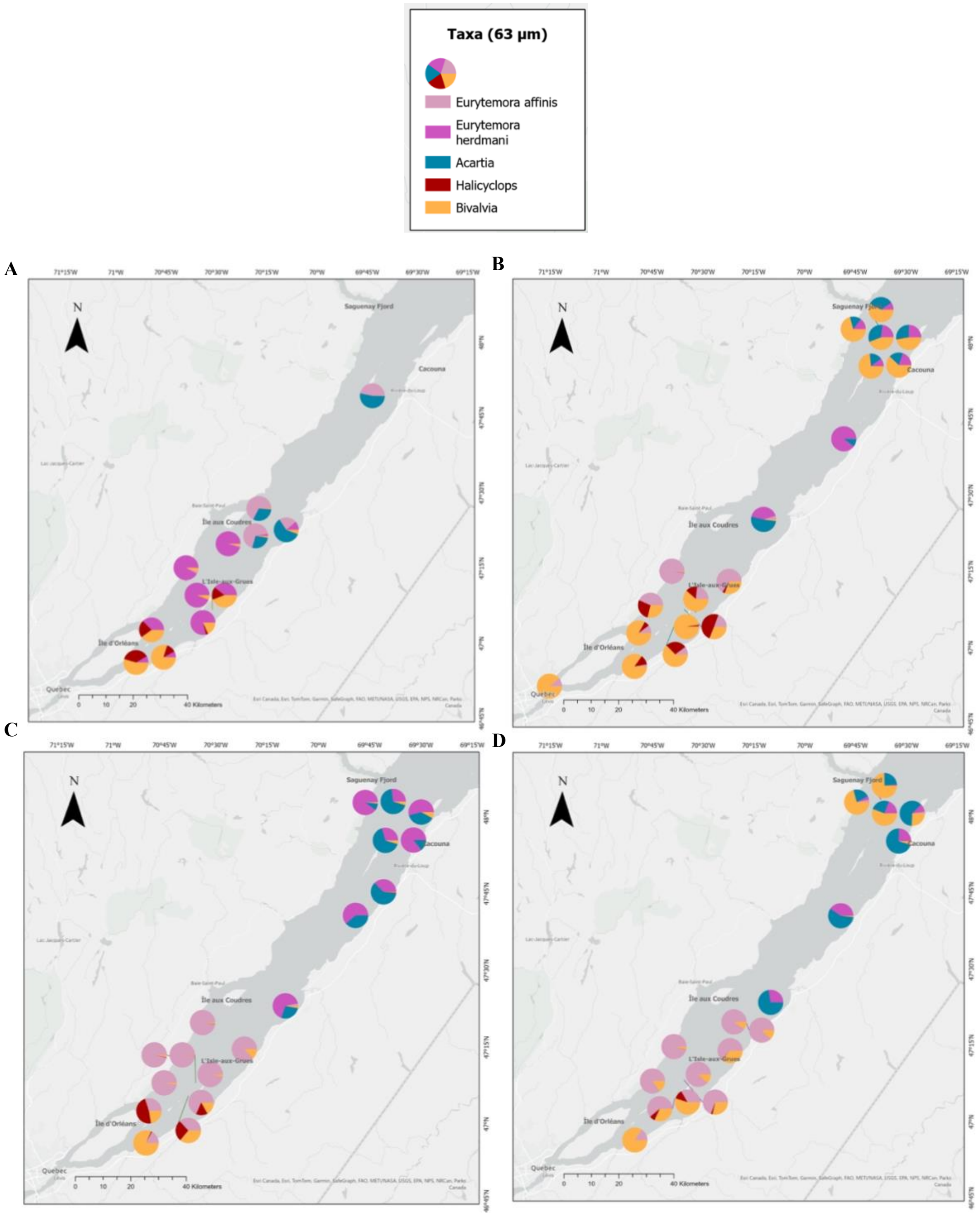


Figure 7. Spatial distribution of some of the taxa that contribute the most to community differences according to SIMPER analysis (Table A9) by station in 2019 (A), 2020 (B), 2021 (C) and 2022 (D) for the 63 µm net and in 2019 (E), 2020 (F), 2021 (G) and 2022 (H) for the 200 µm net.

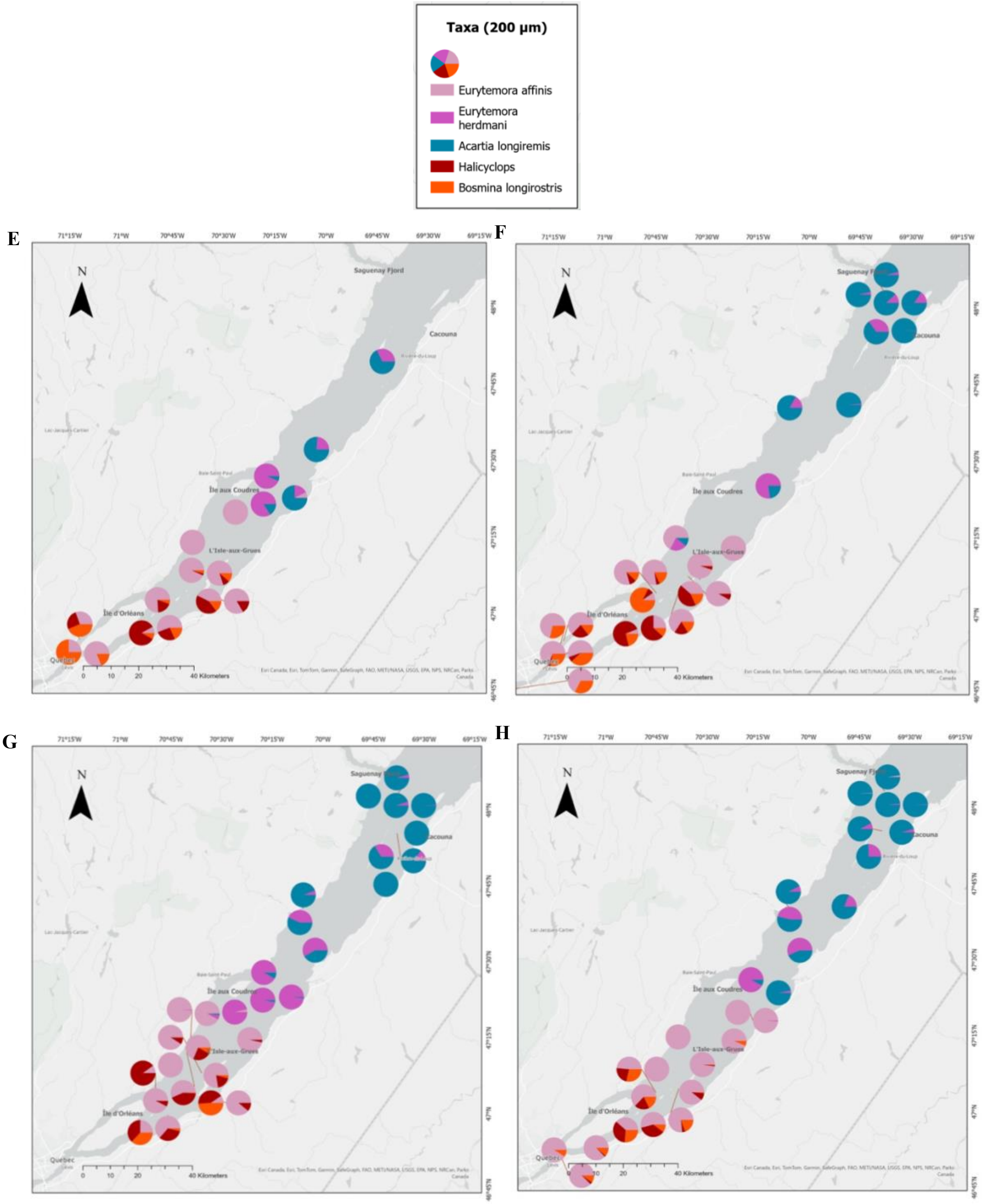


Figure 7 (continued).

Taxonomic diversity

A total of 144 different taxa and 43 species were identified across all samples (Table A2). Community composition varied among all salinity zones and was highly variable in time (Fig. 8). The 63 µm community differed between the year pairs: 2019 and 2020, 2020 and 2021, as well as 2021 and 2022 ($p_{Year} < 0.05$; Table A4). The 200 µm community, on the other hand, differed among every year except 2019 and 2021 ($p_{Year} < 0.05$; Table A4).

With the exception of 2019, most zooplankton communities were mainly composed of copepods, with a highly varying proportion of nauplii (Fig. 8A & B). *Bivalvia* are the second most important group in terms of density in freshwater and gradually decrease in contribution with increasing salinity. *Branchiopoda* were also almost exclusively found in small quantities in freshwater. Although this varied with the years, polyhaline communities were also composed, in lesser proportions, of *Eurotatoria*, *Gastropoda*, *Polychaeta* and *Thecostraca*. The copepodites and adult stages of copepods were very distinct in different salinity zones (Fig. 8C & D). Freshwater was mainly composed of *Eurytemora affinis*, Halicyclops and *Harpactiocoida*, while oligohaline waters shifted to a bigger proportion of Halicyclops and *Eurytemora* spp.. The high concentration of *Eurytemora* spp. in brackish water (Fig. 8C & D) is reflected by the overwhelming proportions of the first copepodite stage (C1) which could not be distinguished between *E. affinis* and *E. herdmani* and was therefore identified as *Eurytemora*. Mesohaline communities resemble oligohaline, but with the addition of a small proportion of *Acartia* spp. and *Eurytemora herdmani*. These two taxa get significantly more present in polyhaline waters, where *Acartia* spp. makes up around half of the populations. The nauplii composition follows a very similar pattern to the copepodites and adults but with a lesser presence of *Harpacticoida* (Fig. 8E).

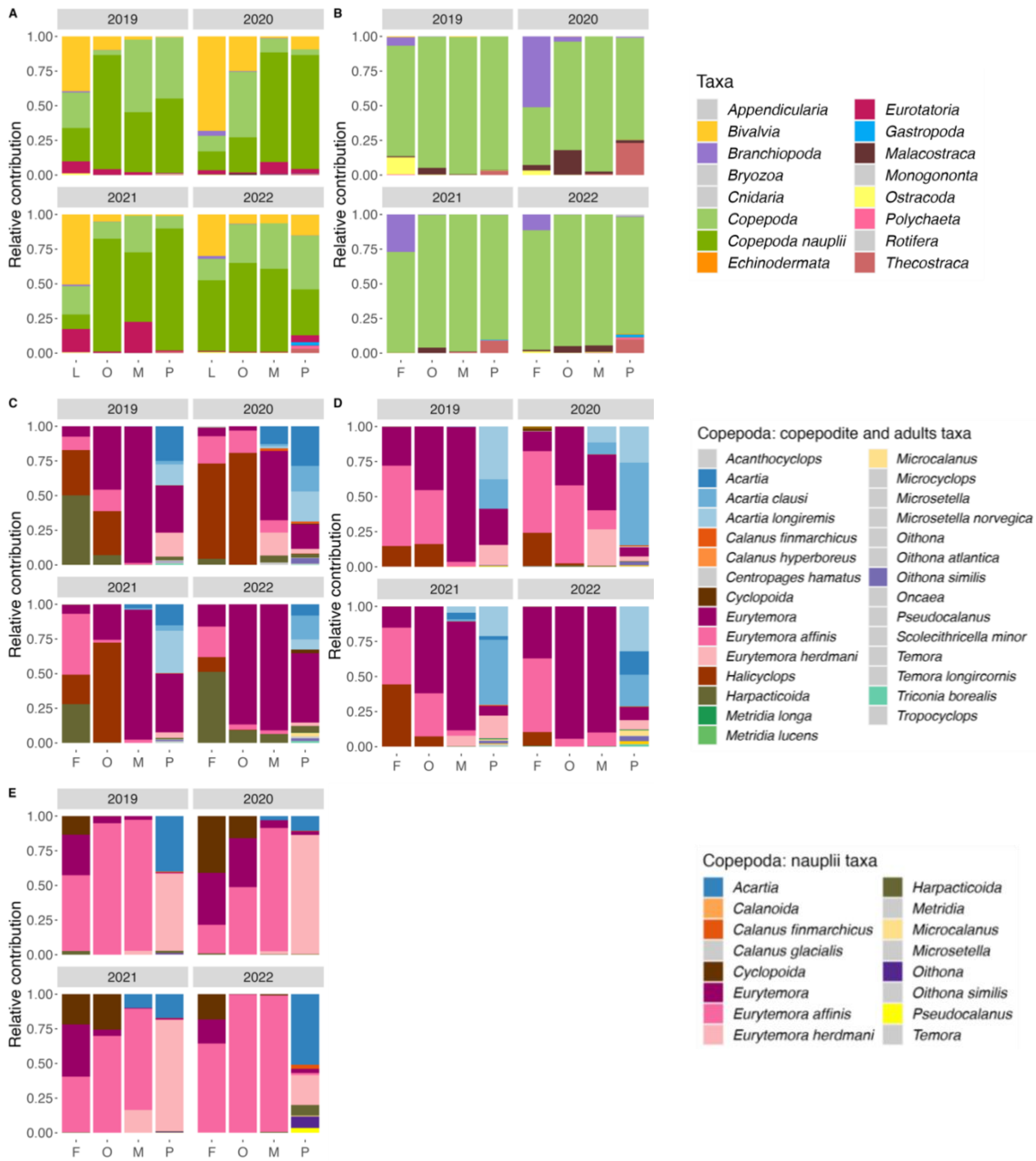


Figure 8. Average composition in relative contribution by salinity zone and year of taxa for 63 µm (A) and 200 µm (B), adults and copepodite copepods for 63 µm (C) and 200 µm (D) and nauplii for 63 µm (E) for freshwater (F), oligohaline (O), mesohaline (M) and polyhaline (P) waters from 2019 to 2022.

For 63 µm nets, taxa richness varied from 5 taxa in oligohaline and mesohaline waters to 26 taxa in freshwater (Fig. 9A), while species richness, based on the number of species identified, varied between 1 species in freshwater, oligohaline and mesohaline zones to 8 species in the polyhaline zone (Fig. 9B). The number of taxa identified in polyhaline samples was generally higher than in freshwater samples, and both oligohaline and mesohaline samples had lower taxa richness compared to freshwater. The lower number of species identified made it harder to detect any trend. Values for Shannon diversity index varied from 0.202 for freshwater to 2.38 in polyhaline waters (Fig. 9C), while Pielou varied from 0.02, also in freshwater, to 0.39 in mesohaline waters (Fig. 9D). Shannon diversity index followed a similar pattern to taxa richness as the polyhaline mean value was higher than oligohaline and mesohaline. Pielou diversity index, on the other hand, was the only taxonomic index for the 63 µm net that did not show any significant influence from salinity zones, years nor their interactions.

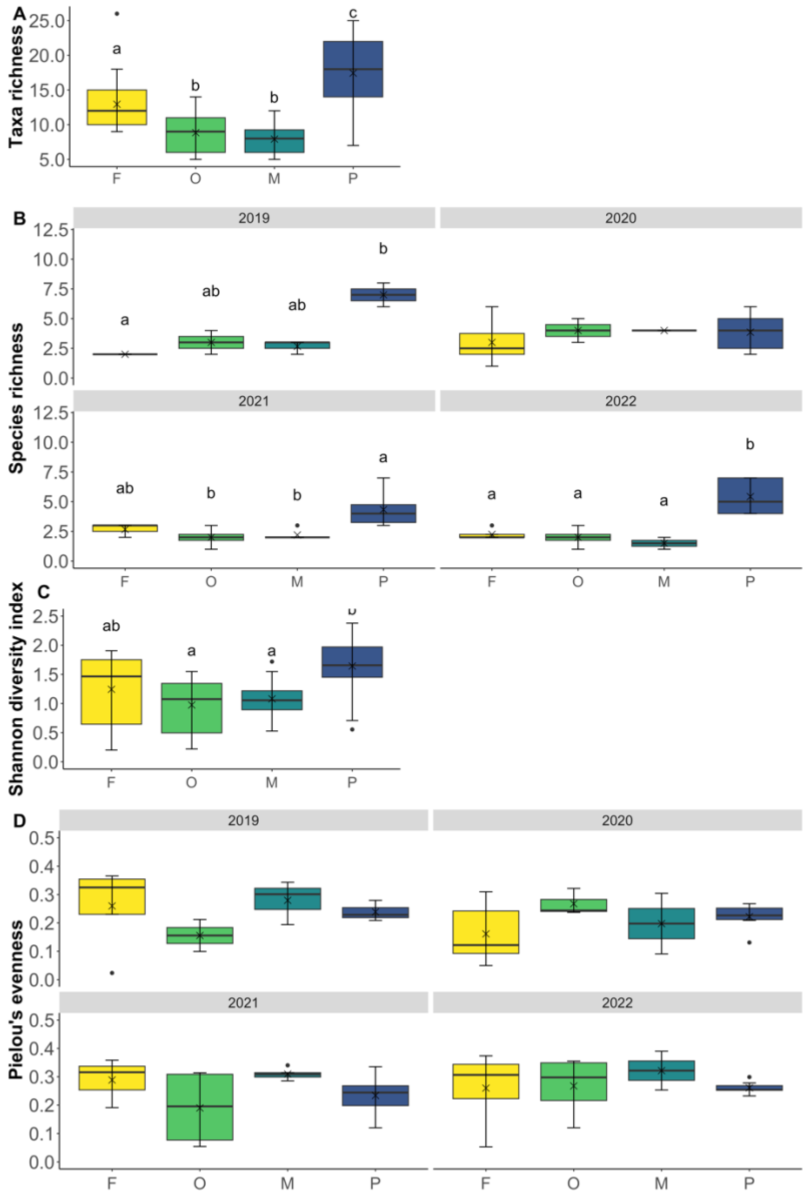


Figure 9. Median taxonomic indices values for freshwater (F, yellow), oligohaline (O, green), mesohaline (M, turquoise) and polyhaline (P, blue) waters from 2019 to 2022 : for 63 µm nets, taxa richness by salinity zone (A), species richness by year and salinity zone (B), Shannon diversity index by salinity zone (C) and Pielou's evenness by year and salinity zone (D); for 200 µm nets, taxa richness by year (E) and salinity zone (F) independently, species richness by year and salinity zone (G), Shannon diversity index by year (H) and salinity zone (I) independently and Pielou's evenness by year and salinity zone µm (J). Different letters indicate significant differences according to PERMANOVAs ($p_{Year*salinity\ zone} < 0.05$; Table A8). The box represents the interquartile range (25th percentile to 75th percentile) while the median is the thick line inside it and the black cross is the mean. The whiskers extend to the most extreme data points and black dots indicate outliers.

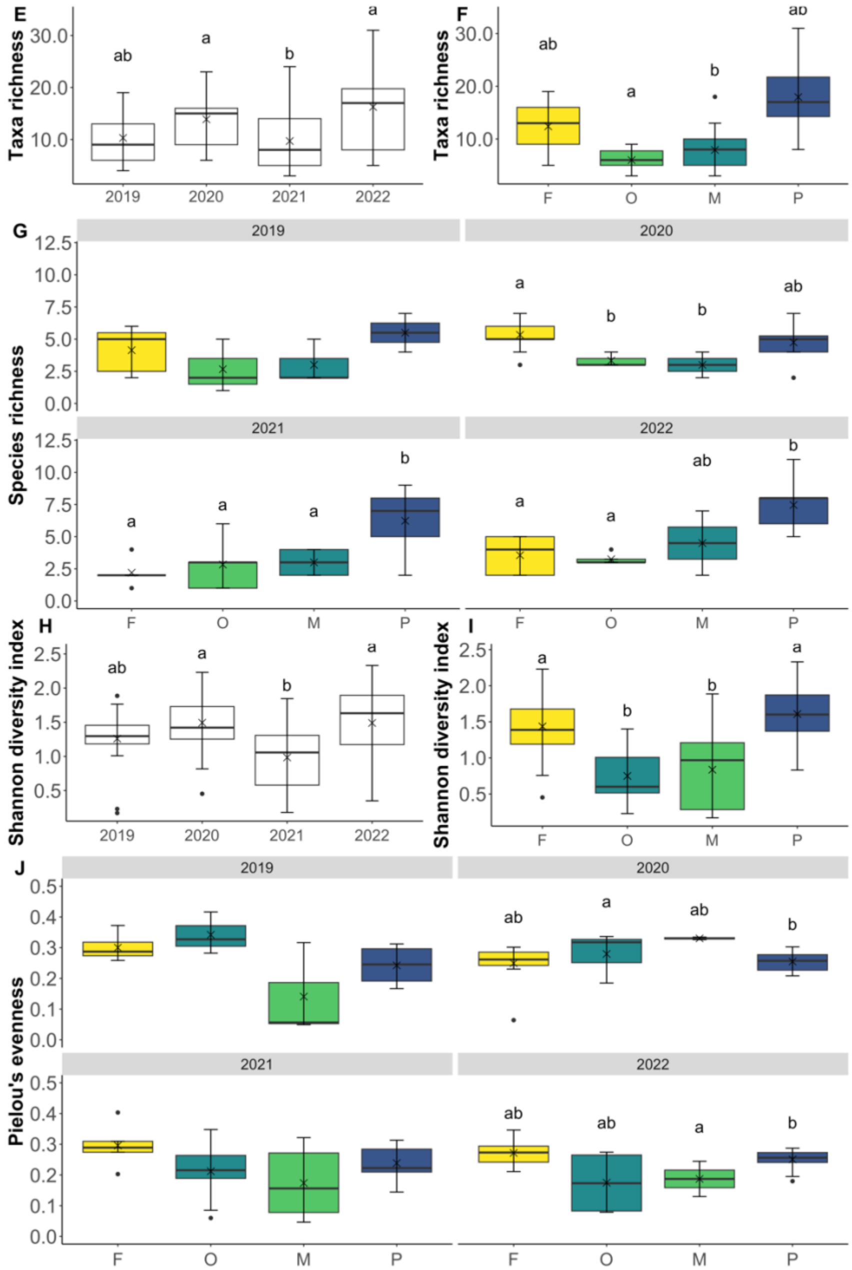
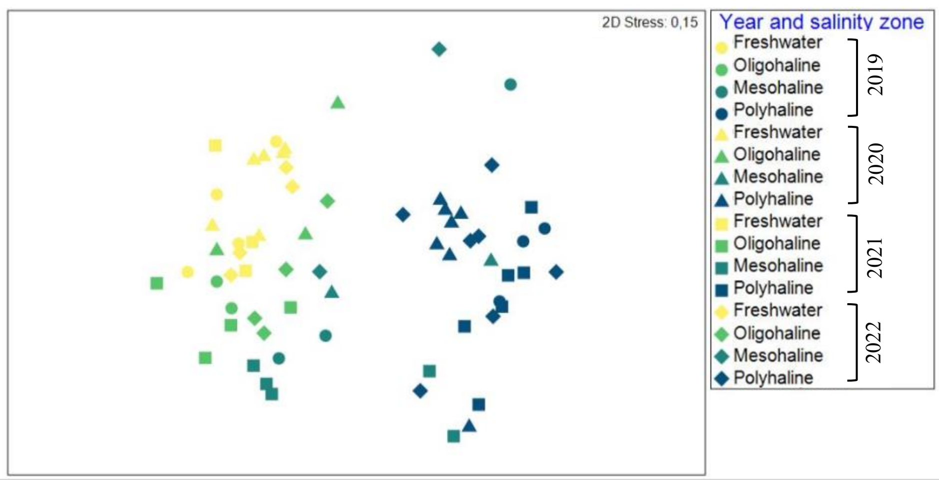


Figure 9 (continued).

The values and trends observed for taxonomic diversity indices behaved very similarly for 200 µm nets compared to 63 µm nets. One slight exception is the significant differences between years for taxa richness (Fig. 9E) and Shannon's diversity index (Fig. 9H), where mean values were higher in 2020 and 2022 than in 2021. Similar to 63 µm, Pielou diversity index for 200 µm nets appears highly variable (Fig. 9J).

A



B

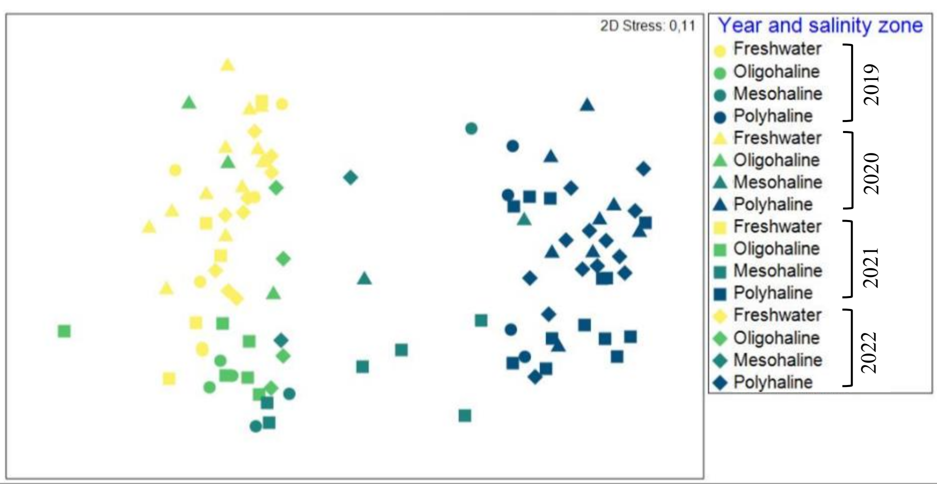


Figure 10. Visualisation of sample similarity by year and salinity zone with a scatter plot created with an nMDS analysis for 63 µm (A) and 200 µm nets (B) for freshwater, oligohaline, mesohaline and polyhaline waters from 2019 to 2022.

Overall two main groups emerged along the first axis, setting apart mostly the polyhaline zone (nMDS; Fig. 10A & B). The first group is composed of freshwater and oligohaline zones while the second one is mostly polyhaline. Mesohaline samples are scattered between both groups. This pattern is much clearer in 200 µm samples compared to 63 µm as shown by multiple significant differences in community composition in an interaction term of year and salinity zone ($p_{Year*Salinity\ zone} < 0.05$; Table A8). Polyhaline communities from the 200 µm samples are indeed significantly different from all other salinity zones in all four years ($p_{Year*Salinity\ zone} < 0.05$; Table A8) with the exception of mesohaline in 2019. The communities of the oligohaline and mesohaline zones (63µm and 200µm) were similar except in 2021 (Table A8). ~~Regarding the second axis, it seems that samples from 2021 tend to remain at the bottom of the figure, while the top is dominated by samples from 2020~~.

Functional diversity

The majority of taxa considered were holoplankton, with only *Crangon septemspinosa* being part of meroplankton. Similar to taxonomic groups (Fig. 8), functional groups for both 63 µm and 200 µm nets vary interannually and are dependent on salinity zones (Fig. 11).

The majority of all organisms sampled with the 63 µm net were herbivorous and current feeders, independent of the salinity zone (Fig. 11A & C). As for other metrics, the trophic strategies are spread in two main groups, the first for freshwater and oligohaline, and the second for mesohaline and polyhaline. Freshwater and oligohaline communities are composed of taxa that are carnivorous, omnivorous and herbivorous as well. Taxa that are both herbivorous and omnivorous become more present in mesohaline and polyhaline communities, along with omnivorous organisms (Fig. 11A). As for feeding methods, in addition to current feeders, exclusively active ambush feeders were the second most present group in freshwater and oligohaline zones, while waters with higher salinities were dominated by current feeders and active ambush feeders. Cruise feeders did not show any clear pattern, appearing in important proportions in all salinity zones but oligohaline depending on the year (Fig. 11C).

A similar pattern emerged in the distribution of feeding methods for the 200 µm samples. The trophic strategies changed with the salinity, with the proportion of herbivores vanishing as the salinity increased (Fig. 11B). On the contrary, the proportion of omnivorous taxa increased with salinity. Oligohaline and mesohaline communities were generally dominated by taxa that are both omnivorous and herbivorous. Almost no cruise feeders were found in 200 µm samples, and the dominating group in polyhaline communities was composed of taxa that were both current feeders and active ambush feeders. Very few carnivorous and detritivores taxa were found in the samples.

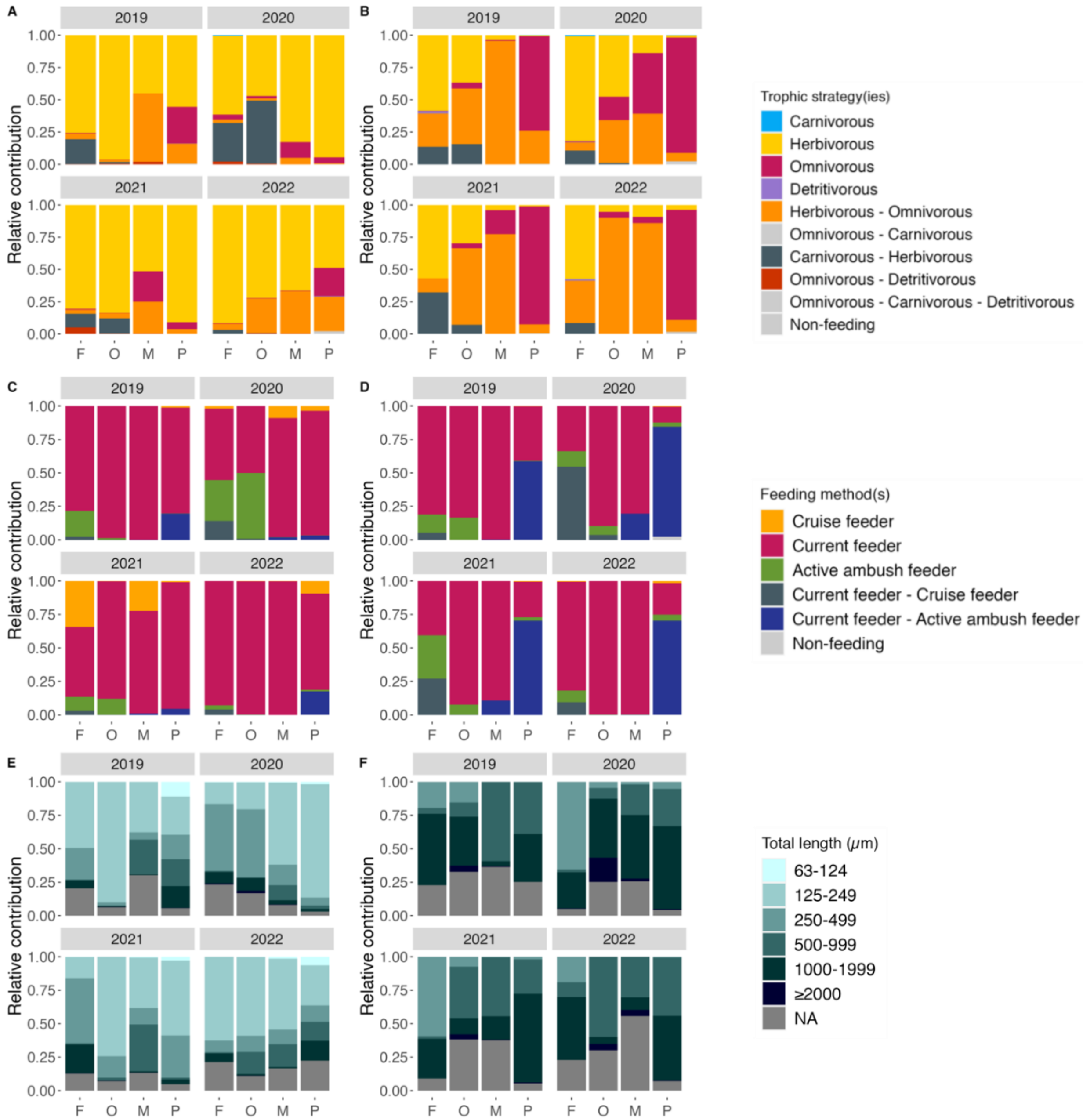


Figure 11. Relative contribution of functional groups by year and salinity zone for trophic strategies from nets 63 µm (A) and 200 µm (B) samples, for the feeding method trait from 63 µm (C) and 200 µm (D) nets and for total length categories from 63 µm (E) and 200 µm (F) nets for freshwater (F), oligohaline (O), mesohaline (M) and polyhaline (P) zones sampled between 2019 and 2022.

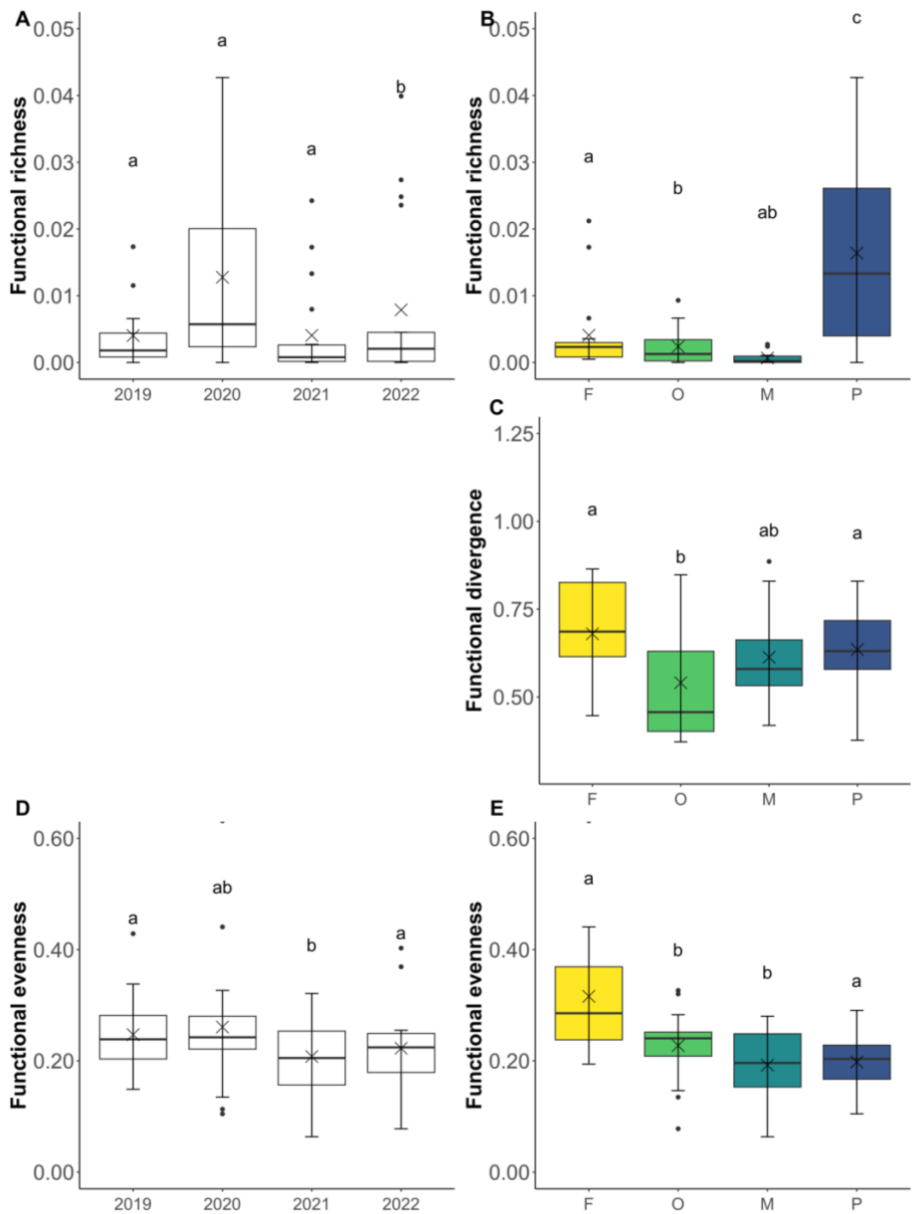


Figure 12. Median functional diversity indices values for freshwater (F, yellow), oligohaline (O, green), mesohaline (M, turquoise) and polyhaline (P, blue) salinity zones from 2019 to 2022: for 63 µm nets, functional richness by year (A) and salinity zone (B), functional divergence by salinity zone (C) and functional evenness by year (D) and salinity zone (E); for 200 µm nets, functional richness by year (F) and salinity zone (G), functional divergence by salinity zone (H) and functional evenness by year (I) and salinity zone (J). Different letters indicate significant differences according to PERMANOVAs ($p_{Year} < 0.05$; Table A4) ($p_{Salinity\ zone} < 0.05$; Table A5). The box represents the interquartile range (25th percentile to 75th percentile) while the median is the thick line inside it and the black cross is the mean. The whiskers extend to the most extreme data points and black dots indicate outliers.

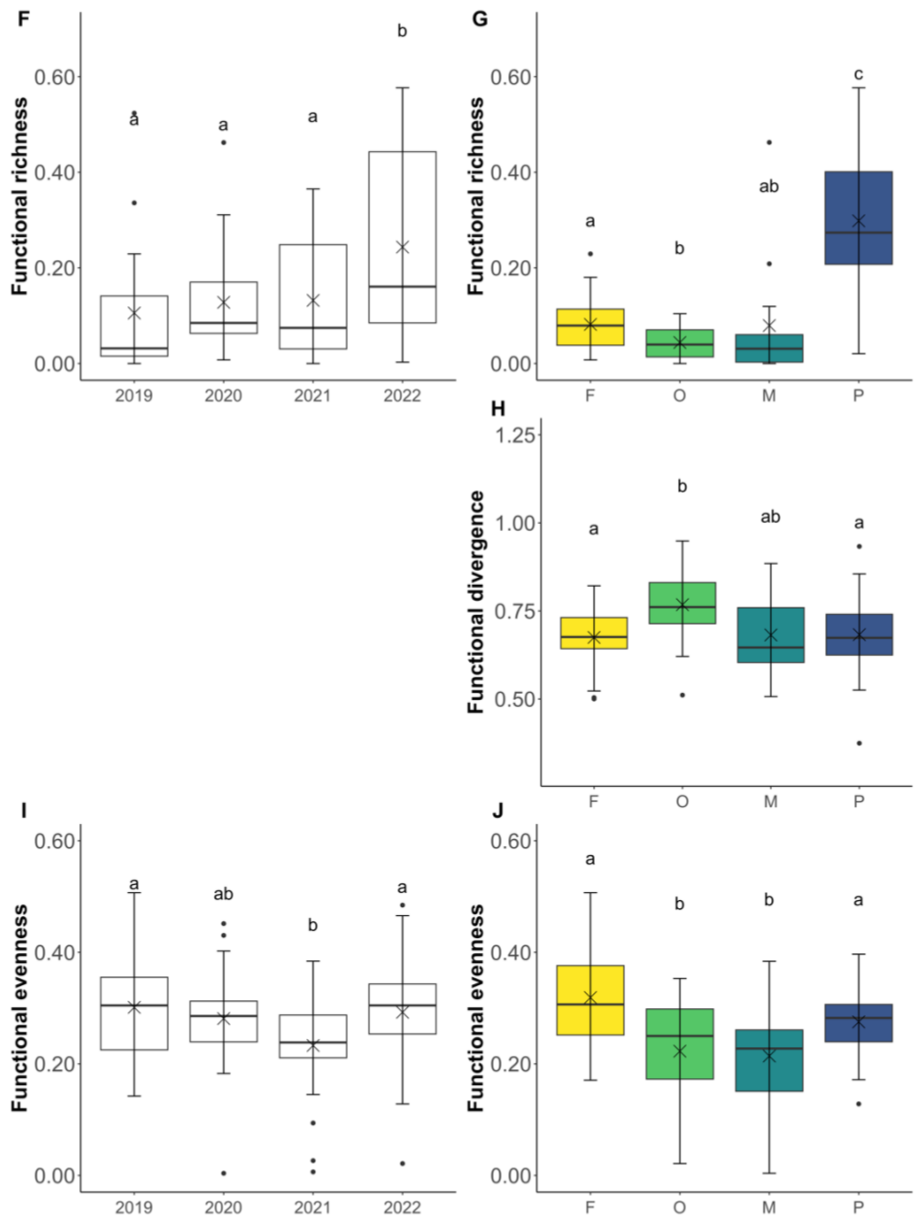


Figure 12 (continued).

Functional richness and evenness are significantly different among years for both nets (Fig. 12) ($p_{Year} < 0.05$; Table A3; Table A6). Functional richness, divergence and evenness are all significantly different among salinity zones for both nets (Fig. 12; Table A7) ($p_{Salinity\ zone} < 0.05$; Table A3). Polyhaline functional richness is higher than in all other salinity zones (Fig. 12B), and variance of functional richness values is noticeably higher zones for both nets (Fig. 12B).

In the 63 µm nets, the functional divergence is higher in the freshwater and polyhaline zones than in the oligohaline zone (Fig. 12C; Table A5), but the functional evenness is higher in freshwater compared to higher salinity zones (Fig. 12E; Table A5). Functional richness is higher in 2020 with variance that is higher than in other years (Fig. 12A; Table A4), while functional evenness is slightly lower in 2021 (Fig. 12D; Table A4). For 200 µm nets, functional richness is higher in 2022 (Fig. 12F; Table A4), while functional evenness, like for 63 µm nets, is slightly lower in 2021 (Fig. 12I; Table A4).

Environmental influence on zooplankton communities

In the 63 µm net freshwater zone, around half of the total community variation (51.6%), was explained by the first axis (Fig. 13A). Fluorescence, SPM and nitrite and nitrate concentrations (NO_2NO_3) contributed the most to this axis. Freshwater communities from 2020 seemed to be mostly influenced by NO_2NO_3. As for the second axis, 18.4% of the total variation was explained (Fig. 13A). Picocyanobacteria and POM were the only environmental factors with a clear discriminant role on this axis, even though only one station from 2021 and one station from 2022 had a considerable influence by these factors. Variation in the oligohaline zone was mainly explained first by nanoeukaryote, second by bacteria, the two of them being about equally present on both axis, which respectively explained 46.9% and 23.1% of total variation (Fig. 13B). Chlorophyll *a* and fluorescence were also about as influent as bacteria but were more present on the second axis (Fig. 13B). In the mesohaline zone, both axis explained an important proportion of the total community variation, with the first axis representing 39.1% of total variation and the second axis, 31.9% of total variation (Fig. 13C). The first axis was mostly explained by picocyanobacteria, while the second axis was explained by picoeukaryotes and temperature. Nanoeukaryote was also an important factor on both axis. Samples from 2021 were dispersed in two groups and seemed to be mostly influenced by picocyanobacteria and picoeukaryotes. They are distinct from 2020 samples, which were mostly influenced by SPM, and from 2022 samples, which were mostly influenced by phaeopigments. In polyhaline waters, a lesser proportion of the total variation was explained by the environmental factors considered, with 27.8% of total variation explained by the first axis and 14.4% by the second axis (Fig. 13D). Temperature explained the most on the first axis, followed by nanocyanobacteria. The second axis was explained by multiple factors in similar proportions. Samples from 2022 were widely spread, while 2020 samples were most explained by POM and SPM, and 2021 was mainly influenced by temperature.

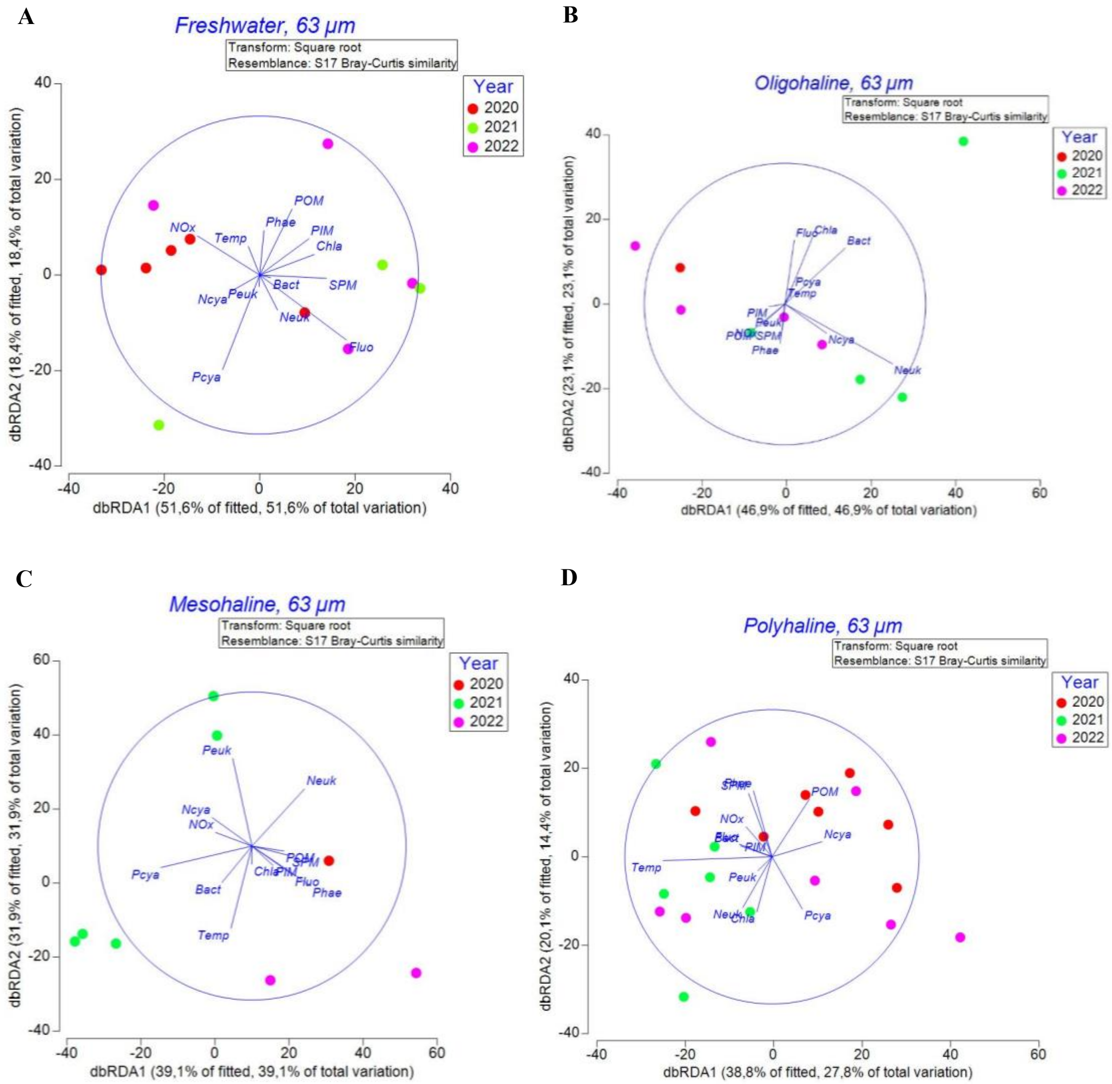


Figure 13. Proportions of community variation explained by environmental factors by an redundancy analysis (RDA) for stations sampled in 2020, 2021 and 2022. For 63 µm nets, freshwater (A), oligohaline (B), mesohaline (C) and polyhaline (D) stations, and for 200 µm nets, freshwater (E), oligohaline (F), mesohaline (G) and polyhaline (H) stations. Environmental variables shown for each year were chosen according to the BEST analysis results. Stations sampled in 2019 as well as 4 stations in 2020 (ETZ-19, ETZ-20, ETZ-21, ETZ-22) were excluded from this analysis due to missing data points.

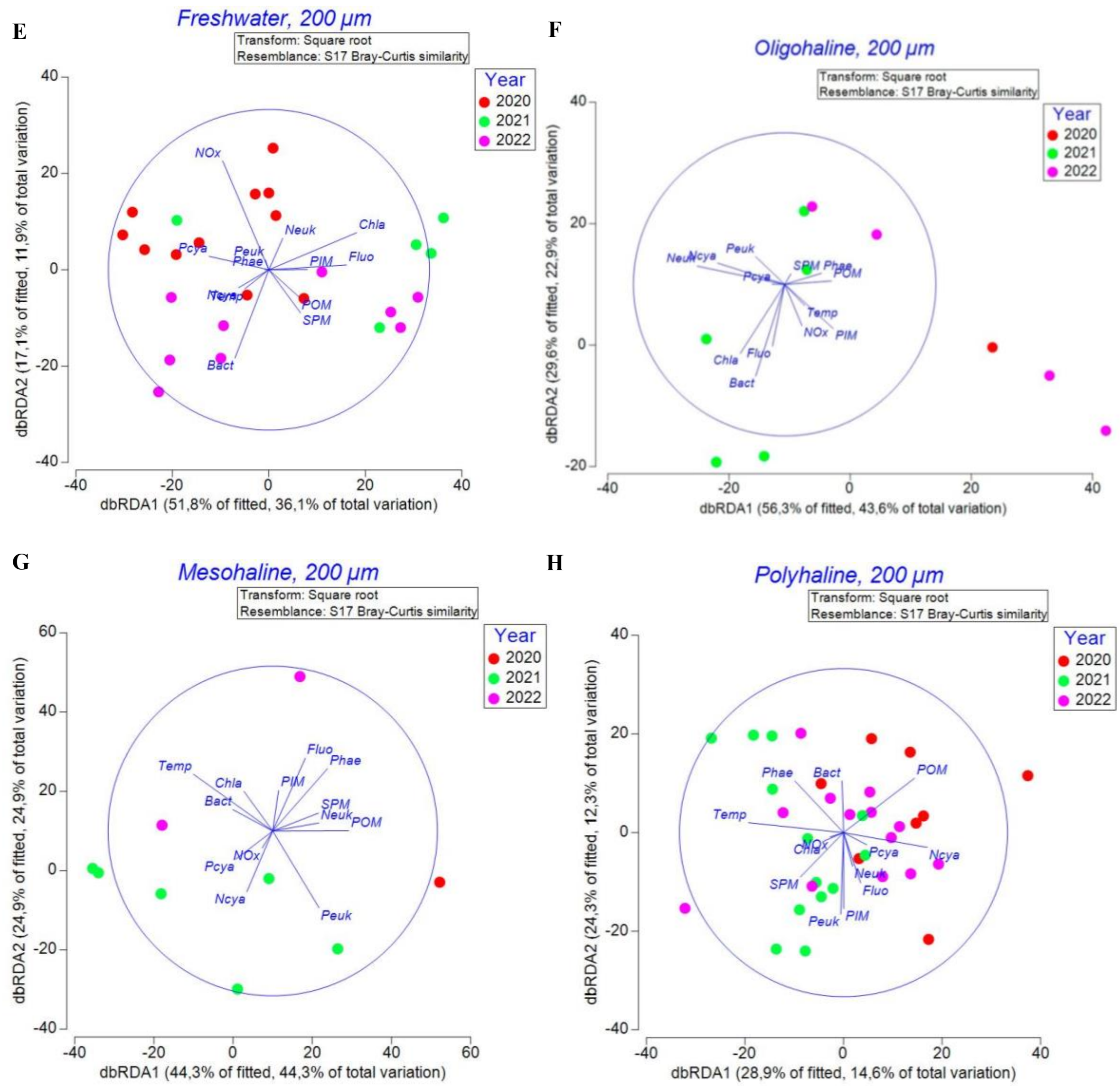


Figure 13 (continued).

In freshwater, regarding the 200 µm samples, the most influential factors retained by the analysis often remained similar to 63 µm samples. The most important factors on the first axis (36.1% of total variation) were chlorophyll a and fluorescence; NO_2NO_3 and bacteria as the important factors on the second axis (11.9% of total variation) (Fig. 13E). Samples from 2020 to 2022 were almost all grouped by year but influenced by different factors: 2020 was mostly influenced by NO_2NO_3 and pycocyanobacteria while 2022 was mostly influenced by bacteria and POM. 2021 was influenced mostly positively from chlorophyll a and fluorescence. For both oligohaline (Fig. 13G) and mesohaline waters (Fig. 13F), samples were also mostly grouped by year. However, in 2020, only one oligohaline and one mesohaline station were sampled in 2020, making it hard to detect any tendencies for that year with such low sample sizes. For oligohaline waters, nanoeukaryotes and nanocyanobacteria were the most important factors of the first axis which explained 43.6% of total variation (Fig. 13F). Bacteria was the most influential factor of the second axis, with chlorophyll a and fluorescence having a similar influence, which explained 22.9% of total variation. The year 2021 was mostly influenced by bacteria and chlorophyll a, while 2020 and 2022 were mostly influenced by POM and PIM. In mesohaline stations of the 200 µm net, the first axis accounted for 44.3% of total variation and was explained mostly by POM and temperature (Fig. 13G). The years 2021 and 2022 were mostly influenced by temperature while 2020 was mostly influenced by POM, although the latter has only one station (Fig. 13G). The second axis explained 24.9% of total variation and the factors most responsible were picoeukaryotes and fluorescence. Similar to 63 µm, polyhaline stations in 200 µm had the smallest percentage of total variation explained, respectively 14.6% on the first axis and 12.3% on the second axis (Fig. 13H). The first axis was mostly explained by temperature and nanocyanobateria, while the second axis was most influenced by picoeukaryotes and PIM. There is overall a high overlap between samples of different years in all salinity zones.

Two important results from zooplankton of both nets are that data points are mostly grouped by year and that there was no single forcing that could explain these groupings across salinity groups or years. Across 2020 to 2022 in all salinity zones, samples from 2020 and 2022 often overlapped while 2021 remained more separate and therefore influenced differently by the factors considered. However, the lesser quantity of data in oligohaline mesohaline zones made it harder to define trends in these salinities, especially for the year 2020.

DISCUSSION

The zooplankton community in the estuarine transition zone of the St. Lawrence was divided into three distinct and consistent assemblages based on salinity, with similar communities in mesohaline and oligohaline zones for both nets. Pattern of distinct communities were less clear for the 63µm net. The four years studied from 2019 to 2022 during the month of August represent the first survey of the entire ETZ range since the 1990's. This study also includes the novelty of describing the functional diversity of these communities as well the taxonomic diversity. Consistent with the concept of biodiversity change throughout the salinity gradient, we generally found similar patterns between taxonomic and functional diversity throughout the salinity gradient, highest taxonomic and functional diversity in the polyhaline zone and lowest indices in the oligohaline and/or mesohaline zone of the ETZ. Total densities were highly variable within each zone, so that significant differences among the salinity zones were found in two years only. Densities in each salinity zone varied interannually, showing two years of high (2019, 2021) and two years (2020, 2022) of low densities. However, zooplankton composition was primarily structured by salinity zones, with minimal interannual variability. Environmental drivers shaping community structure within each salinity zone over the 4 years varied among salinity zones.

In the following, we will compare and discuss these results considering the new understanding of the structures of the zooplankton communities of the St. Lawrence Estuary provided by the results of this study as well as already established knowledge.

Environmental conditions in August 2019 to 2022

The St. Lawrence Middle Estuary is characterized by an important gradient of environmental conditions, which is reflected in the factors measured between 2019 and 2022. The use of the Venice salinity system explains the broader range and therefore variation of salinity values encompassed in mesohaline and polyhaline waters. These variations are also reflected in temperature distribution across the salinity zones since the two factors are strongly linked

(Nash, 1947; Horner-Devine et al., 2015). Each salinity zone presented specific factors that were more variable than others. Freshwater and oligohaline zones were generally characterized by high values and variability of fluorescence, turbidity, POM and bacteria. The mesohaline zone was defined by generally stable environmental conditions that are similar among years and show little variation, except for salinity and temperature. In the polyhaline zone overall lower concentration of suspended particles, fluorescence and microorganisms were found, while the nutrient phosphate concentration where highest. In an estuarine environment, turbidity typically decreases downstream and is therefore negatively correlated with the salinity due to the neutralisation and precipitation of negatively charged particles (Nash, 1947). The horizontal salinity gradient of the ETZ is one of the main factors affecting particles distribution through baroclinic flow and gravitational circulation, which not only affects patterns of suspended matters but also zooplankton retention and distribution, which will be discussed below (Simons et al., 2006; St-Onge-Drouin et al., 2014). The high current velocity upstream combined with important variations in bathymetry, which is often shallow, leads to higher levels of turbidity in the low salinity zone (Hamblin, 1989) as well as zooplankton retention and sometimes separation between cryptic species such as *Eurytemora affinis* North Atlantic clade and *E. carolleeae* (Simons et al., 2006; St-Onge-Drouin et al., 2014). Phytoplankton and bacterial dynamics are also affected by these circulation and retention processes, as longer cell retention time in the Maximum Turbidity Zone (MTZ) promotes increased concentrations and high taxonomic diversity, especially in the warmer freshwaters of the summer months (Frenette et al., 1995; Painchaud et al., 1995; Lovejoy et al., 2000), confirming patterns found in the present study. This therefore makes the freshwater and oligohaline zone very biologically productive (Frenette et al., 1995, Vincent et al., 1996).

Some variability was found among years for fluorescence, showing interactions among salinity zones that tend to distinguish 2019 and 2020 conditions from 2021 and 2022. The oligohaline zone had higher levels than freshwater in 2019 and 2020, while the opposite was observed in 2021 and 2022. Freshwater runoff has been shown to have a strong influence on phytoplankton distribution in the St. Lawrence estuary during high discharge periods (spring and fall), but this shift towards a more important influence by other physical processes during the summer months from June to September (Therriault and Levasseur, 1986). Phytoplankton distribution then is more influenced by localized river plumes (Therriault and Levasseur, 1985; Therriault and Levasseur, 1986) which may explain in part these patterns observed between 2019 and 2022. Furthermore, higher discharge in September 2019 (11177 $m^3 s^{-1}$) and August 2020 (11427 $m^3 s^{-1}$) might have pushed the peak phytoplankton concentrations into the oligohaline zone, while lower discharge in August 2021 (10073 $m^3 s^{-1}$) and 2022 (10895 $m^3 s^{-1}$) may allow for higher concentrations in the freshwater zone (for discharge values see: Fisheries and Oceans Canada, 2023).

Spatial and annual pattern in the zooplankton community

a. Zooplankton community composition and densities

Taxonomic composition for the zooplankton communities of the St. Lawrence's estuary mainly depends on salinity zones with a few important and structuring taxa varying in densities across them. As already described in the literature, the salinity gradient is generally the main environmental constraint structuring zooplankton communities in the St. Lawrence estuary (Laprise and Dodson, 1994; Winkler et al. 2003; Favier and Winkler 2014). These studies highlight communities along the salinity gradient constituted of different taxa based on their physiological tolerance. Three distinct groups seem to emerge from these results, one being composed of freshwater oligohaline assemblages, a mesohaline assemblage, overlapping with the freshwater/oligohaline and the polyhaline assemblage. The mesohaline zone encompasses what is known as the "nucleus" of an estuary, or the critical salinity zone of 5-8 PSU, which forms a barrier zone of abiotic properties limiting the presence of taxa depending on their physiological tolerances, while the highest numbers of species are usually found around 30 PSU (Telesh et Khlebovich, 2010). In our samples, taxonomic composition reflected those differences between salinity zones. Taxa such as Harpactiocoida, Halicyclops and *Eurytemora affinis* constituted most of freshwater and oligohaline densities, while *Acartia* spp. (mainly *Acartia hudsonica* and *A. longiremis*) and *Eurytemora herdmani* formed most of the density in the polyhaline zone. The mesohaline zone was constituted of the main taxa found in both lower salinities and higher salinities, with the exception of freshwater taxa. Some of those taxa emerge as the most structuring of the communities, such as the freshwater Branchiopoda *Bosmina longirostris*. Multiple taxa are also only present in polyhaline waters, indicating an important impact of marine stenohaline taxa such as *Calanus* spp. on the community distinction, while the steep salinity gradient in the oligohaline and mesohaline zone is mostly dominated by euryhaline species, such as *E. affinis*.

The mesh size with which zooplankton is collected also allows for different but complementary assemblages of the same community to be sampled, which in turn can reflect different diversity patterns that otherwise might not have been described (Pansera et al., 2014). In the present study, we sampled different size categories of zooplankton (63 µm and 200 µm net). For both the 63 µm and 200 µm communities, the years 2020 and 2022 showed considerably lower density values across most salinity zones, indicating simultaneous variations in densities of different size classes and life stages of zooplankton. In the 63 µm samples, we found an important proportions of meroplanktonic Bivalvia veligers and Copepoda nauplii that were not present in 200 µm samples. Although Bivalvia veligers from the samples were not identified at the species level, lower densities in brackish waters and consistently higher densities in freshwater and polyhaline samples indicates the presence of distinct stenohaline species. Previous reports have found multiple saltwater taxa in the lower Estuary and the Gulf St. Lawrence, such as the order Mytiloida in polyhaline waters (Nozères et al., 2015), while the St. Lawrence River, including the tidal freshwater and oligohaline zone, has been colonized by the introduced *Dreissena* mussels such as the zebra mussel (*Dreissena polymorpha*), and the quagga mussel (*Dreissena bugensis*) since their introduction in North America around 1986 (Ricciardi et al., 1996). This invasion has threatened and reduced native freshwater bivalve populations of the St. Lawrence River (Ricciardi et al., 1996) and very high densities of *Dreissena* veligers are found in the limnetic and oligohaline zone of the estuary (Barnard et al. 2003, Winkler et al. 2005). However, these high densities of veligers did not disrupt the zooplankton community in the early 2000's

(Winkler et al. 2005). The other major taxon that composes the 63 µm samples was the class Copepoda, the majority being larval stages (nauplii), while only more developed life stages were retained by the 200 µm. The species composition of copepods for the copepodites stages and adults was relatively similar in the mesohaline and polyhaline zones, but varied more for the freshwater and oligohaline zones. This is mainly due to a higher presence of *Halicyclops* in the 63 µm nets as well as harpacticoids, which were absent from the 200 µm nets and have generally been found to be composed of the freshwater species *Halectinosoma curticorne.*

Zooplankton densities were higher in the oligohaline and mesohaline zones, explained by physical and biotic factors. As discussed earlier, this can be traced back to the hydrodynamic retention process of the MTZ (Simons et al., 2006, St-Onge-Drouin et al., 2014), leading to elevated concentrations of suspended matters (d'Anglejan et Smith, 1973) that sustain high levels of phytoplankton (Frenette et al., 1995), which in turn support high densities of zooplankton through trophic coupling (Dodson et al., 1989, Winkler et al., 2003, Favier et Winkler, 2014).

b. Species composition and functional traits

Using both taxonomic and functional approaches to reveal diversity in zooplankton has proven to be of advantage to highlight different structural changes observed in aquatic ecosystems and to correctly assess ecosystem functioning (Heneghan et al., 2020; McLaskey et al., 2024; Santo et al., 2024; Benedetti et al., 2025). While Copepoda remained the dominant taxon through most years, salinity zones and sampling nets, important variations were found in proportions of different feeding methods (Fig. 5 & Fig. 8).

In this study, the most present trophic functional groups the 63 µm samples were herbivorous and current feeders (Fig. 8), based on a large functional group that includes multiple smaller-size calanoids (Benedetti et al., 2016). Herbivores were by far the dominant trophic level in 63 µm nets but were only dominant in freshwater in 200 µm nets (Fig. 8), suggesting that the majority of species sampled composing the herbivorous group were of small size. This is most likely due to the very high proportion of Copepoda nauplii in most 63 µm samples (Fig. 5A), which are almost all classified as herbivorous and filter feeding due to their small size and early developmental stage (McLaskey et al., 2024).

Samples from 200 µm are still generally dominated by current feeders, except in polyhaline communities where most taxa are also active ambush feeders. Results from this net showed distinctively more variation in functional composition with increasing salinity, resulting in more differences between nets in the polyhaline zone compared to the other zones. Contrary to 63 µm nets, the proportion of herbivores in 200 µm nets consistently decreased with increasing salinity, while the proportion of omnivores increased. Most zooplankton bigger than 200 µm in the polyhaline zone were both current feeders and active ambush feeders, hinting towards a higher presence of a group of small mixed-feeders (Benedetti et al., 2016). These differences indicate more variation in functional composition along the salinity gradient for bigger sized zooplankton.

The dominance of exclusively herbivorous or omnivorous taxa in freshwater and polyhaline waters, respectively is linked to the prevalence of specialist taxa in these habitats (Fig. 8B). The environmental constraints of brackish waters only allows for the presence of generalist taxa with a higher tolerance to stress, which are often harder to classify into a single trophic strategy (David et al., 2016). This habitat heterogeneity, which has been observed in previous studies, is also defined by a gradient of spatial conditions heavily influenced by Île d'Orléans and Île-aux-Coudres (Runge and Simard, 1990). Freshwater taxa, such as Bivalvia, *Halicyclops* and *Bosmina longirostris* (Fig. 4 & Fig. 5) were most present in the zone south of Ile d'Orléans around Montmagny, while *E. affinis* dominated the community west towards Quebec City and east past Montmagny up until La Pocatière (Fig. 4 & Fig. 5). The emblematic estuarine copepods *E. affinis* and *Acartia* spp. were found to have mostly distinct spatial distributions in the estuarine transition zone, with *E. affinis* dominating between Quebec City and Île aux Coudres while *Acartia* spp. dominated between Île aux Coudres and the Saguenay fjord. These findings are interesting considering that these two species have also been found to coexist in the same areas in other ecosystems such as the mesohaline fjord Schlei, in Germany, with seasonal successions related to differences in reproductive strategies between *Eurytemora* and *Acartia* (Hirche, 1992) or other estuaries such as the Gironde (David et al. 2016). This therefore shows a variation in niche differentiation depending on the system considered, which in these two examples differed between spatial and seasonal species separation, and has been found to be influenced by functional traits such as reproductive strategies (Hirche, 1992). In the ETZ, the presence of *Eurytemora herdmani*, might influence also the distribution pattern of *E. affinis* and *Acartia* spp. *E. herdmani* is not present in Europe, but has been found in this study to overlap the spatial distribution of both *E. affinis* and *Acartia* spp.

c. Taxonomic and functional diversity

In addition to taxonomic and functional groups, diversity indices are another way of looking at changes in a zooplankton community and comparing taxonomic and functional diversity, as well as studying the links between them (Villéger et al., 2008). There was a high number of taxa in freshwater and polyhaline waters (Fig. 6A & F), while the limited number of species that can tolerate brackish waters explain the lower species and taxa richness in oligohaline and mesohaline waters observed in the ETZ of the St. Lawrence (Fig. 6A & F) and elsewhere such as the Gironde Estuary, the Baltic Sea and the Duliujian River (David et al., 2016, Telesh et Khlebovich, 2010; Sun et al., 2023), which is consistent with the critical salinity zone (Telesh et Khlebovich, 2010).

When it comes to functional diversity, functional richness is considered the equivalent of taxa richness, providing an estimation of the number of functional traits while functional evenness and functional divergence describe how these traits are distributed in the functional space, providing different facets of the community diversity (Villéger et al., 2008). The latter two are equivalents to the Shannon-Wiener and the Pielou’s evenness, respectively and are discussed below. Both nets showed annual variations in functional diversity, with functional richness being higher in 2022 and functional evenness being lower in 2021. Functional richness, similarly to taxa richness, was significantly higher and more variable in the polyhaline zone compared to the three other salinity zones (Fig. 12B & G), but did not show an increase in the freshwater zone as was observed for taxa richness. Overall, this indicates more differentiation in composition and functional traits in the polyhaline zone, maintaining higher regional diversity. Functional richness is known to increase and follow similar trends as species richness (Mason et al., 2013; Veríssimo et al., 2017), which is observed in this study except in freshwater where the low functional richness did not reflect the high taxonomic diversity. These freshwater communities were, however, composed of more evenly distributed functional traits compared to the three other salinity zones, pointing towards a higher presence of specialist species. Communities in brackish waters were characterized by lower functional richness and evenness, indicating that they tend to be dominated by a few specific traits and are mostly composed of few generalist species that can exploit a broader range of resources. Stable environments foster more competition among taxa, typically leading to higher functional diversity and more diverse traits, which allows co-existence (Kneitel et Chase, 2004). In the case of the St. Lawrence ETZ, the stability in environmental conditions in freshwater combined with the presence of abundant resources as shown by fluorescence and suspended matter concentrations (turbidity and POM) may allow for a more even distribution of functional traits.

Taxonomic and functional diversity results suggest that ecological roles in the freshwater community are more evenly distributed across taxa, unlike in higher salinity zones where a few traits may dominate. As discussed earlier, the proportion of copepods found in the zooplankton increased with salinity and largely dominated the community in polyhaline waters. Considering these various taxa of copepods often share the same functional traits, this can reduce the functional evenness in those habitats while still maintaining the same taxonomic distribution as other salinities. The functional diversity of zooplankton communities in the St. Lawrence ETZ therefore points towards a higher degree of specialization among species in freshwater communities. The fact that there are less functional roles in freshwater, oligohaline and mesohaline communities might potentially ensure a higher resistance to the high environmental variability in this zone (Kneitel et Chase, 2004). On the contrary, more stable conditions in polyhaline ecosystems makes competition for resources an important factor in biological communities leading to niche specialisation to exploit limiting resources differently. In this context, the presence of more diverse specialized taxa enable co-existence, with an especially broader range of functional traits occupied in polyhaline waters and therefore most likely occupying more ecological niches (Helenius et al., 2017).

Furthermore, functional richness values indicate a higher number of functional traits present in organisms larger than 200 µm compared to the ones sampled by a 63 µm net. This is logical considering that a large part of the latter is composed of organisms of earlier life stages, which often share a restricted range of functional traits due to their limited physiological capacities and smaller size (Heneghan et al., 2020). Resource use is highly related to zooplankton size, with around 89% herbivory level in zooplankton smaller than 125 µm (McLaskey et al., 2024). Copepod nauplii, for example, were all classified as herbivorous current feeders even though the more developed life stages of multiple taxa often divided in different functional feeding groups (Koski et al., 2006).

Environmental influence on zooplankton communities

Considering that taxonomic and functional results showed that the ETZ's zooplankton communities were highly structured by salinity (Table A7), we were interested in describing the influence of environmental drivers on zooplankton community variation within each salinity zone. The general trend observed is that the main structuring environmental drivers on zooplankton change depending on the salinity zones. These factors tend to be similar between different zooplankton size classes, here being zooplankton bigger than 63 µm and bigger than 200 µm but still show some level of variation.

Multiple components could explain the variation in environmental influences for communities along the salinity gradient, such as the interactions between resource availability, abiotic conditions and predation (Kneitel et Chase, 2004) as well as the differences in tolerance of each taxa to environmental variations. A study on the variations in abundances of *Pseudocalanus elongatus*, *Acartia hudsonica*, *Calanus finmarchicus* and Hyperiidea in the north-east Atlantic and the North Sea indicated that each species responds individually to its environment rather than as a group (Colebrook, 1985). This suggest that communities with different taxa composition due to different habitats will respond differently to their environmental influences based on each taxa present. Studies in various aquatic ecosystems have found zooplankton to respond differently to environmental factors along the salinity gradient, as well as specific factors influencing some taxa more than others (Telesh et Khlebovich, 2010; Sun et al., 2023; Laprise et Dodson, 1994). Important factors for the zooplankton communities were notably found to be total nitrogen, water depth, pH and salinity (Sun et al., 2023). Our findings add some knowledge to this understanding by specifying that while nutrients such as $NO_2^-+NO_3^-$ are indeed an important environmental factor explaining variation in the zooplankton communities in the freshwater and the oligohaline zones, they have a rather small impact compared to other abiotic factors in higher salinity environment such as in the mesohaline and polyhaline zones (Table A10). Anthropogenic eutrophication in the ETZ occurs largely through carbon and nutrients inflow from freshwater discharge, therefore having a significant impact upstream where the largest inflows occur (Hudon et al., 2017). Because the primary production of most freshwater systems is known to be limited by phosphorus (P) supply, governmental regulations have been put in place to prevent large inputs of P while uncontrolled nitrogen (N) additions stimulate primary production and can lead to harmful algual blooms (Bricker et al., 2008; Hudon et al., 2017). Bacterial abundance is another reoccurring environmental factor that structure communities in lower salinities and has been shown to be an important contribution to the carbon flux of the ETZ (Vincent et al., 1996). It has been observed that both short-term and long-term ecosystem processes, such as freshwater outflow or sediment resuspension, control the distribution of bacteria in the upper St. Lawrence estuary (Painchaud et al., 1995).

Knowing that estuarine microorganisms are highly impacted by variations in temperature and salinity explains that bacterial influence varies in different years and habitats (Morita et al., 1973), as shown by the important variations of bacterial concentrations in this study.

Mean total densities, taxonomic community composition and functional diversity of zooplankton in the ETZ show important interannual variability (Table A7), which can be linked to multiple environmental factors. As shown by the dbRDA, zooplankton communities were influenced in similar ways by the environment in 2020 and 2022, as stations of different years overlap in most salinity zones. This could explain that these communities showed similar structures. Communities from these two years had lower total densities, but a higher taxonomic and functional diversity. Temperature is one of the environmental factors that stands out as one of the most influential between these years in polyhaline waters, influencing 2021 generally in the opposite way from 2020 and 2022. Mean temperature was slightly higher in 2021 in the polyhaline zone, which could explain the different impact observed on zooplankton communities. Communities in 2021 had lower taxa richness, Shannon diversity and functional evenness but higher total densities, which could indicate that specific taxa with higher presence have a higher acclimatization capacity in regards to temperature variations.This is consistent with reports in the larger St. Lawrence system, such as the Lower St. Lawrence Estuary (LSLE) and the Gulf showing that sea surface temperatures showed major variations between those years. While May to November average sea surface temperature in the Gulf was globally normal in 2020, it was lower than average in 2019 (Blais et al., 2021b) and higher than average in 2021 (Blais et al., 2023a; Galbraith et al., 2022). Temperature has been found to be a factor that influences the larval development rate of benthic invertebrates (Reitzel et al., 2004) and their community structure in the St. Lawrence (Lévesque, 2009). This could explain the lower abundances of Bivalvia veliger observed in the polyhaline zone in 2021, as our results show that temperature was positively correlated with zooplankton communities in these communities. Temperature is also an important factor affecting winter conditions found in the St. Lawrence estuary from 2019 to 2022 (Table A10), which has been suggested to be directly linked to interannual variations in plankton abundances through how differently each species respond to winter conditions (Colebrook, 1985). While the volume of sea ice recorded was normal in 2019 and 2022 in the adjacent LSLE and Gulf, it was below normal in 2020 and nearly ice-free in 2021 (Blais et al., 2021a; Blais et al., 2021b; Blais et al., 2023a; Blais et al., 2023b). The winter season of 2021 is one of the few winters in the record with air temperature anomalies of +2.4 °C in the Gulf from December to March as well as nearly ice-free conditions, with an ice cover that formed much later than usual in the Estuary (Galbraith et al., 2024). Warmer-than-normal winters are typically associated with low winter convection, which is a critical process to bring deep nutrient-rich waters to the surface that support spring primary production (Blais et al., 2023a).

Other than winter conditions, freshwater runoff has been determined as one of the principal external factors shaping zooplankton communities in estuaries through their influence on nutrients concentrations and dissolved organic matter (Benfield, 2012; Chou et al., 2012; Mukherjee et al., 2018; Sun et al., 2020). Freshwater runoff account for up to 35% of nutrient input to the St. Lawrence estuary (Blais et al., 2023b). Higher levels of nutrients and detrital organic matters brought by river runoff are typically positively correlated with phytoplankton as well as zooplankton production and density (Benfield, 2012; Sun et al., 2020) and simultaneously structure phytoplankton composition (Bharathi et al., 2018). At Quebec City, the peak of freshwater runoff usually happens in April and May and can reach up to 22000 m^3s^{-1} of water (Fisheries and Oceans Canada, 2023). Between 2019 and 2022, data shows that freshwater runoffs in the St. Lawrence estuary were the lowest in 2021 compared to the three other years (Fisheries and Oceans Canada, 2023), while being slightly above normal in 2020 and normal in 2022 (Galbraith et al., 2023). In 2019 however, the freshwater discharge in the estuary recorded was at its highest since 1976 (Galbraith et al., 2022). Very low freshwater discharge in 2021, combined with a reduced winter convection, might have led to overall less available nutrients in the Estuary and therefore lower spring primary production (Blais et al., 2023a). In other estuaries, such as the Liaohe Estuary, a decreasing trend in zooplankton density has been observed from spring to autumn, which is consistent with the seasonal water runoff patterns in that area (Sun et al., 2020). In the St. Lawrence estuary, strong seasonal patterns have also been found between spring and summer, with decreasing densities of mesozooplankton such as *E. affinis* and *B. longirostris* potentially due to predation, while there is an increase in microzooplankton (Laprise et Dodson, 1994).

Early phytoplankton blooms have been linked to higher survival rates in copepod offsprings (Seebens et al., 2009), and previous data suggested a strong and early phytoplankton bloom around Rimouski in 2019 (Blais et al., 2023b). It is, however, hard to know to what extend chl *a* influenced the structure and high densities of zooplankton sampled in 2019 in the ETZ, as no data were available early in the year 2019. Average fluorescence levels and chl *a* concentrations in the ETZ were higher in 2020 and 2021 than 2019 and 2022. However, these differences are mainly due to the freshwater and oligohaline zones since fluorescence values in mesohaline and polyhaline waters did not vary much among years. Fluorescence and chl *a* were shown to be some of the main structuring factors of freshwater and oligohaline communities. Phytoplankton blooms with a high magnitude can lead to increased zooplankton egg productivity (Durbin et al., 2003). A positive correlation was found between these factors with most of the communities of 2021, while in 2021 a negative correlation with communities was observed, which may explain partially the higher zooplankton densities found in the year 2021.

Physical, chemical and biological conditions described above between 2019 and 2022 likely influenced other environmental factors and therefore the zooplankton communities indirectly as well. Interannual and spatial variations in zooplankton observed in this study seem to be in large parts driven by physical environmental factors, which is consistent with previous research (Laprise et Dodson, 1994; Winkler et al., 2005; Santo, 2023). Furthermore, other biological factors of zooplankton that are known to impact interannual variations but were not measured could also have influenced the communities. These include reproduction, mortality, predation and food conditions (Winkler et al., 2003; Kneitel et Chase, 2004; Winkler et al., 2005). For example mysids such as *Neomysis americana* and *Mysis stenolepis* show temporal and spatial prey-switching behavior, therefore potentially having an important influence on zooplankton structure (Winkler et al., 2007).

CONCLUSION

This study is the first project since the 2000's to present a portrait of the current state of the zooplankton communities in the ETZ of the St. Lawrence and to analyze the functional diversity of these communities. These new data reveal zooplankton communities whose structure closely follows that of the zones from the Venice Salinity System and where the mesohaline zone represents a clear transition zone between lower and higher salinities, both in terms of environmental influences and dominant zooplankton species and traits. While densities were highly dominated by a few structuring taxa, Copepoda was, by far, the most present group across the salinity gradient. Varying proportions of trophic functional groups revealed a more even distribution of functional traits in freshwater where resources are abundant, compared to a higher presence of specialist species in the polyhaline zone. Functional richness was sometimes contrasted with the observed taxonomic indices, with communities from 2020 and 2022 being more diverse taxonomically and functionally in the 200 µm nets despite lower densities. Our results also highlight the complexity of the different environmental conditions shaping the structure and function of these communities, with the most influential environmental factors varying with years and salinity zone. This study confirms the necessity of a long-term and seasonal survey of the zooplankton of the St. Lawrence transition zone to better understand this highly variable system. In the context of ongoing anthropic and environmental changes that will most likely impact the functioning of the whole ecosystem.

CONCLUSION GÉNÉRALE

Ce projet est le premier à analyser les données provenant d'un suivi des dernières années (de 2019 à 2022) sur les communautés zooplanctoniques de la ZTE du Saint-Laurent. Les objectifs de ce projet étaient d'approfondir nos connaissances sur le zooplancton de la ZTE du Saint-Laurent sous l'angle de la diversité taxonomique et fonctionnelle et en lien avec les variations environnementales. Ces résultats s'inscrivent également dans le contexte plus large de l'amélioration de la compréhension du fonctionnement des estuaires qui sont des écosystèmes très dynamiques et complexes (Bousfield et al. 1975). Les communautés zooplanctoniques échantillonnées de la ZTE du Saint-Laurent de 2019 à 2022 sont fortement structurées par le gradient de salinité. Les communautés de la zone mésohaline représentent une communauté de transition claire entre les salinités plus basses et plus élevées. Les copépodes formaient la grande majorité de ces assemblages, qui se distinguaient particulièrement par la présence de certaines espèces limnétiques ou marines. Une tendance temporelle distingue les années 2019 et 2021 des années 2020 et 2022, puisque les densités de zooplancton étaient plus élevées en 2019 et 2021 et s'accompagnaient d'une richesse taxonomique et fonctionnelle plus faible, ce qui démontre que la ZTE du Saint-Laurent est une zone dynamique et très variable d'une année à l'autre. Les facteurs environnementaux les plus influant sur les communautés zooplanctoniques observées varient avec les années et les zones de salinité, démontrant la complexité des interactions entre les différents facteurs de ce système. La température a eu une influence particulièrement importante dans les zones mésohaline et polyhaline. Les zones d'eau douce étaient davantage influencées par les concentrations de NO_2NO_3, qui ont eu une influence positive sur les communautés de 2020, et la fluorescence.

Limites de l'étude

Dans le contexte d'échantillonnage pluriannuel, un manque d'uniformité dans les données recueillies à travers les années a empêché certaines analyses d'être réalisées, en particulier parce que plusieurs données environnementales n'ont pas été mesurées durant l'année 2019. Les analyses de redondances visant à mesurer les influences environnementales sur les communautés nécessitent qu'il n'y ait aucune donnée manquante, ce qui explique pourquoi l'année 2019 ainsi que certains facteurs environnementaux ont dû être retirés de ces analyses. De plus, en raison des restrictions techniques liées au travail de terrain et à l'imprévisibilité des conditions, l'échantillonnage ne s'est pas produit exactement aux mêmes dates à chaque année, ce qui peut induire un biais dans les résultats considérant l'importance de la saisonnalité chez les communautés zooplanctoniques (Colebrook, 1985 ; Seebens et al., 2009; Sun et al., 2020), particulièrement dans des environnements dynamiques comme les estuaires. Il est ainsi difficile de conclure si certaines différences observées dans les communautés de 2019 pourraient être attribuées à un échantillonnage légèrement tardif en début septembre par rapport aux trois autres années échantillonnées en août. L'identification visuelle réalisée du zooplancton comporte également ses limites. Les copépodes étaient souvent le seul groupe dont les individus pouvaient être identifiés jusqu'à l'espèce, tandis que plusieurs autres taxa ont dû être identifiés à des niveaux taxonomiques supérieurs en raison de contraintes techniques. Ceci implique donc nécessairement un niveau de précision variable dans les zones de salinité qui continent moins de copépodes.

Il est difficile de comprendre les forces influant le zooplancton sur une base de données de 4 ans seulement considérant que ces communautés sont fortement dynamiques et variables. Les données actuelles permettent uniquement de formuler des hypothèses sur les conditions environnementales semblant avoir eu un impact sur la composition et la diversité des communautés durant certaines années spécifiques. Il est toutefois difficile de déterminer des liens de causalité exactes en raison de la complexité et des interactions entre les facteurs physiques, chimiques et biologiques à considérer. Par exemple, les années 2019 et 2021 montrant des communautés zooplanctoniques avec des densités et des compositions similaires, mais une grande partie des facteurs environnementaux observés ont des valeurs très variables entre ces deux années. De plus, il ne nous est pas possible de distinguer les influences des paramètres environnementaux des dynamiques saisonnières avec ce jeu de données obtenu pendant une courte période de l'été/automne, une situation similaire à d'autres estuaires (Sun et al., 2020).

Implications et perspectives de recherche

Ce projet soutient l'importance de poursuivre un suivi annuel du zooplancton de l'estuaire du Saint-Laurent pour combler un manque de données important. Les études s'intéressant au zooplancton de l'Estuaire du Saint-Laurent sont peu nombreuses, et la majorité des connaissances sur ces communautés sont basées sur des études qui précèdent les années 2000 (Bousfield et al. 1975; Runge et Simard, 1990; Laprise et Dodson, 1994). Dans ce contexte, les données zooplanctoniques et environnementales utilisées pour ce projet ont le potentiel de devenir une base de données de référence pour des travaux futurs. Il est essentiel de construire une base de données détaillée à partir d'un suivi temporel à plus long terme du zooplancton de l'Estuaire du Saint-Laurent. Une compréhension approfondie des tendances temporelles en lien des variations environnementales contribuerait à une meilleure anticipation des changements futurs des communautés de l'Estuaire et de leurs conséquences sur les réseaux trophiques et les services écosystémiques. Cette compréhension est aussi importante pour distinguer les variations de ces changements dans chaque zone de salinité dans le contexte où les résultats de ce projet montrent que l'importance de différents facteurs environnementaux n'est pas la même le long du gradient de salinité. Le rôle central du zooplancton dans les transferts d'énergie et les réseaux trophiques des écosystèmes estuariens lui procure un rôle essentiel comme indicateur de l'état de ces écosystèmes (Ferdous et Muktadir, 2009). Des projets de « recherche écologique à long-terme » sont généralement considérés comme tel lorsque des données ont été récoltées de façon systématique et régulière sur une période d'au moins 10 ans, permettant de distinguer les fluctuations naturelles des tendances à long terme souvent attribuables aux changements climatiques (Lindenmayer et al., 2012; Ratnarajah et al., 2023). Ce sont ces travaux de recherche à long terme qui ont une importance au niveau légal et permettent de mettre en œuvre des politiques environnementales visant à la conservation de ces habitats (Hughes et al., 2017). Une attention particulière devrait également être portée à la phénologie des espèces caractéristiques de l'Estuaire, considérant qu'il a été observé que les cycles de croissance du zooplancton deviennent de plus en plus hâtifs et répondent particulièrement rapidement aux changements environnementaux (Cooley et al., 2022; Ratnarajah et al., 2023). Ceci peut, entre autres, être réalisé à l'aide de l'identification des stades de développement, ce qui a été réalisée dans cette étude pour la majorité des espèces de copépodes mais n'a pas pu être inclus dans les analyses par manque de temps. Des échantillonnages durant plusieurs saisons permettraient également d'approfondir notre compréhension sur les tendances saisonnières des communautés (Laprise et Dodson, 1994) qui pourraient avoir joué des rôles importants dans les différences interannuelles des assemblages observées dans cette étude.

À cette meilleure compréhension de la compréhension des communautés zooplanctoniques de l'Estuaire s'ajoute plusieurs perspectives de recherche sur les impacts anthropiques sur ces communautés. Ces impacts incluent ceux liés à la présence de microoplastiques ou de contaminants, ainsi qu'au réchauffement des eaux (Martins et al., 2023). L'ajout de données se penchant davantage sur d'autres facteurs n'ayant pas été considérés dans la présente étude mais ayant un impact sur le zooplancton serait nécessaire afin de déterminer avec une plus grande certitude les variations environnementales structurant les communautés. Les interactions trophiques ont été suggérées comme ayant un impact important sur les dynamiques spatio-temporelles des assemblages de zooplancton (Laprise et Dodson, 1994). La prédation, non mesurés dans cette étude, peut interagir avec d'autres facteurs et ainsi avoir des impacts substantiels sur la façon dont les communautés zooplanctoniques réagissent aux variations environnementales (Kneitel et Chase, 2004). De plus, deux des quatre traits fonctionnels considérés dans cette étude ont trait à l'alimentation, soit le groupe trophique et la méthode d'alimentation. Avec l'amélioration de la quantité de traits fonctionnels documentés pour le zooplancton dans la littérature, il serait pertinent d'inclure des traits pouvant renseigner sur d'autres fonctions écologiques comme la croissance, la reproduction et la survie (Litchman et al., 2013).

En plus d'améliorer notre compréhension de la structure des communautés zooplanctoniques de l'estuaire moyen du Saint-Laurent, ce projet a le potentiel d'être le début d'un suivi à long-terme de ces communautés qui sont au cœur des écosystèmes. Il sera donc par la suite essentiel que les ressources nécessaires soient investies dans la prise et l'analyses de ces données, afin de prévoir et favoriser le maintien du fonctionnement des écosystèmes du Saint-Laurent et de tous les services qui en découlent.

ANNEXES

Table A1. *Coordinates of stations sampled by year with the 63 µm and/or 200 µm plankton nets and their corresponding salinity zone (freshwater = F, oligohaline = O, mesohaline = M, polyhaline = P) and coordinates. The salinity zones were attributed based on the median of the salinities measured throughout the entire water column and the Venice system.*

Station Name	Year	Coordinates		Salinity zone	Sampled	
		Longitude	Latitude		63 µm	200 µm
ED-01	2019	-71.1285	46.8872	F	x	x
	2020	-71.1285	46.8866	F	x	x
	2021	71.07607	46.53338	F	x	x
ED-02	2019	-71.063	46.84025	F	x	x
	2022	-70.978	46.8548	F	x	x
ED-03	2020	-71.1545	46.8394	F	x	x
	2021	71.09250	46.49992	F	x	x
	2022	-71.154	46.8347	F	x	x
ED-07	2019	-71.1244	46.4767	F	x	x
	2020	-71.2215	46.79235	F	x	x
ED-10	2019	-71.2074	46.4342	F	x	x
	2020	-71.3455	46.72435	F	x	x
ED-BB	2019	-71.179	46.8434	F	x	x
	2020	-71.178	46.8426	F	x	x
	2021	71.11008	46.50454	F	x	x
	2022	-71.1795	46.84285	F	x	x
ETZ-01	2020	-69.5165	47.98105	P	x	x
	2021	-69.524	47.9987	P	x	x
	2022	-69.508	47.9855	P	x	x
ETZ-02	2020	-69.7105	48.0425	P	x	x
	2021	-69.719	48.0432	P	x	x
	2022	-69.714	48.04465	P	x	x
ETZ-03	2020	-69.622	48.0464	P	x	x
	2021	-69.631	48.0474	P	x	x
	2022	-69.6205	48.05315	P	x	x
ETZ-04	2020	-69.617	47.98725	P	x	x
	2021	-69.633	47.9916	P		x
	2022	-69.603	47.99785	P	x	x
ETZ-4,5	2020	-69.631	47.9217	P	x	x
	2021	-69.626	47.9208	P	x	x
	2022	-69.629	47.9221	P	x	x
ETZ-05	2020	-69.5285	47.9262	P	x	x
	2021	-69.53	47.9228	P	x	x
	2022	-69.532	47.9185	P	x	x
ETZ-06	2019	-69.714	47.8194	P	x	x
	2021	-69.702	47.8303	P	x	x
	2022	-69.6925	47.83675	P	x	x
ETZ-07	2021	-69.677	47.7525	M	x	x
ETZ-08	2020	-69.791	47.68115	P	x	x
	2021	-69.804	47.6744	M	x	x
	2022	-69.808	47.67045	P	x	x

Table A1 (continued).

Station Name	Year	Coordinates		Salnity zone	Sampled	
		Longitude	Latitude		63 µm	200 µm
ETZ-09	2020	-70.077	47.6676	P	x	X
	2021	-70.078	47.6682	P	x	x
	2022	-70.0805	47.6669	P	x	x
ETZ-10	2021	-70.093	47.6036	P	x	x
	2022	-70.073	47.62485	P	x	x
ETZ-11	2019	-70.024	47.5277	P		x
	2021	-70.016	47.5312	P	x	x
	2022	-70.02	47.5235	P	x	x
ETZ-12	2019	-70.1315	47.36815	M	x	x
	2020	-70.172	47.4112	M	x	x
	2021	-70.132	47.3752	P	x	x
	2022	-70.139	47.38165	P	x	x
ETZ-13	2019	-70.2595	47.41765	P	x	x
	2021	-70.262	47.4164	P	x	x
	2022	-70.2545	47.4231	P	x	x
ETZ-14	2021	-70.265	47.3628	P	x	x
	2022	-70.2705	47.33915	M	x	x
ETZ-15	2019	-70.3175	47.345025	P	x	x
	2021	-70.526	47.3139	M	x	x
ETZ-16	2019	-70.4057	47.3172	M	x	x
	2021	-70.399	47.3153	M	x	x
	2022	-70.314	47.3147	M	x	x
ETZ-17	2020	-70.3315	47.20505	O	x	x
	2021	-70.323	47.2313	O	x	x
	2022	-70.329	47.22	O	x	x
ETZ-19	2019	-70.606	47.1905	M	x	x
	2020	-70.6065	47.19145	M	x	x
	2021	-70.61	47.1826	M	x	x
	2022	-70.5985	47.1924	P	x	x
ETZ-20	2019	-70.5497	47.1245	O	x	x
	2020	-70.544	47.10915	O	x	x
	2021	-70.551	47.1173	O	x	x
	2022	-70.547	47.1197	F	x	x
ETZ-21	2020	-70.585	47.0627	F	x	x
	2021	-70.584	47.0733	F	x	x
	2022	-70.59	47.0579	F	x	x
ETZ-22	2020	-70.706	47.10885	O	x	x
	2021	-70.701	47.112	M	x	x
	2022	-70.6985	47.1135	O	x	x
ETZ-23	2019	-70.4737	47.0971	F	x	x
	2020	-70.4875	47.1002	F	x	x
	2021	-70.481	47.1063	O	x	x
	2022	-70.478	47.1085	O	x	x
ETZ-24	2019	-70.518	47.0533	O	x	x
	2020	-70.531	47.0527	F	x	x
	2021	-70.522	47.0538	F	x	x
	2022	-70.527	47.0475	F	x	x

Table A1 (continued).

Station Name	Year	Coordinates		Salnity zone	Sampled	
		Longitude	Latitude		63 µm	200 µm
ETZ-25	2019	-70.522	47.0245	O	x	x
	2021	-70.516	47.0197	F	x	x
ETZ-26	2019	-70.774	46.9153	F	x	x
	2020	-70.7745	46.91715	F	x	x
	2021	-70.778	46.9167	F	x	x
	2022	-70.774	46.91825	F	x	x
ETZ-27	2019	-70.706	46.9748	F	x	x
	2020	-70.704	46.9703	F	x	x
	2021	-70.708	46.9748	F	x	x
	2022	-70.709	46.976	F	x	x
ETZ-28	2020	-70.694	47.0515	F	x	x
	2021	-70.689	47.05	O	x	x
	2022	-70.6995	47.04395	F	x	x
ETZ-29	2019	-70.766	47.0239	F	x	x
	2020	-70.759	47.0273	F	x	x
	2021	-70.769	47.0216	O	x	x
	2022	-70.7575	47.0275	F	x	x
ETZ-29	2021	-70.769	47.0216	O		x

Table A2. *Summary of presence-absence for all identified taxa in each year and salinity zone (freshwater = F, oligohaline = O, mesohaline = M, polyhaline = P) for 63 µm and 200 µm plankton net mesh.*

Taxa	63 µm																200 µm															
	2019				2020				2021				2022				2019				2020				2021				2022			
	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
Acantharea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1
Acanthocyclops spp.	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0
Acartia clausi	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Acartia longiremis	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1
Acartia spp.	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1
Aetideidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Alona spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Anonyx sarsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ascidiacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Ascomorpha sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asplanchna sp.	0	0	1	1	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0	1	0	0	0	1
Bosmina longirostris	1	1	0	0	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0
Brachionidae sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachionus sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachionus variabilis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bradyidius similis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Calanoida	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Calanus finmarchicus	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1
Calanus finmarchicus glacialis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Calanus glacialis hyperboreus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Calanus hyperboreus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Camptocercus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Centropages hamatus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Ceriodaphnia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
Chaetognatha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Chaetognatha (> 1cm)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chydoridae	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Cirripedia	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	1
Cnidaria	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1
Cnidaria (> 1cm)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Colurella sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochiloides sp.	0	1	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilus sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copepoda	1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	1	1	0	1	1	1	1	0	0	1	1	0	1	0	0	0	1
Crangon septemspinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ctenophora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ctenophora (> 1cm)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cumacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cyclopoida	1	1	1	0	1	1	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Daphnia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Decapoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1

Table A2 (continued).

Taxa	63 µm																200 µm															
	2019				2020				2021				2022				2019				2020				2021				2022			
	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
Diacyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Diacyclops thomassi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplostraca	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1
Echinodermata	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Ectoprocta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Epischura lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euchlanis alata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euchlanis sp.	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Euphausiidae	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	1
Eurycercus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Eurytemora affinis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eurytemora herdmani	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1
Eurytemora spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Evadne sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Facetotecta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Foraminiferida	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	1
Fritillaria sp.	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Gadidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gammaridae	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	0	1	1	1	1
Gasterosteus aculeatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gastropoda	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	1	1	1	1	1
Halicyclops sp.	1	1	0	0	1	1	0	1	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0
Harpacticoida	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1
Hydrozoa	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ichtyoplancton	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	1
Ilyocryptus sp.	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Ilyocryptus spinifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Invertebrate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	0	1
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Kellicotia bostoniensis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Keratella cochlearis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Keratella sp.	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Keratella tecta	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lecane cornuta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lecane sp.	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepadella sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodiaptomus sicilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodiaptomus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Mesocyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Metridia longa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Metridia lucens	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Metridia spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

Table A2 (continued).

Taxa	63 µm																200 µm															
	2019				2020				2021				2022				2019				2020				2021				2022			
	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
Microcalanus spp.	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Microcyclops rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Microcyclops sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Microgadus tomcod	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
Microsetella norvegica	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Microsetella sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Monospilus dispar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Monostyla bulla	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monostyla sp.	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monstrilla sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Mysidacea	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Mysis stenolepis	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	1	1	0	1	1	1
Neomysis americana	0	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	0	1	1	1
Notholca sp.	1	1	0	0	1	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notommata sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oithona atlantica	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oithona similis	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Oithona sp1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oithona spp.	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Oncaea sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Orthocyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmerus mordax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0
Osphranticum labronectum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ostracoda	1	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1
Paraeuchaeta norvegica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Ploesoma truncatum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Podon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Polyarthra sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	1	0	1	1	1	0	0	1	1	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1
Proales sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocalanus spp.	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Rotifera	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scolecithricella minor	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1
Scolecithricella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Sida crystallina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0
Streblocerus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Synchaeta sp.	0	0	1	0	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tardigrade	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Temora longicornis	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1
Temora sp.	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Table A2 (continued).

Taxa	63 µm																200 µm															
	2019				2020				2021				2022				2019				2020				2021				2022			
	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
Testudinellidae sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thysanoessa raschii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Tintinnina	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Tortanus discaudatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trichocerca sp.	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triconia borealis	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Triconia sp.	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tropocyclops sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Table A3. *Two-factor PERMANOVA (year, salinity zone) results of community composition, density, taxonomic indices (taxa richness, species richness, Shannon's diversity, Pilou's eveness) and function indices (functional richness, functional divergence, functional eveness.*

		Df	SS	MS	Pseudo-F	P(perm)	
Community composition							
63 µm	Year	3	10918	3639	2,49	0,002	**
	Salinity zone	3	66128	22043	15,07	0,001	***
	Year * salinity zone	9	17729	1970	1,35	0,035	*
	Residual	49	71695	1463			
	Total	64	171950				
200 µm	Year	3	16083	5361	4,31	0,001	***
	Salinity zone	3	109320	36439	29,29	0,001	***
	Year * salinity zone	9	21051	2339	1,88	0,001	***
	Residual	84	104510	1244			
	Total	99	278920				
Density							
63 µm	Year	3	4,24E+10	1,41E+10	6,88	0,002	**
	Salinity zone	3	2,77E+10	9,24E+09	4,50	0,013	*
	Year * salinity zone	9	4,27E+10	4,75E+09	2,31	0,036	*
	Residual	49	1,01E+11	2,05E+09			
	Total	64	2,09E+11				
200 µm	Year	3	9,68E+07	3,23E+07	10,95	0,001	***
	Salinity zone	3	1,64E+07	5,48E+06	1,86	0,158	
	Year * salinity zone	9	2,58E+07	2,86E+06	0,97	0,445	
	Residual	84	2,48E+08	2,95E+06			
	Total	99	3,94E+08				
Taxa richness							
63 µm	Year	3	121,91	40,64	2,75	0,061	
	Salinity zone	3	868,91	289,64	19,60	0,001	***
	Year * salinity zone	9	183,01	20,34	1,38	0,216	
	Residual	49	724,10	14,78			
	Total	64	2007,00				
200 µm	Year	3	229,19	76,40	4,41	0,005	**
	Salinity zone	3	1446,80	482,28	27,82	0,001	***
	Year * salinity zone	9	202,29	22,48	1,30	0,242	
	Residual	90	1560,20	17,34			
	Total	105	4468,50				
Species richness							
63 µm	Year	3	11,37	3,79	2,31	0,091	
	Salinity zone	3	94,26	31,42	19,11	0,001	***
	Year * salinity zone	9	41,09	4,57	2,78	0,007	**
	Residual	49	80,58	1,64			
	Total	64	212,15				
200 µm	Year	3	14,43	4,81	1,89	0,129	
	Salinity zone	3	128,06	42,69	16,79	0,001	***
	Year * salinity zone	9	69,06	7,67	3,02	0,003	**
	Residual	90	228,83	2,54			
	Total	105	508,35				

Table A3 (continued).

		Df	SS	MS	Pseudo-F	P(perm)	
Shannon's diversity							
63 µm	Year	3	0,28	0,09	0,38	0,755	
	Salinity zone	3	4,04	1,35	5,36	0,003	**
	Year * salinity zone	9	1,92	0,21	0,85	0,585	
	Residual	49	12,31	0,25			
	Total	64	19,72				
200 µm	Year	3	2,13	0,71	5,27	0,002	**
	Salinity zone	3	6,94	2,31	17,19	0,001	***
	Year * salinity zone	9	1,43	0,16	1,18	0,307	
	Residual	90	12,12	0,13			
	Total	105	29,44				
Pielou's eveness							
63 µm	Year	3	0,034	0,011	1,34	0,266	
	Salinity zone	3	0,019	0,006	0,73	0,512	
	Year * salinity zone	9	0,062	0,007	0,81	0,643	
	Residual	49	0,419	0,009			
	Total	64	0,549				
200 µm	Year	3	0,035	0,012	2,57	0,060	
	Salinity zone	3	0,043	0,014	3,16	0,030	*
	Year * salinity zone	9	0,111	0,012	2,71	0,015	*
	Residual	90	0,411	0,005			
	Total	105	0,602				
Functional richness							
63 µm	Year	3	0,13416	0,044719	4,6148	0,006	**
	Salinity zone	3	0,91304	0,30435	31,407	0,001	***
	Year * salinity zone	9	0,11102	0,012335	1,2729	0,278	
	Residual	84	0,81399	0,0096904			
	Total	99	2,3359				
200 µm	Year	3	0,13416	0,044719	4,6148	0,006	**
	Salinity zone	3	0,91304	0,30435	31,407	0,001	***
	Year * salinity zone	9	0,11102	0,012335	1,2729	0,265	
	Residual	84	0,81399	0,0096904			
	Total	99	2,3359				
Functional divergence							
63 µm	Year	3	0,034224	0,011408	0,95352	0,384	
	Salinity zone	3	0,13499	0,044997	3,761	0,006	**
	Year * salinity zone	9	0,088021	0,0097801	0,81745	0,616	
	Residual	84	1,005	0,011964			
	Total	99	1,2619				
200 µm	Year	3	0,034224	0,011408	0,95352	0,437	
	Salinity zone	3	0,13499	0,044997	3,761	0,012	**
	Year * salinity zone	9	0,088021	0,0097801	0,81745	0,600	
	Residual	84	1,005	0,011964			
	Total	99	1,2619				
Functional eveness							
63 µm	Year	3	0,07235	0,024117	3,3537	0,019	*
	Salinity zone	3	0,097826	0,032609	4,5346	0,007	**
	Year * salinity zone	9	0,07044	0,0078267	1,0884	0,375	
	Residual	84	0,60405	0,0071911			
	Total	99	0,8729				
200 µm	Year	3	0,07235	0,024117	3,3537	0,030	*
	Salinity zone	3	0,097826	0,032609	4,5346	0,006	**
	Year * salinity zone	9	0,07044	0,0078267	1,0884	0,406	
	Residual	84	0,60405	0,0071911			
	Total	99	0,8729				

Table A4. *Post-hoc comparisons of years (PERMANOVA) of community composition, density, taxonomic indices and functional indices per year for significantly different factors (<0.05).*

Plankton net			P-values			
			2019	2020	2021	2022
Community composition	63 µm	2019	NA	NA	NA	NA
		2020	0.020	NA	NA	NA
		2021	0.153	0,001	NA	NA
		2022	0.071	0.117	0.003	NA
	200 µm	2019	NA	NA	NA	NA
		2020	0.001	NA	NA	NA
		2021	0.129	0.001	NA	NA
		2022	0.005	0.005	0.001	NA
Density	63 µm	2019	NA	NA	NA	NA
		2020	0.056	NA	NA	NA
		2021	0.118	0.007	NA	NA
		2022	0.032	0.991	0.001	NA
	200 µm	2019	NA	NA	NA	NA
		2020	0.002	NA	NA	NA
		2021	0.900	0.001	NA	NA
		2022	0.001	0.365	0.001	NA
Taxa richness	200 µm	2019	NA	NA	NA	NA
		2020	0.224	NA	NA	NA
		2021	0.494	0.029	NA	NA
		2022	0.052	0.269	0.001	NA
Shannon's diversity	200 µm	2019	NA	NA	NA	NA
		2020	0.183	NA	NA	NA
		2021	0.054	0.002	NA	NA
		2022	0.689	0.258	0.01	NA
Functional richness	63 µm	2019	NA	NA	NA	NA
		2020	0.808	NA	NA	NA
		2021	0.974	0.700	NA	NA
		2022	0.018	0.008	0.001	NA
	200 µm	2019	NA	NA	NA	NA
		2020	0.781	NA	NA	NA
		2021	0.984	0.687	NA	NA
		2022	0.024	0.010	0.004	NA
Functional eveness	63 µm	2019	NA	NA	NA	NA
		2020	0.097	NA	NA	NA
		2021	0.008	0.457	NA	NA
		2022	0.670	0.140	0.021	NA
	200 µm	2019	NA	NA	NA	NA
		2020	0.084	NA	NA	NA
		2021	0.015	0.446	NA	NA
		2022	0.698	0.144	0.020	NA

Table A5. *Post-hoc comparisons of salinity zones (PERMANOVA) of community composition, density, taxonomic indices and functional indices per salinity zone (freshwater = F, oligohaline = O, mesohaline = M, polyhaline = P) for significantly different factors (<0.05).*

	Plankton net mesh		P-values			
			F	O	M	P
Community composition	63 µm	F	NA	NA	NA	NA
		O	0.001	NA	NA	NA
		M	0.001	0.003	NA	NA
		P	0.001	0.001	0.001	NA
	200 µm	F	NA	NA	NA	NA
		O	0.001	NA	NA	NA
		M	0.001	0.001	NA	NA
		P	0.001	0.001	0.001	NA
Density	63 µm	F	NA	NA	NA	NA
		O	0.131	NA	NA	NA
		M	0.443	0.128	NA	NA
		P	0.01	0.002	0.287	NA
Taxa richness	63 µm	F	NA	NA	NA	NA
		O	0.019	NA	NA	NA
		M	0.01	0.286	NA	NA
		P	0.002	0.001	0.001	NA
	200 µm	F	NA	NA	NA	NA
		O	0.001	NA	NA	NA
		M	0.025	0.149	NA	NA
		P	0.001	0.001	0.001	NA
Species richness	63 µm	F	NA	NA	NA	NA
		O	0.765	NA	NA	NA
		M	0.907	0.745	NA	NA
		P	0.001	0.001	0.001	NA
	200 µm	F	NA	NA	NA	NA
		O	0.063	NA	NA	NA
		M	0.405	0.586	NA	NA
		P	0.001	0.001	0.001	NA
Shannon's diversity	63 µm	F	NA	NA	NA	NA
		O	0.185	NA	NA	NA
		M	0.362	0.501	NA	NA
		P	0.068	0.002	0.003	NA
	200 µm	F	NA	NA	NA	NA
		O	0.001	NA	NA	NA
		M	0.007	0.702	NA	NA
		P	0.059	0.001	0.001	NA
Pielou	200 µm	F	NA	NA	NA	NA
		O	0.196	NA	NA	NA
		M	0.016	0.26	NA	NA
		P	0.018	0.787	0.11	NA
Functional richness	63 µm	F	NA	NA	NA	NA
		O	0.041	NA	NA	NA
		M	0.650	0.222	NA	NA
		P	0.001	0.01	0.001	NA
	200 µm	F	NA	NA	NA	NA
		O	0.039	NA	NA	NA
		M	0.657	0.215	NA	NA
		P	0.001	0.001	0.001	NA
Functional divergence	63 µm	F	NA	NA	NA	NA
		O	0.002	NA	NA	NA
		M	0.327	0.166	NA	NA
		P	0.322	0.014	0.697	NA
	200 µm	F	NA	NA	NA	NA
		O	0.001	NA	NA	NA
		M	0.307	0.150	NA	NA
		P	0.328	0.009	0.713	NA

Table A5 (continued).

	Plankton net mesh		P-values			
			F	O	M	P
Functional eveness	63 µm	F	NA	NA	NA	NA
		O	0.017	NA	NA	NA
		M	0.016	0.818	NA	NA
		P	0.164	0.032	0.024	NA
	200 µm	F	NA	NA	NA	NA
		O	0.008	NA	NA	NA
		M	0.015	0.837	NA	NA
		P	0.160	0.038	0.019	NA

Table A6. *Summary of PERMANOVA results of significantly different community composition, density, taxonomic indices and functional indices per year. Where: CC = community composition, Den = density, Tric = taxonomic richness, SpRich =species richness, Sha = Shannon's indice, Pie = Pielou's eveness indice, Fric = functional richness, Fdiv = functional divergence and Feve = functional eveness.*

		2019	2020	2021	2022
63 µm	2019				
	2020	CC			
	2021	Feve	CC, Den		
	2022	Den, Fric	Fric	CC, Den, Fric, Feve	
200 µm	2019				
	2020	CC, Den			
	2021	Feve	CC, Den, Tric, Sha		
	2022	CC, Den, Fric	CC, Fric	CC, Den, Tric, Sha, Fric, Feve	

Table A7. *Summary of PERMANOVA results of community composition, density, taxonomic indices and functional indices per salinity zone (freshwater = F, oligohaline = O, mesohaline = M, polyhaline = P). Where: CC = community composition, Den = density, Tric = taxonomic richness, SpRich = species richness, Sha = Shannon's indice, Pie = Pielou's eveness indice, Fric = functional richness, Fdiv = functional divergence and Feve = functional eveness.*

		F	O	M	P
63 µm	F				
	O	CC, Tric, Fric, Fdiv, Feve			
	M	CC, Tric, Feve	CC		
	P	CC, Den, Tric, SpRich, Fric	CC, Den, Tric SpRich, Sha, Fric, Fdiv, Feve	CC, Tric, SpRich, Sha, Fric, Feve	
200 µm	F				
	O	CC, Tric, Sha, Fric, Feve, Fdiv			
	M	CC, Tric, Sha, Pie, Feve	CC		
	P	CC, Tric, SpRich, Pie, Fric	CC, Tric, SpRich, Sha, Fric, Feve, Fdiv	CC, Tric, SpRich, Sha, Fric, Feve	

Table A8. *Results of post-hoc comparisons (pair-wise PERMANOVA) of interaction terms (year (2019-2022)*salinity zone (freshwater = F, oligohaline = O, mesohaline = M, polyhaline = P)) of community composition, density, taxonomic indices for significantly different factors (<0.05). Only p-values of significant interaction terms between year and salinity zone are shown.*

				2019				2020				2021				2022			
				F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
Community composition	63 µm	2019	F																
			O																
			M	0.038															
			P	0.021															
		2020	F																
			O					0.025											
			M					0.027											
			P				0.035	0.002	0.018										
		2021	F																
			O																
			M									0.02							
			P									0.012	0.006	0.003					
		2022	F																
			O																
			M											0.049					
			P				0.048									0.006	0.007	0.034	
	200 µm	2019	F																
			O	0.05															
			M	0.043															
			P	0.005	0.035														
		2020	F																
			O					0.009											
			M					0.012											
			P				0.021	0.001	0.005	0.018									
		2021	F																
			O						0.019			0.015							
			M									0.005	0.007						
			P								0.003	0.001	0.001	0.001					
		2022	F	0.02															
			O										0.013			0.003			
			M													0.013			
			P				0.007				0.001				0.017	0.001	0.002	0.009	
Density	63 µm	2019	F																
			O																
			M																
			P																
		2020	F	0.047															
			O																
			M					0.038											
			P																
		2021	F																
			O																
			M																
			P										0.013	0.024					
		2022	F																
			O																
			M																
			P																

Table A8 (continued).

				2019				2020				2021				2022			
				F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
Species richness	63 µm	2019	F																
			O																
			M																
			P	0.026															
		2020	F																
			O																
			M																
			P				0.037												
		2021	F																
			O																
			M																
			P										0.02	0.025					
		2022	F																
			O																
			M																
			P													0.013	0.003	0.04	
	200 µm	2019	F																
			O																
			M																
			P																
		2020	F																
			O					0.023											
			M					0.048											
			P																
		2021	F					0.002											
			O																
			M																
			P									0.003	0.001	0.007					
		2022	F					0.008											
			O																
			M																
			P								0.002					0.001	0.001		
Pielou's eveness	200 µm	2019	F																
			O																
			M																
			P																
		2020	F																
			O																
			M																
			P							0.02									
		2021	F																
			O		0.032														
			M																
			P																
		2022	F																
			O																
			M																
			P														0.032		

Table A9. *Summary of a one-way similarity percentage analysis (SIMPER) dissimilarity matrix (%) of taxa composition resemblance using Bray-Curtis similarity between year and salinity zone (freshwater = F, oligohaline = O, mesohaline = M, polyhaline = P) with a square-root transformation.* Dissimilarity values in blue are between years in the same salinity zone and values in white are between salinity zones in the same year.

			2019				2020				2021				2022			
			F	O	M	P	F	O	M	P	F	O	M	P	F	O	M	P
63 µm	2019	F																
		O	48,96															
		M	78,31	67,20														
		P	90,26	91,06	75,64													
	2020	F	40,69															
		O		57,25			54,97											
		M			65,97		79,57	69,45										
		P				56,81	77,49	76,78	62,91									
	2021	F	46,17				49,63											
		O		38,15				64,45			60,70							
		M			68,81				72,28		77,02	60,99						
		P				50,17				56,30	87,92	89,46	74,11					
	2022	F	46,44				46,93				46,23							
		O		50,97				51,15				52,99			54,74			
		M			65,24				62,10				83,80		73,90	62,89		
		P				58,48				55,64				56,21	82,30	82,86	85,52	
200 µm	2019	F																
		O	57,04															
		M	75,01	60,28														
		P	84,89	82,93	73,66													
	2020	F	55,72															
		O		70,46			58,15											
		M			64,84		77,52	68,79										
		P				56,16	91,24	91,24	60,33									
	2021	F	56,07				55,95											
		O		34,14				65,38			58,55							
		M			54,34				63,92		76,69	55,20						
		P				52,93				56,24	91,42	91,83	73,41					
	2022	F	52,28				49,16				50,78							
		O		53,63				47,64				49,41			57,18			
		M			59,75				60,67				60,87		58,73	40,69		
		P				54,32				51,24				50,93	89,96	89,18	83,41	

Table A10. *Summary of a BEST analysis on normalised environmental data (Fl = fluorescence, Tu = turbidity, Ch = chlorophyl a, NO = NO_2+NO_3, PO4 = PO_4^{3-}, PIM = particulate inorganic matter, POM = particulate organic matter, SP = suspended particulate matter, Picoc = picocyanobacteria, Nanoc = nanocyanobacteria, Ph = phaeopigments, Ba = bacteria, Te = temperature) and taxa composition resemblance using Euclidian distance, with the BIOENV method. Data from 2019 as well as a few other stations between 2020 and 2022 were excluded from this analysis due to missing data points.*

		No.Vars	Corr	Selections
63 µm	F	5	0,831	Fl,Tu,NO,PIM,Picoc
		5	0,801	Te,Fl,Tu,PIM,Picoc
		5	0,800	Fl,Tu,NO,Picoc
	O	1	0,477	Ba
		2	0,460	Picoe, Ba
		2	0,455	Te, Ba
	M	5	0,750	Tu,POM,PIM,Ph,Ba
		5	0,741	Tu,SP,PIM,Ph,Ba
		5	0,734	Tu,PIM,Ph,Nanoc,Ba
	P	5	0,286	Te,Fl,Tu,SP,Ph
		4	0,283	Te,Fl,Tu,Ph
		5	0,283	Te,Fl,Tu,PIM,Ph
200 µm	F	5	0,469	Fl,PO4,Picoe,Nanoe,Ba
		4	0,469	Fl,PO4,Nanoe,Ba
		4	0,468	Fl,Picoe,Nanoe,Ba
	O	3	0,449	Te,PIM,Ba
		4	0,440	Te,PIM,Picoe,Ba
		4	0,427	Te,PIM,Nanoc,Ba
	M	2	0,651	POM, PIM
		4	0,607	SP,POM,PIM,Nanoc
		3	0,606	SP,POM,PIM
	P	4	0,273	SP,POM,Ch,Ph
		5	0,270	SP,POM,PIM,Ch,Ph
		3	0,268	SP,POM,Ph

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