



**Variabilité spatio-temporelle des assemblages d'invertébrés dans
l'estuaire moyen du Saint-Laurent**

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RÉSUMÉ

Les estuaires, ces zones de transition marquées de gradients environnementaux, supportent des habitats hétérogènes et comptent parmi les milieux les plus productifs. Grâce à ses ressources alimentaires foisonnantes, la zone de turbidité maximale de l'estuaire du Saint-Laurent soutient une zone d'alevinage cruciale pour plusieurs espèces de poisson.

La maîtrise a pour objectif de décrire et comparer les assemblages des invertébrés pélagiques et littoraux le long du gradient estuarien. Accessoirement, l'étude vise à associer l'occurrence des premiers stades de vie du bar rayé aux assemblages d'invertébrés, et ce, durant toute de la saison de croissance de l'espèce, de juin à septembre. Elle permet également d'améliorer les connaissances sur les habitats estuariens littoraux, par ailleurs peu caractérisés à travers le monde, en offrant une première description de la composition des invertébrés planctoniques et supra-benthiques littoraux à proximité de l'intertidal dans l'estuaire fluvial et moyen du Saint-Laurent.

De juin à septembre 2014, 54 stations pélagiques et 188 stations littorales ont été échantillonnées au moyen de filet bongo, seine de rivage et sonde CTD. Une sous-sélection de 20 stations pélagiques et 68 stations littorales a été analysée. Ces stations ont été caractérisées en termes de physicochimie, de présence de bar rayé et d'assemblages d'invertébrés, notamment de zooplancton. Trois habitats estuariens ont été préalablement circonscrits : un habitat en amont associé à l'estuaire fluvial (Up); un habitat correspondant à la portion amont de la zone de turbidité maximale dans l'estuaire moyen (ETM); et finalement un habitat en aval de la zone de turbidité maximale de l'estuaire moyen (Down). Les suivis de juin à septembre 2014 ont permis l'identification de 122 taxons et stades de développement parmi les habitats Up, ETM et Down, de juin à septembre.

En juin, en milieu pélagique, l'assemblage Up était plus riche, plus équitable et plus diversifié sur la base des données d'abondance. Les larves de bar rayé étaient plus abondantes dans l'habitat ETM, dont l'assemblage était constitué de Gammaridae, de *Bosmina* sp. et d'*Eurytemora affinis*. Par ailleurs, la composition des assemblages Up et ETM ne se distinguait pas, probablement en raison de leur faible salinité, et seul l'assemblage Down était circonscrit, caractérisé par les calanoïdes de stades nauplii et copépodites C1-C3. En milieu littorale de juillet à septembre, les assemblages Up, ETM et Down ne se distinguaient pas en composition. Les taxons qui contribuaient en abondance à la similarité étaient *E. affinis*, Gammaridae, *Neomysis americana*, Ostracoda, Diptera, Hemiptera, Hydracarina et Gasteropoda, ce qui a mis en évidence la contribution des organismes supra-benthiques dans les eaux peu profondes. La distribution de ces taxons parmi les habitats était stable au cours de la saison. Finalement, nos résultats en lien avec les premiers stades de vie du bar rayé étaient en adéquation avec les conclusions d'études récentes qui fournissaient des informations révélatrices sur le comportement alimentaire du bar rayé, qui semblait adopter un régime opportuniste en consommant les taxons les plus abondants de son environnement.

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LISTE DES ABRÉVIATIONS FRANÇAISES

Chl-a : Chlorophylle-a

ESL : Estuaire du Saint-Laurent

ZTM : Zone de Turbidité Maximale

LIST OF ENGLISH ABBREVIATIONS

Chl-a: Chlorophyll-a

CPUE: Catch Per Unit Effort

ETM: Estuary Turbidity Maximal

PSU: Practical Salinity Unit

SLE: St. Lawrence Estuary

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INTRODUCTION GÉNÉRALE

Les estuaires sont des écosystèmes de transition très productifs (Potter *et al.* 2015), caractérisés par des gradients environnementaux créant des habitats hétérogènes (Dame 2008). Le gradient de salinité exerce une grande influence sur les assemblages d'invertébrés, structurant la composition du zooplancton le long de celui-ci (Telesh et Khlebovich 2010). La distribution des espèces est donc limitée puisque chacune a ses propres besoins et niveaux de tolérance physiologiques. Elles forment ainsi des communautés réparties au long de la zone de transition estuarienne selon des caractéristiques biophysiques particulières (McLusky et Elliott 2004). Les estuaires constituent également des zones d'alevinage cruciales pour de nombreuses espèces de poissons (Haedrich 1983; Beck *et al.* 2001).

L'estuaire du Saint-Laurent (ESL), un des plus grands estuaires du monde, est subdivisé en trois sections (Centre Saint-Laurent 1996). En amont, à la suite du tronçon fluvial, commence l'estuaire fluvial (appelé en anglais *upper estuary*) à partir du Lac Saint-Pierre aux environs de Trois-Rivières. Les eaux douces qui y coulent sont soumises aux marées. Cette section s'étend jusqu'à la pointe Est de l'Île d'Orléans. Là débute l'estuaire moyen (appelé en anglais *middle estuary*) qui court jusqu'à l'embouchure du Saguenay. Les eaux douces et salées s'y rencontrent. La portion en amont de l'Isle-aux-Coudres est particulièrement turbide, alors que les eaux en aval sont davantage stratifiées et salées. L'estuaire maritime (appelé en anglais *lower estuary*), est pourvu d'eaux profondes et salées. Il couvre le secteur entre Tadoussac et Pointe-des-Monts, avant de devenir se poursuit le Golfe du Saint-Laurent.

L'ESL présente des propriétés abiotiques et biotiques particulières. Un mélange se produit à l'interface entre l'eau douce et l'eau saumâtre et entraîne le piégeage des particules, créant une zone de turbidité élevée appelée zone de turbidité maximale (ZTM). Selon Bowers et Yeats (1978), la ZTM de l'ESL débute à 15 km en amont du front de salinité, lui-même situé aux environs de la pointe Est de l'Île d'Orléans. Elle présente des gradients importants de propriétés abiotiques (Vincent *et al.* 1996). Elle est caractérisée par une bathymétrie complexe, de forts courants de marée et de grandes quantités de sédiments qui expliquent ses propriétés physiques distinctes : recirculation estuarienne, stratification semi-diurne et mélange associé aux marées, piégeage des sédiments et turbidité élevée (Vincent et Dodson 1999). Le débit d'eau douce influence l'hydrodynamisme de toute la zone (D'Anglejan et Smith 1973). Il agit directement sur la position du front de salinité, ce qui fait varier de façon saisonnière la position et l'étendue de la ZTM, de 70 à 120 km (Silverberg et Sundby 1979). La ZTM de l'ESL est connue pour sa forte production primaire (Vincent et Dodson 1999), son abondance de zooplancton (Bousfield *et al.* 1975; Dodson *et al.* 1989) et sa biomasse (Dodson *et al.* 1989; Runge et Simard 1990). Bousfield *et al.* (1975) ont produit la première étude approfondie le long de l'estuaire moyen, décrivant la distribution estivale longitudinale et verticale du mésozooplancton, principalement des copépodes, en amont de l'Isle-aux-Coudres, dans le chenal Nord. Laprise et Dodson (1994) ont par la suite distingué trois assemblages de zooplancton, soit des associations plus étroites d'espèces coexistant entre elles, en réponse à toutes les interactions abiotiques et biotiques. Ils ont fourni une description plus détaillée de la distribution spatio-temporelle du zooplancton, expliquée principalement par la salinité et la

stratification verticale. Winkler *et al.* (2003) ont confirmé, tel que précédemment décrit, la succession d'assemblages de zooplancton le long de la ZTM. Ainsi, trois assemblages distincts ont été identifiés à plusieurs reprises le long de la zone pélagique de l'estuaire (Bousfield *et al.* 1975; Laprise et Dodson 1994; Winkler *et al.* 2003; Favier et Winkler 2014).

Le zooplancton constitue une ressource alimentaire indispensable dans la survie des premiers stades de vie des poissons (Cushing 1990). Son rôle écologique en tant que proie est crucial afin de transmettre l'énergie vers les niveaux trophiques supérieurs (Newton 1996). Dans la ZTM de l'ESL, Winkler *et al.* (2003) ont défini les processus de couplage entre les niveaux trophiques des producteurs primaires, des herbivores et des planctivores, soutenant la zone comme une importante aire d'alevinage pour les poissons lors des stades larvaires. Parmi les espèces qui en dépendent, il y a le poulamon de l'Atlantique (*Microgadus tomcod*), l'éperlan arc-en-ciel (*Osmerus mordax*) (Dodson *et al.* 1989; Vincent et Dodson 1999; Sirois et Dodson 2000a; Sirois et Dodson 2000b; Winkler *et al.* 2003), l'alose savoureuse (*Alosa sapidissima*), le baret (*Morone americana*) et, plus récemment, la population réintroduite de bar rayé (*Morone saxatilis*) du Saint-Laurent (Pelletier *et al.* 2011; Morissette *et al.* 2016; Vanalderweireldt *et al.* 2019a; 2019b; 2020).

Le bar rayé présente un intérêt particulier pour la présente étude. Cette espèce anadrome s'identifie à ses flancs arborant sept à huit rayures foncées (Scott et Scott 1988). Parfaitement adapté aux variations drastiques des milieux estuariens auxquels il est étroitement associé, il supporte des changements rapides de température, de salinité et de turbidité (Robitaille *et al.* 2011). Il occupe un niveau

trophique élevé, ce qui fait de lui un des piscivores les plus importants des communautés estuariennes de la côte est de l'Amérique du Nord et ses estuaires (Robitaille *et al.* 2011). Au Canada, les aires de répartition des cinq populations indigènes se limitent à trois secteurs : la baie de Fundy, le sud du golfe du Saint-Laurent et l'ESL, correspondant chacun à une unité désignable de conservation déterminée par le Comité sur la situation des espèces en péril au Canada (COSEPAC). Le secteur de l'estuaire du Saint-Laurent comptait une seule population reproductrice isolée (Robitaille 2004). La surexploitation par les pêches commerciales et sportives ainsi que l'altération des habitats par la pollution et les activités de dragage sont mises en cause dans la disparition du bar rayé des eaux du Saint-Laurent, constatée à la fin des années soixante (Robitaille 2002). En 2002, le MFFP lance un programme de réintroduction du bar rayé en ensemencement des individus issus de la population du sud du golfe. Plusieurs signes encourageants de rétablissement de la nouvelle population se sont manifestés. Notamment, la confirmation d'événements de reproduction naturelle en 2008 (Pelletier 2009; Pelletier *et al.* 2011) ainsi que l'élargissement de l'aire de répartition connu de l'ancienne la population qui atteint maintenant les eaux de la Rivière Saguenay (Valiquette *et al.* 2017). Trois stratégies migratoires ont été identifiées à travers la nouvelle population de bar rayé du Saint-Laurent, soit la résidence en eau douce, l'utilisation du milieu oligohalin de la ZTM de l'ESL et l'utilisation du milieu mésohalin (Morissette *et al.* 2016). L'expression de stratégies variées et absentes de la population d'origine est caractéristique des populations colonisant de nouveaux habitats et révèle une dynamique de population en phase d'établissement. La dernière modification en vertu de la *Loi sur les espèces en péril* (L.C. 2002, ch. 29)

a été faite en 2019 et confère à la population du fleuve Saint-Laurent le statut en voie de disparition.

Les saisons exercent une influence déterminante sur la répartition spatio-temporelle de la nouvelle population de bar rayé du Saint-Laurent. Au printemps, les adultes sexuellement matures, c'est-à-dire les mâles de trois ans et plus ainsi que les femelles à partir de quatre ou cinq ans, se regroupent généralement entre les sites d'hivernage et les sites de reproduction et y demeurent en attendant la fraie (L'Italien *et al.* 2020). Le site de Rivière Ouelle en est un exemple. Fréquenté en majorité par des femelles matures à cette période, il présenterait des conditions idéales pour la maturation de leurs gonades (L'Italien *et al.* 2020). Une brusque augmentation de la température de l'eau entre la fin mai et le début juin, indiquant l'atteinte des conditions de reproduction adéquates, déclencherait la migration des adultes vers les sites de reproduction (L'Italien *et al.* 2020). Actuellement, deux frayères sont connues pour leur contribution active au recrutement de la nouvelle population, soit l'extrémité des installations portuaires à Beauport dans l'estuaire fluvial et l'embouchure de la Rivière du Sud à Montmagny dans l'estuaire moyen (L'Italien *et al.* 2020). Les reproducteurs quittent rapidement ces sites une fois la fraie terminée pour se diriger vers les aires d'alimentation en aval dans l'estuaire moyen (Pêches et Océans Canada 2017). Les œufs de bar rayé sont largués dans le courant et éclosent généralement trois jours plus tard. Les larves n'ont aucune capacité natatoire à ce stade et poursuivent leur dérive en milieu pélagique jusqu'à la résorption du sac vitellin qui survient environ cinq à huit jours après l'éclosion (L'Italien *et al.* 2020). Leur survie au moment du passage à l'alimentation exogène

dépend de la disponibilité des proies dans le milieu, particulièrement du zooplancton pélagique (Kernehan *et al.* 1981). Comme mentionné précédemment, la ZTM leur offre un habitat de croissance idéale où le zooplancton se concentre en abondance (Bousfield *et al.* 1975; Dodson *et al.* 1989) et où les conditions osmotiques sont favorables pour l'espèce tout en abritant les larves des prédateurs visuels (L'Italien *et al.* 2020; Vanalderweireldt *et al.* 2019a). Le passage du stade larvaire à celui de juvénile se produit au cours du mois de juillet alors que les bars rayés atteignent l'âge de 35 à 50 jours et mesurent approximativement 20 mm. À ce stade, ils tolèrent mieux les variations des conditions environnementales et sont associés aux milieux littoraux (Pêches et Océans Canada 2021). L'espèce est d'ailleurs connue pour sa forte association avec la zone intertidale, de zéro à cinq mètres de profondeur, qui est essentielle à la croissance des juvéniles (Pêches et Océans Canada 2017). Les juvéniles dévalent le long du gradient de salinité vers l'eau saumâtre puis salée. Ils sont également observés en amont et en aval de la ZTM dans des habitats énergétiquement moins intéressants, mais plus susceptibles de diminuer la compétition intraspécifique pour l'accès aux ressources alimentaires. Leur diète est principalement constituée d'invertébrés (Vanalderweireldt *et al.* 2019a). Durant cette période, les adultes au régime alimentaire piscivore ont tendance à poursuivre leurs déplacements en aval ou demeurent dans l'estuaire fluvial pour se nourrir. À l'automne, les individus migrent et se regroupent dans des aires d'hivernage à proximité des sites de fraie et les comportements d'alimentation cessent (Beaulieu 1985; L'Italien *et al.* 2020; Robitaille *et al.* 2011). La taille alors atteinte par les jeunes de l'année constitue un indicateur clé de la survie au terme du premier hiver, car la nouvelle population de bar rayé est soumise à une importante mortalité sélective en

fonction de ce facteur (Peres *et al.* 2022). Les aires d'hivernages connues sont situées près de la ville de Québec, au sud de l'Île aux Grues (Pêches et Océans Canada 2017) et dans la Rivière Richelieu, le Lac Saint-Pierre et son archipel (MFFP, données non publiées).

En somme, le bar rayé est tout désigné pour ce projet de recherche en tant que représentant des espèces de poissons de l'estuaire dépendant des zones d'alevinage de la ZTM de l'ESL et exploitant les ressources alimentaires des habitats littoraux. Cependant, à l'inverse des milieux pélagiques, les habitats littoraux de l'ESL n'ont pas été décrits. D'ailleurs, peu d'estuaires à travers le monde ont ainsi été caractérisés, et peu d'informations sont collectées sur leurs communautés d'invertébrés supra-benthiques et planctoniques. Une première description de la composition de l'assemblage de ces invertébrés dans les habitats littoraux améliorera les connaissances de ces milieux. Cela permettra de mieux cerner les conditions favorables aux premiers stades de vie des espèces de poissons de l'estuaire, particulièrement en ce qui a trait à la disponibilité des proies potentielles. Ceci est d'autant plus pertinent pour assurer la bonne gestion des espèces et le succès du rétablissement de celles dont la situation est précaire.

L'objectif général de cette étude est de décrire la composition des invertébrés pélagiques et littoraux dans l'estuaire fluvial et moyen du Saint-Laurent, qui supportent d'importants habitats d'alimentation, pendant la saison de croissance du bar rayé, une espèce de poisson estuarien emblématique associée au littoral.

Pour y parvenir, nous visons d'abord à décrire et comparer les assemblages d'invertébrés sur la base de divers traits caractéristiques, dont les indices de diversité, l'abondance et la biomasse en zooplancton, et en matière de composition des taxons et stades de développement. Ces comparaisons se feront d'une part entre les assemblages des habitats pélagiques en juin et d'autre part entre ceux des habitats littoraux de juillet à septembre, le long du gradient estuarien. L'hypothèse avancée est que les assemblages d'invertébrés pélagiques et littoraux devraient être distingués le long du gradient de salinité-turbidité estuarien selon trois habitats : un habitat en amont associé à l'estuaire fluvial (Up); un habitat correspondant à la portion oligohaline amont de la zone de turbidité maximale dans l'estuaire moyen (ETM); et finalement un habitat correspondant à la portion mésohaline aval de la zone de turbidité maximale de l'estuaire moyen (Down), en se basant sur les connaissances acquises en milieu pélagique (Bousfield *et al.* 1975; Laprise et Dodson 1994; Winkler *et al.* 2003).

Accessoirement, nous tentons d'associer qualitativement l'occurrence des premiers stades de vie du bar rayé durant toute sa saison de croissance aux assemblages d'invertébrés pélagiques et littoraux. L'hypothèse avancée veut que les plus fortes abondances de larves et de juvéniles soient observées en association avec de fortes concentrations d'invertébrés, respectivement pélagiques puis littoraux, selon le stade de développement. Ceci se produit dans l'habitat oligohalin de la zone de turbidité maximale estuarienne (ZTM), car il présente des conditions optimales connues pour le bar rayé telles qu'une faible salinité et une turbidité élevée (North et Houde 2003; Morissette *et al.* 2016; Vanalderweireldt *et al.* 2019a).

CHAPITRE I

SPATIO-TEMPORAL VARIABILITY OF INVERTEBRATE ASSEMBLAGES IN THE ST. LAWRENCE MIDDLE ESTUARY

1.1 INTRODUCTION

Estuaries are highly productive (Potter *et al.* 2015) and play a crucial nursery role for many fish species (Haedrich 1983; Beck *et al.* 2001). Environmental gradients characterizing these transitional ecosystems create heterogeneous habitats (Dame 2008). For instance, the salinity gradient is known as a strong limiting factor, structuring numerous living communities along it, including zooplankton composition (Telesh and Khlebovich 2010) as species have their own needs and physiological tolerance levels (McLusky and Elliott 2004).

The St. Lawrence Estuary (SLE) range from Lac Saint-Pierre, near Trois-Rivières, to Pointe-des-Monts encompassing three distinct zones, the upper, the middle, and the lower estuaries. Its estuarine turbidity maximum (ETM) is generated by the confluence of freshwater and brackish water that takes place in the vicinity of the eastern tip of Île d'Orléans. The ETM of the SLE features sharp gradients in abiotic properties (Vincent *et al.* 1996; Vincent and Dodson 1999) as a result of many processes, such as the exchanges of large amounts of sediment from surrounding marshes, the complex bathymetry of the area and the influence of the strong tide current (Vincent and Dodson 1999). It is also known for its high primary production (Vincent and Dodson 1999), zooplankton abundance (Bousfield *et al.* 1975; Dodson *et al.* 1989) and biomass (Dodson *et al.* 1989; Runge and Simard 1990).

The longitudinal and vertical summer distribution of mesozooplankton along the middle estuary, which extends from the eastern tip of Île d'Orléans to the mouth of the Saguenay River, was first described by Bousfield *et al.* (1975). Three zooplankton assemblages, defined as narrower associations of species that co-occur because of all abiotic and biotic interactions, were then identified by Laprise and Dodson (1994), thus providing a more detailed description of the spatio-temporal distribution, explained mainly by salinity and vertical stratification. Winkler *et al.* (2003) confirmed the previously described succession of seasonally stable assemblages of zooplankton along the ETM. Hence, three distinct assemblages have been repeatedly identified along the well-described ETM's pelagic zone (Bousfield *et al.* 1975; Laprise and Dodson 1994; Winkler *et al.* 2003; Favier and Winkler 2014).

Zooplankton is a major food source transferring material and energy to higher trophic levels (Newton 1996) and ensures a key role in the survival of fish early life stages when switching to exogenous feeding (Cushing 1990). The SLE ETM has been found to be a food-rich nursery site for larval fishes, sustained by processes of coupling between trophic levels (Winkler *et al.* 2003). Furthermore, several species depend on it, such as the Atlantic tomcod (*Microgadus tomcod*), the rainbow smelt (*Osmerus mordax*) (Dodson *et al.* 1989; Vincent and Dodson 1999; Sirois and Dodson 2000a; Sirois and Dodson 2000b; Winkler *et al.* 2003), the American shad (*Alosa sapidissima*), the white perch (*Morone americana*) and, more recently, the St. Lawrence reintroduced population of striped bass (*Morone saxatilis*) (Pelletier *et al.* 2011; Morissette *et al.* 2016; Vanalderweireldt *et al.* 2019a; 2019b; 2020). The latter

is of special interest given its status with respect to the *Species at Risk Act* (L.C. 2002, ch. 29) and its ecological role in the vicinity of the intertidal zone, from a depth of 0 to 5 m (Pêches et Océans Canada 2017). Striped bass, as other estuarine fish species, hatch in the pelagic environment of the ETM and move to the littoral zone as early as a few weeks after hatching up until adult stages and therefore exploits these feeding habitats (Robichaud-LeBlanc *et al.* 1997; Vanalderweireldt *et al.* 2020).

However, littoral habitats of the SLE remain uncharacterized, as for most estuaries. Little information is collected on invertebrate communities there found. This reinforces the importance of conducting a first description of the composition of littoral invertebrates. Improving baseline knowledge of the littoral habitats will offer insights of favourable conditions for early life stages of estuarine fish species.

The general objective of this study was to describe the composition of pelagic and littoral invertebrates in the SLE, throughout the growing season of the striped bass, an iconic species of estuarine fish associated with the littoral habitat. We aimed at comparing invertebrate assemblages based on various characteristics, including indices of diversity, abundance and biomass of zooplankton, and in terms of taxa and developmental stages composition. Comparisons were made among pelagic habitats in June and littoral habitats from July to September along the estuarine gradient. Based on the knowledge acquired in the pelagic zone (Bousfield *et al.* 1975; Laprise and Dodson 1994; Winkler *et al.* 2003), we proposed the hypothesis of a differing composition of pelagic and littoral invertebrate assemblages along the estuarine gradient according to three habitats: an upstream freshwater (Up) habitat,

an estuarine turbidity maximum (ETM) habitat, and a downstream mesohaline and polyhaline (Down) habitat. Incidentally, we associated qualitatively the occurrence of early life stages of striped bass throughout its growing season with the pelagic and littoral invertebrate assemblages. We suggested that high abundances of juvenile striped bass occur in habitat with high abundances of pelagic and littoral invertebrates. Whether the juveniles are found in the pelagic or the littoral habitats would depend on the developmental stage. The oligohaline habitat of the estuarine turbidity maximum (ETM) is predicted to have the highest abundance of striped bass compared to other habitats. This habitat is known for its optimal characteristics for striped bass due to low salinity and high turbidity conditions (North and Houde 2003; Morissette *et al.* 2016; Vanalderweireldt *et al.* 2019a).

1.2 METHODS

1.2.1 Study Area

We targeted two of the three sections of the estuary. The upper estuary (also referred to as the fluvial estuary), characterized by fresh water subjected to tides, begins at the eastern edge of Lac Saint-Pierre, near Trois-Rivières, and runs for 160 km to the eastern tip of Île d'Orléans. It corresponded to the upstream freshwater (Up) habitat (Figure 1). From there, the middle estuary (also referred to as the upper estuary) runs for 150 km to the mouth of the Saguenay River. It is considered the estuarine transition zone, encompassing a salinity gradient from 0 to 25 PSU (Centre Saint-Laurent 1996). The estuarine turbidity maximum (ETM) habitat corresponded to the upper oligohaline section of the middle estuary ranging from the eastern tip of Île d'Orléans to Montmagny (Figure 1). According to Silverberg and Sundby 1979, it extends for 70 to 120 km, depending on water discharge. It displays high concentrations of suspended matter in the water column namely due to large longitudinal and lateral salinity gradients, strong tidal and river flows. In addition, this area presents a complex bathymetry with a lateral variation of depth, including a deep northern channel, shallower middle and southern channels separated by islands, sand banks and shallow shoals with an extensive littoral zone (Simons *et al.* 2010). The area of interest for this study extends to Isle-aux-Coudres on the Northern shore and Rivière-du-Loup on the Southern shore, which corresponded to a downstream mesohaline and polyhaline (Down) habitat (Figure 1).

1.2.2 Field surveys

Invertebrates' communities and early life stages of striped bass were collected in the St. Lawrence upper and middle estuary in 2014. We performed three pelagic survey in June (4th to 8th, 12th to 17th, and 21st to 28th), and three littoral surveys in July (7th to 16th), August (8th to 12th) and September (8th to 22nd) according to Vanalderweireldt *et al.* (2019a).

Environmental abiotic data, namely the physico-chemical variables of salinity, turbidity, temperature and fluorescence, were monitored at each station for all surveys with a CTD probe (SBE19, Sea-Bird Electronics, Inc.). A profile was obtained from 1 to 2 m below the surface. To quantify chlorophyll-*a* concentrations to calibrate the CTD fluorescence measurements, a total of 55 water samples were collected, throughout all surveys, in brown Nalgene bottles at a 0.5 m depth.

In June 2014, 54 stations located on the 5 m isobaths and distributed throughout the entire study area were sampled on three occasions. Surveys were performed using 0.5 m diameter opening Bongo nets of two different mesh sizes. We used a 158 μm mesh to collect zooplankton and a 333 μm mesh to collect fish larvae. Each net was equipped with a general oceanic flowmeter measuring the volume of filtered water. Tows of 10 minutes were made along longitudinal transects, reaching a maximum depth of 5 m. All sampled larvae were anesthetized in a mixed solution of cloves, ethyl-alcohol 95% and estuarine water. Both sets of samples, zooplankton and early life stages of striped bass, were preserved in ethyl-alcohol 95% until identification.

In July, August, and September 2014, littoral surveys of respectively 43, 44, and 101 stations were conducted across the entire study area according to the sampling grid of 101 stations defined as part of the annual striped bass monitoring network of the Ministère des Forêts, de la Faune et des Parcs du Québec (*Ministry of Forest, Fauna and Parks of Quebec*). The survey was performed using a rectangular net (3.75 m long; 1 m high; 1.2 m deep; 500 µm mesh size) to collect invertebrates (188 samples). The net was dragged against the current along a 15 m transect parallel to the shoreline. Samples were preserved frozen until identification. To collect fishes of early life stages (188 samples), we used a beach seine (15 m long; 1.8 m high; 0.95 cm and 0.63 cm mesh sizes respectively for the wings and the central pouch). All sampled fishes were anesthetized in a mixed solution of cloves, ethyl-alcohol 95% and estuarine water. Samples were preserved in ethyl-alcohol 95% until identification.

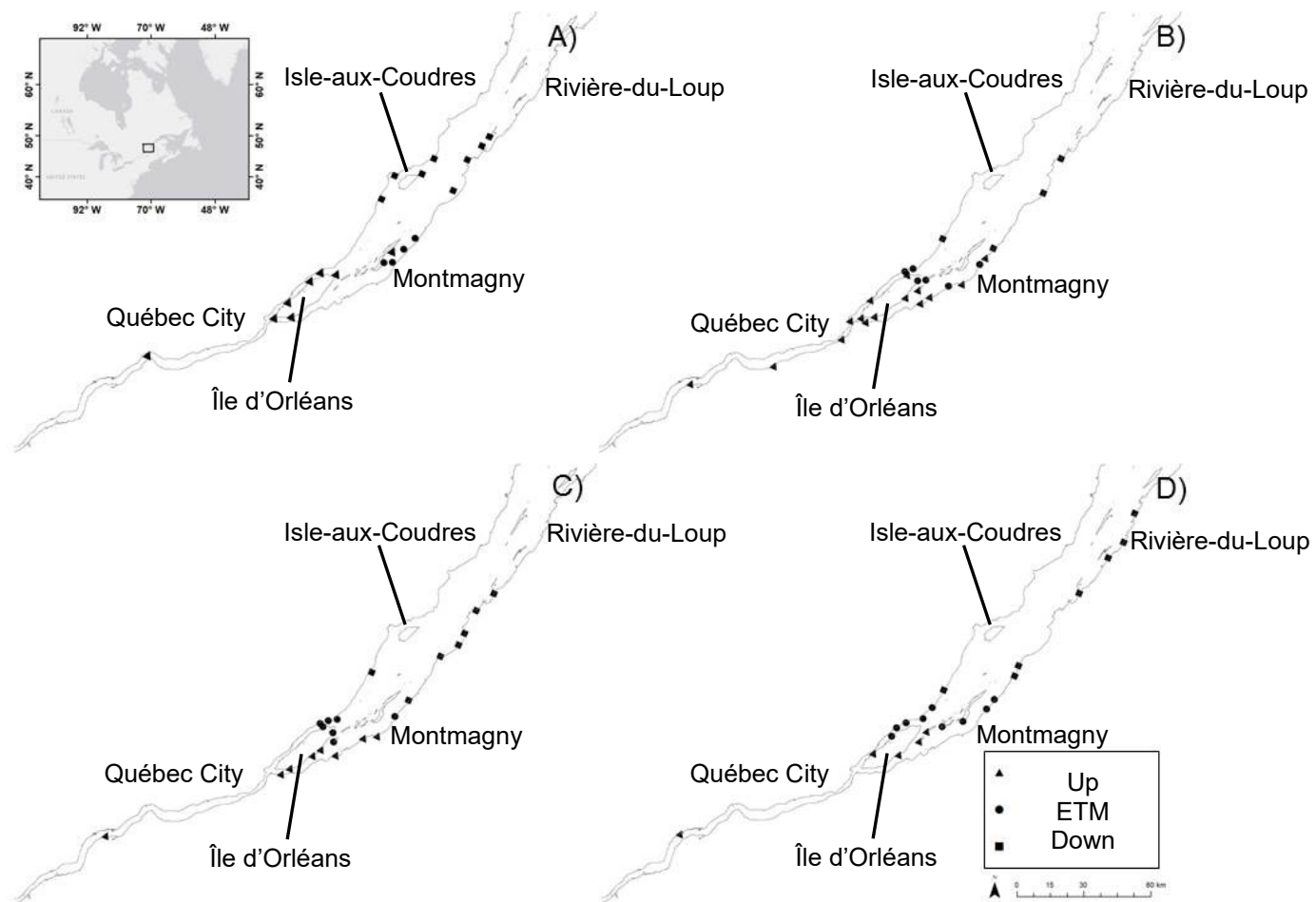


Figure 1. Maps of sub-selected sampling stations in the pelagic zone in June (A) and in the littoral zone in July (B) August (C) and September (D) along the SLE. The three habitats are illustrated: Up (triangles), ETM (circles) and Down (squares).

1.2.3 Laboratory procedures

1.2.3.1 Chlorophyll-a

The algal biomass can effectively be measured by chlorophyll-a (chl-a) concentrations (Steinman *et al.* 1996). For each station, chl-a was quantified based on the CTD fluorescence probe data. Calibration of the fluorescence measurements of the CTD probe has been conducted according to Vanalderweireldt *et al.* (2019a). To summarize, collected surface water samples were filtered in the field through GF/F filters (47 mm diameter) into two replicates immediately frozen on dry ice, and then stored at -60 °C until analysis. Extraction of chl-a was performed following Nusch (1980) and Jeffrey and Welschmeyer (1997). Measurements of chl-a were taken by fluorescence using a mass spectrophotometer paired with the Cary Win UV software and used to calculate a calibration curve

$(\log [\text{chl-a } (\mu\text{g}\cdot\text{L}^{-1})] = 0.6405 \times \ln [\text{fluorescence measurements } (\mu\text{g}\cdot\text{L}^{-1})] + 0.7019 ;$
 $n = 55 ; R^2 = 0.73).$

1.2.3.2 Early life stages of striped bass

Fish larvae and juveniles were measured and identified under a Leica, MZ 12.5 stereomicroscope (Pearson 1938; Auer 1982; Waldman *et al.* 1999) according to Vanalderweireldt *et al.* (2019a). Abundance of striped bass was expressed in density ($\text{ind}\cdot\text{m}^{-3}$) for pelagic larvae and in catch per unit effort (CPUE) for littoral juveniles.

1.2.3.3 Invertebrate assemblages

For this study, several stations from the field surveys were sub-selected before performing the laboratory procedures. This sub-selection was carried out

independently for each month. All sampling stations, where at least 1 striped bass has been identified (June [n=7], July [n=18], August [n=13], September [n=19]), were selected for the analysis. To widen coverage of the study area, a random selection of stations without striped bass (June [n=13], July [n=7], August [n=9], September [n=2]) was performed to reach between 20 and 25 total stations per month (June [n=20], July [n=25], August [n=22], September [n=21]; Figure 1).

Invertebrate samples were divided in 3 size fractions by sieving over 6.3 mm and 1000 μm . The entire large size fraction was analyzed, while the middle and small size fractions were subsampled to examine at least a hundred individuals per sample (Greenberg *et al.* 1992). Samples were split with a Folsom splitter and subsequent aliquots were taken with a Hensen-Stempel pipette. We identified the individuals to the lowest possible taxon and determined the developmental stages according to specific morphological characteristics and size (Edmondson 1959; Préfontaine and Brunel 1962; Vidal 1971; Pennak 1978; Smith and Fernando 1978; Czaika 1982; Merritt and Cummins 1996; Brunel *et al.* 1998) under a Leica, MZ 12.5 stereomicroscope. In this manuscript, *Eurytemora affinis* refers to the cryptic species complex of two morphologically similar, yet genetically distinct clades, including *Eurytemora carolleae* formerly *E. affinis* Atlantic clade and the North-Atlantic clade. These two co-occurring clades are found in the SLE (Winkler *et al.* 2008; Winkler *et al.* 2016); however, we did not conduct any genetic analysis to discriminate them. Abundance of zooplankton and invertebrates was expressed in density ($\text{ind}\cdot\text{m}^{-3}$) for the pelagic survey in June and in surface abundance ($\text{ind}\cdot\text{m}^{-2}$) for littoral surveys in

July, August, and September. Biomass was estimated based on length-weight regressions for each individual (Annexe 2).

1.2.4 Data analysis

1.2.4.1 Habitat

Each station was assigned one of the *a priori* defined habitats according to Vanalderweireldt *et al.* (2019a). Briefly, for each month, cluster analyses were performed based on log-10 transformed salinity and the square root of turbidity, using the average linkage method with Euclidean distance. For the purpose of this manuscript, we distinguished three habitats along the study area instead of four, using a level of among-habitat dissimilarity of 40%. The equivalences with Vanalderweireldt *et al.* (2019a) are as follows: the upstream section (UP) here named "Up", the ETM section (O-ETM) here named "ETM", and finally the M-ETM and the polyhaline section DOWN were merged here into the habitat named "Down".

The means of the physico-chemical variables (salinity, turbidity, temperature and chl-*a*) were calculated for each habitat. We first tested the respect of normality and homoscedasticity assumptions by verifying the spread of residuals (Quinn and Keough 2002). In the pelagic zone in June, the criteria of assumptions were met by the variables of salinity, turbidity, and temperature. An ANOVA followed by a Tukey HSD test was performed to compare habitats. The criteria of assumptions were not met by the dependent variables of the chl-*a* so that a Kruskal-Wallis test followed by Dunn's test was performed. For samples from the littoral zone in July, August, and September, the criteria of assumptions were met by the variables of salinity, turbidity,

temperature, and chl-*a*. An ANOVA followed by a Tukey HSD test was performed to compare habitats.

The mean abundance of striped bass was calculated for each habitat. In the pelagic zone in June, differences in the abundance (ind·m⁻³) of striped bass among habitats were tested performing an ANOVA followed by a Tukey HSD test. In the littoral zone in July, August, and September, a Kruskal-Wallis test followed by Dunn's test were performed independently for each month to test for differences in abundance (CPUE) of the striped bass among habitats.

1.2.4.2 Invertebrate assemblages

Since similarities among rare species have little meaning and tend to confuse the resemblance matrix, we first carried out taxonomic groupings within the dataset (Clarke and Warwick 2001; Drouin *et al.* 2009). They were made according to the frequency of taxa, determined by two thresholds. To be included into the analysis matrix a taxon had to count at least 30 individuals or had to be found in at least 5% of the stations. If at least one of these conditions was not met, the individuals were grouped together at the next higher taxonomic level. The only exception was Plecoptera. This taxon was retained even though the two selection criteria were not met, because Plecoptera is a major contributor to fish diet (Lehmkuhl 1979).

Once the data matrix on abundance and biomass was completed, diversity indices were calculated, and univariate and multivariate analyses were performed using PRIMER v6+ statistical package (Clarke and Warwick 2001). Both matrices of

abundance and biomass were used for the pelagic samples collected in June, while only the abundance resemblance matrix was used for the littoral samples collected in the remaining months of July, August, and September. Invertebrate assemblages were named after the three habitats (Up, ETM and Down).

We calculated three different diversity indices: Richness (S), Pielou's evenness (J') and Shannon-Wiener diversity (H'). We tested the assumptions of normality and homoscedasticity by verifying the spread of residuals (Quinn and Keough 2002). We then performed a one-way ANOVA followed by a Tukey HSD test for each diversity index and each month to compare the three habitats.

In the pelagic zone in June, we used the abundance, expressed in density ($\text{ind}\cdot\text{m}^{-3}$), and biomass ($\text{mg}\cdot\text{m}^{-3}$) of zooplankton as univariate variables. In the littoral zone in July, August, and September, only the abundance ($\text{ind}\cdot\text{m}^{-2}$) of zooplankton (and other invertebrates) was used. When the normality and homoscedasticity assumptions were not met, the Kruskal-Wallis test followed by the Dunn's test were performed to compare the three habitats.

We transformed abundance and biomass data matrix using a fourth-root transformation ($\sqrt[4]{x}$), followed by a Bray-Curtis resemblance matrix. The fourth-root transformation down weighted the importance of very abundant taxa to consider the less common ones (Clarke and Warwick 2001, Drouin *et al.* 2009). The following analyses were performed to characterize the composition of invertebrate assemblages of each habitat.

The SIMPER analysis was used to determine the percentage of similarity and dissimilarity among assemblages based on habitat (Clarke and Warwick 2001). It discriminated taxa that contributed to in-group similarities as well as those that contributed most to differentiation among assemblages. Non-metric multidimensional scaling (nMDS) ordinations were carried out to provide a visual representation of the position of habitats and associated invertebrate assemblages (Clarke and Warwick 2001). The one-way analysis of similarity (ANOSIM) was performed to test for differentiation among assemblages. Statistic R values ranging from 0 to 1 indicate discrimination between sites (Clarke and Warwick 2001).

The mean abundance of taxa that contributed most to assemblage similarity were compared among habitats (Up, ETM and Down) for July, August, and September, using a single Kruskal-Wallis test followed by Dunn's test (Quinn and Keough 2002).

1.3 RESULTS

1.3.1 Habitats

Three habitats were distinguished along the study area based on salinity and turbidity: 1) The Up habitat was characterized by tidal freshwater (< 0.5 psu) and low turbidity, 2) the ETM habitat also characterized by tidal freshwater but high turbidity, and 3) the Down habitat characterized by mesohaline conditions (3-16 psu) and lower turbidity compared to the ETM habitat (Table 1 and 2). In the pelagic and the littoral zones, salinity was not different between the Up and the ETM habitats but was significantly higher in the Down habitat (Table 1 and 2). Turbidity was higher in the ETM except in September where it was highly variable in all habitats. Water temperature was higher upstream in June and July but was not statistically different among habitats in August and September. Chl-a was higher in the ETM, although it was not different between the Up and the ETM in June and the Down was not distinct from the other habitats in August (Table 1 and 2).

1.3.2 Describing the pelagic and littoral invertebrate assemblages along the estuarine gradient, through the striped bass growing season, from June to September

A total of 122 taxa and developmental stages were identified over all three habitats from June to September (Annexe 1). These include, among others, copepods (26 taxa and 4 developmental stages), diplostracans (20 taxa), mysids (2 taxa), amphipods (5 taxa), other crustaceans (8 taxa), insects (20 taxa), molluscs (3 taxa) and rotifers (18 taxa).

1.3.2.1 The pelagic zone

Average zooplankton abundance and biomass did not significantly differ among assemblages. Diversity indices based on abundance revealed that Richness (S) was significantly higher in the Up ($p = 0.0001$). The Up was also more even (J') ($p = 0.0131$) and diverse (H') ($p = 0.0007$) than the Down but did not differ significantly from the ETM assemblage (Table 1). Highest abundance of striped bass larvae was found in the ETM habitat ($\text{ind}\cdot\text{m}^{-3}$, $p = 0.0014$) and no striped bass larvae were found the Down habitat (Table 1).

In the pelagic zone in June, 10 taxa or developmental stages were responsible for assemblage similarities within each habitat (Table 3). In the Up and the ETM habitats Cyclopoida copepodites and *Bosmina* sp. abundances contributed the most to the habitat similarity. Cyclopoida copepodites and Diptera biomass were responsible for the similarity in the Up habitat, while it was due to Cyclopoida copepodites, *Eurytemora affinis*, Gammaridae and *Bosmina* sp. in the ETM. In the Down habitat, Calanoida nauplii and copepodites C1-C3 explained similarity based on abundance and biomass data (Table 3).

The Down assemblage differed in species composition, whereas the assemblages of the Up and the ETM habitats overlapped (nMDS, Figure 2; ANOSIM, Table 5). Differences in the assemblages between the Down and the Up habitats were characterized as follows. The Down showed higher abundance and biomass of Calanoida nauplii and copepodites C1-C3 along with higher biomass of insects, Calanoida nauplii and copepodites C1-C3. In comparison, the Up displayed higher abundance of *Bosmina* sp., Cyclopoida copepodites C1-C3 as well as higher

biomass of *E. affinis*, Cyclopoida copepodites C1-C3, *Bosmina* sp. (SIMPER, Table 7). The assemblages found in the Down and ETM habitats were also distinguished. A higher abundance and biomass of Calanoida nauplii and copepodites C1-C3 was found in the Down, while the ETM showed a higher abundance of diplostracans and Cyclopoida copepodites along with a higher biomass of Gammaridae, diplostracans, *E. affinis*, and Cyclopoida copepodites (Table 7).

1.3.2.2 The littoral zone

Mean abundance of invertebrates in July was greater in the ETM than in the Up habitat ($p = 0.0105$). Higher mean abundance in the ETM habitat was also observed in September, however not significantly (Table 2). The diversity indices were similar among habitats (Table 2). Early stages of striped bass were found in all three habitats in July, August, and September. No significant differences in abundances were detected among the different habitats. However, there was a tendency of higher abundances in the Up habitat in July. In August and September, the mean abundances were slightly shifted towards higher numbers in the two downstream habitats compared to the Up habitat (Table 2).

In the littoral zone, within assemblage similarity was related to the abundance of 8 taxa (SIMPER, Table 4). In July, most of the similarity was due to Diptera and Hemiptera in the Up habitat, Gammaridae, Hemiptera and Diptera in the ETM habitat and Gammaridae in the Down habitat. In August, similarity was namely due to Hemiptera in the Up habitat, Gammaridae and *E. affinis* in the ETM habitat and Gammaridae in the Down habitat. Finally, in September, contributing taxa to within assemblage similarity were Gammaridae and Diptera in the Up habitat, Hemiptera

and Gammaridae in the ETM habitat and Gammaridae and *Neomysis americana* in the Down habitat (SIMPER, Table 4).

Species composition along the upper and middle estuary littoral habitats showed little differentiation throughout the study period. Assemblages highly overlapped with a maximum differentiation of 35% between the Up and Down habitats in July, of 30% between the ETM and Down habitats in August and finally of 43 % between Up and ETM habitats in September (nMDS, Figure 3; ANOSIM, Table 6).

Differences in assemblages between the Up and the Down habitats in July, were characterized by higher abundance of Hemiptera and Diptera found in the Up habitat. The Down habitat showed a higher abundance of Gammaridae, *N. americana* and *Mysis stenolepis* (SIMPER, Table 8). In August, a higher abundance of *E. affinis*, Hemiptera, Gammaridae, *Bosmina* sp. and Diptera was found in the ETM habitat, while the Down habitat showed a higher abundance of Gasteropoda (SIMPER, Table 8). In September, the differences between the Up and the ETM habitats were due to higher abundance of Diptera in the Up habitat, whereas the ETM habitat showed a higher abundance of Hemiptera and Gammaridae (SIMPER, Table 8).

Comparing the abundance (ind·m⁻²) of single targeted taxa contributing most to in-group similarity of littoral assemblages (SIMPER, Table 4) revealed that 4 taxa showed significant variation of abundance among habitats for some months: Gammaridae, *N. americana*, *E. affinis*, and Hemiptera (Figure 4). In July, abundance of Gammaridae was higher in the ETM habitat than in the Up habitat ($p = 0.0017$)

and the abundance of *N. americana* abundance was higher in the Down habitat compared to the Up ($p = 0.0009$) and the ETM ($p = 0.0331$) habitats. *E. affinis* abundance was significantly higher in the ETM habitat compared to the Up ($p = 0.0067$) and the Down ($p = 0.0036$) habitats in August. In September, abundance of Hemiptera was higher in the ETM habitat than the Down habitat ($p = 0.0011$) in September (Figure 4).

Table 1. Univariate characteristics (physico-chemical variables, zooplankton abundance and associated diversity index: Richness (S), Pielou's evenness (J') and Shannon-Wiener diversity (H'), zooplankton biomass and associated diversity index, and striped bass abundance) of pelagic invertebrate assemblages in June. Statistical analysis performed were Kruskal-Wallis (K-W) and one-way ANOVA tests. Means are presented with standard errors in parentheses. Significant differences are indicated in bold and with different letters (A, B, and AB).

Variables	Test	June			<i>p</i>			
		Up (n=8)	ETM (n=4)	Down (n=8)				
Physico-chemical								
Salinity (PSU)	ANOVA	0.09 (0.01)	B	0.09 (0)	B	10.41 (3.01)	A	<0.0001
Turbidity (NTU)	ANOVA	10.42 (4.77)	B	74.66 (22.3)	A	16.18 (13.8)	B	<0.0001
Temperature (°C)	ANOVA	17.61 (1.24)	A	16.61 (0.62)	A	12.12 (1.31)	B	<0.0001
Chl-a (µg·L ⁻¹)	K-W	57.77 (96.5)	A	15.95 (6.76)	A	4.1 (1.34)	B	0.0015
Abundance								
Zooplankton (ind·m ⁻³)	K-W	483.58 (648.89)		952.61 (551.32)		3452.06 (5966.29)		0.0795
Diversity index								
Richness (S)	ANOVA	16.25 (5.34)	A	12.5 (3.87)	B	7.88 (4.16)	B	0.0001
Evenness (J')	ANOVA	0.6 (0.11)	A	0.53 (0.07)	AB	0.39 (0.16)	B	0.0131
Diversity (H')	ANOVA	1.65 (0.41)	A	1.35 (0.33)	AB	0.81 (0.46)	B	0.0007
Biomass								
Zooplankton (mg·m ⁻³)	K-W	13.29 (9.72)		5.88 (4.63)		43.4 (108.64)		0.3633
Diversity index								
Evenness (J')	ANOVA	0.35 (0.15)		0.58 (0.21)		0.49 (0.15)		0.0664
Diversity (H')	ANOVA	0.89 (0.33)		1.43 (0.51)		0.95 (0.36)		0.0808
Striped bass (ind·100 m ⁻³)	ANOVA	3 (9)	B	66 (61)	A	0 (0)	B	0.0014

Table 2. Univariate characteristics (physico-chemical variables, zooplankton abundance and associated diversity index: Richness (S), Pielou's evenness (J') and Shannon-Wiener diversity (H') and striped bass abundance) of littoral invertebrate assemblages in July, August, and September. Statistical analysis performed were Kruskal-Wallis (K-W) and one-way ANOVA tests. Means are presented with standard errors in parentheses. Significant differences are indicated in bold and with different letters (A, B, and AB).

Variables	Test	July				August				September			
		Up (n=15)	ETM (n=6)	Down (n=4)	<i>p</i>	Up (n=8)	ETM (n=7)	Down (n=7)	<i>p</i>	Up (n=5)	ETM (n=9)	Down (n=7)	<i>p</i>
Physico-chemical													
Salinity (PSU)	ANOVA	0.12 (0.02)	B 0.14 (0.05)	B 11.26 (9.3)	A 0.0001	0.12 (0.03)	B 0.15 (0.03)	B 10.99 (6.45)	A 0.0001	0.1 (0.04)	B 0.25 (0.26)	B 14.72 (8.6)	A 0.0001
Turbidity (NTU)	ANOVA	10.92 (6.05)	B 57.46 (25.21)	A 59.9 (49.04)	A 0.0002	7.7 (5.29)	B 42.43 (13.61)	A 65.52 (38.47)	A 0.0004	7.48 (4.5)	B 38.86 (26.17)	A 26.38 (27.13)	0.0884
Temperature (°C)	ANOVA	22.01 (1.34)	A 22.28 (1.81)	A 17.61 (3.53)	B 0.0014	24.8 (1.27)	B 23.94 (1.21)	22.89 (3.15)	0.2235	17.66 (0.84)	B 18.75 (2.9)	A 15.48 (3.18)	0.0790
Chl-a (µg·L ⁻¹)	ANOVA	22.64 (29.16)	B 160.93 (93.97)	A 17.98 (14.28)	B 0.0001	19.63 (25.32)	B 107.69 (63.11)	A 48.45 (48.64)	AB 0.0066	17.35 (19)	B 86.55 (50.72)	A 23.2 (28.02)	B 0.0068
Abundance													
Zooplankton (ind·m ⁻²)	K-W	8.05 (17.88)	B 43.56 (31.18)	A 19.59 (20.1)	AB 0.0105	57.36 (155.6)	31.71 (38.36)	93.56 (203.48)	0.2441	2.51 (2.05)	192.96 (432.97)	7.23 (12.57)	0.0730
Diversity index													
Richness (S)	ANOVA	7.67 (4.29)	9.67 (2.88)	8.5 (3.51)	0.5740	8 (2.83)	9.86 (1.95)	8.14 (3.98)	0.4468	9.6 (4.28)	7.44 (2.79)	9.71 (4.39)	0.4193
Evenness (J')	ANOVA	0.65 (0.24)	0.66 (0.15)	0.59 (0.2)	0.8625	0.66 (0.28)	0.72 (0.13)	0.64 (0.36)	0.8607	0.73 (0.12)	0.49 (0.31)	0.62 (0.22)	0.1422
Diversity (H')	ANOVA	1.14 (0.58)	1.48 (0.42)	1.19 (0.41)	0.4230	1.27 (0.53)	1.63 (0.31)	1.25 (0.85)	0.4186	1.52 (0.4)	0.89 (0.6)	1.28 (0.61)	0.1408
Striped bass (CPUE)	K-W	31.4 (116.92)	5.33 (6.12)	2.25 (2.06)	0.3100	1.13 (1.55)	4.57 (6.27)	4.29 (6.13)	0.3726	1.4 (1.52)	1.67 (0.87)	3.71 (4.82)	0.4972

Table 3. Results of Similarity percentages analysis (SIMPER) showing in-group similarity of June's pelagic invertebrate assemblages, based on Bray-Curtis resemblance matrix calculated on fourth-root ($\sqrt[4]{x}$) transformed abundance and biomass. Taxa contributing to *circa* 50% of the assemblages' similarity are shown.

	June					
	Abundance			Biomass		
	Up	ETM	Down	Up	ETM	Down
Taxa	Cyclopoida C1-C3	Cyclopoida C1-C3	Calanoida C1-C3	Cyclopoida C1-C3	Cyclopoida C1-C3	Calanoida C1-C3
Contribution to	15.34	16.75	28.36	12.22	13.85	29.11
average similarity (%)	<i>Bosmina</i> sp.	<i>Bosmina</i> sp.	Calanoida nauplii	Diptera	Cyclopoida C4-C5	Calanoida nauplii
	10.2	14.18	23.41	11.53	11.04	16.7
	Calanoida C1-C3	Cyclopoida C4-C5		Hydracarina	<i>Eurytemora affinis</i>	
	9.21	11.77		9.77	9.92	
	Harpacticoida C6	Harpacticoida C6		Calanoida C1-C3	Gammaridae	
	8.53	11.37		7.77	9.57	
	Cyclopoida C4-C5			Cyclopoida C4-C5	<i>Bosmina</i> sp.	
	8.07			7.05	7.78	
Cumulative (%)	51.35	54.07	51.77	48.34	52.16	45.81

Table 4. Results of Similarity percentages analysis (SIMPER) showing in-group similarity of littoral invertebrate assemblages in July, August, and September, based on Bray-Curtis resemblance matrix calculated on fourth-root ($\sqrt[4]{x}$) transformed abundance data. Taxa contributing to *circa* 50% of the assemblages' similarity are shown.

	July			August			September		
	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down
Taxa	Diptera	Gammaridae	Gammaridae	Hemiptera	Ostracoda	Ostracoda	Gammaridae	Hemiptera	Gasteropoda
Contribution to	34.88	24.88	30.14	23.29	18.45	27.27	15.62	38.2	20.5
average similarity (%)	Hemiptera	Hemiptera	Ostracoda	Ostracoda	Gammaridae	Gammaridae	Diptera	Gammaridae	Gammaridae
	18.08	20.55	13.75	22.68	17.74	24.74	14.25	20.3	14.48
		Diptera	Diptera	Gasteropoda	<i>Eurytemora affinis</i>		Gasteropoda		Hydracarina
		13.88	13.27	17.45	16.46		12.31		12.43
							Ostracoda		<i>Neomysis americana</i>
							11.8		7.95
Cumulative (%)	52.96	59.31	57.16	63.42	52.65	52.01	53.98	58.5	55.36

Table 5. Results of Analysis of similarities (ANOSIM) showing differences between June's pelagic invertebrate assemblages in abundance and biomass. Pairwise comparisons between habitats are presented. Significant differences are indicated in bold.

	June		
	Global R (p level)	Pairwise tests	Pairwise R (% level)
Abundance	0.671 (0.001)	Up, ETM	0.296 (4)
		Up, Down	0.722 (0.1)
		ETM, Down	0.653 (0.4)
Biomass	0.485 (0.001)	Up, ETM	0.248 (5.1)
		Up, Down	0.602 (0.1)
		ETM, Down	0.564 (0.4)

Table 6. Results of Analysis of similarities (ANOSIM) showing differences between littoral invertebrate assemblages' abundance in July, August, and September. Pairwise comparisons between habitats are presented. Significant differences are indicated in bold.

	Global R (p level)	Pairwise tests	Pairwise R (% level)
July	0.231 (0.032)	Up, ETM	0.291 (7)
		Up, Down	0.349 (2.9)
		ETM, Down	0.195 (8.2)
August	0.251 (0.004)	Up, ETM	0.294 (1)
		Up, Down	0.181 (1.6)
		ETM, Down	0.303 (1.5)
September	0.309 (0.001)	Up, ETM	0.433 (0.1)
		Up, Down	0.161 (7.8)
		ETM, Down	0.269 (4)

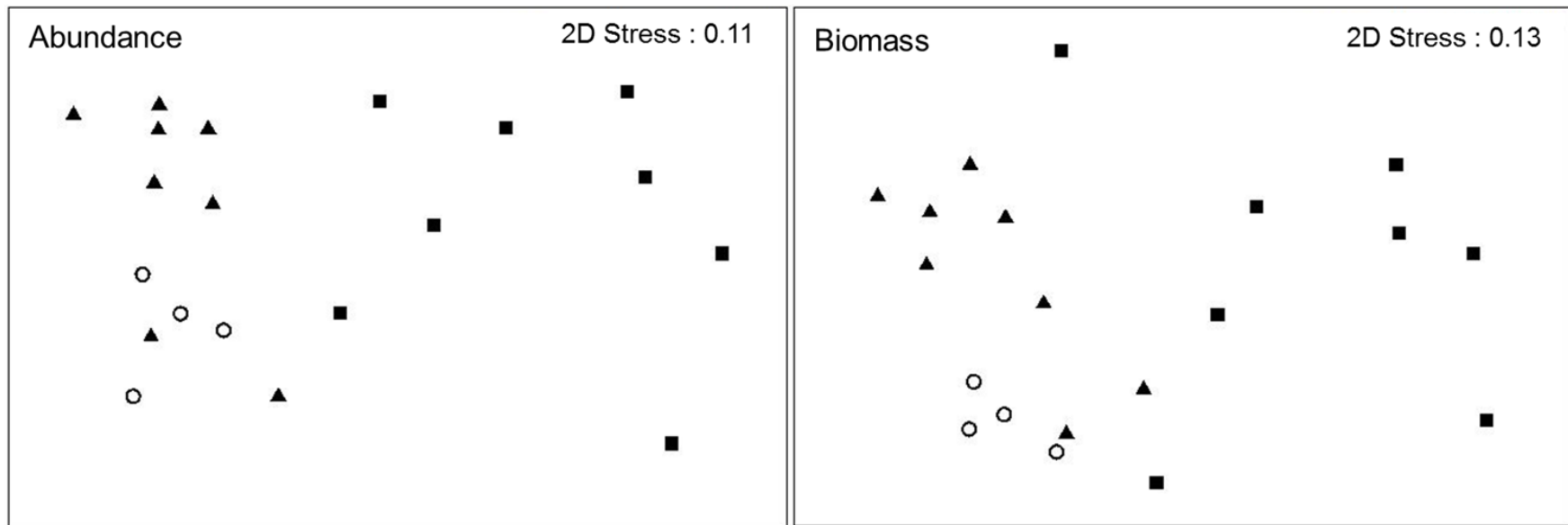


Figure 2. Non-metric multidimensional scaling (nMDS) ordinations, representing pelagic samples in June from the Up habitat (triangles), the ETM habitat (circles) and the Down habitat (squares), based on Bray-Curtis resemblance matrix calculated on fourth-root ($\sqrt[4]{x}$) transformed abundance and biomass.

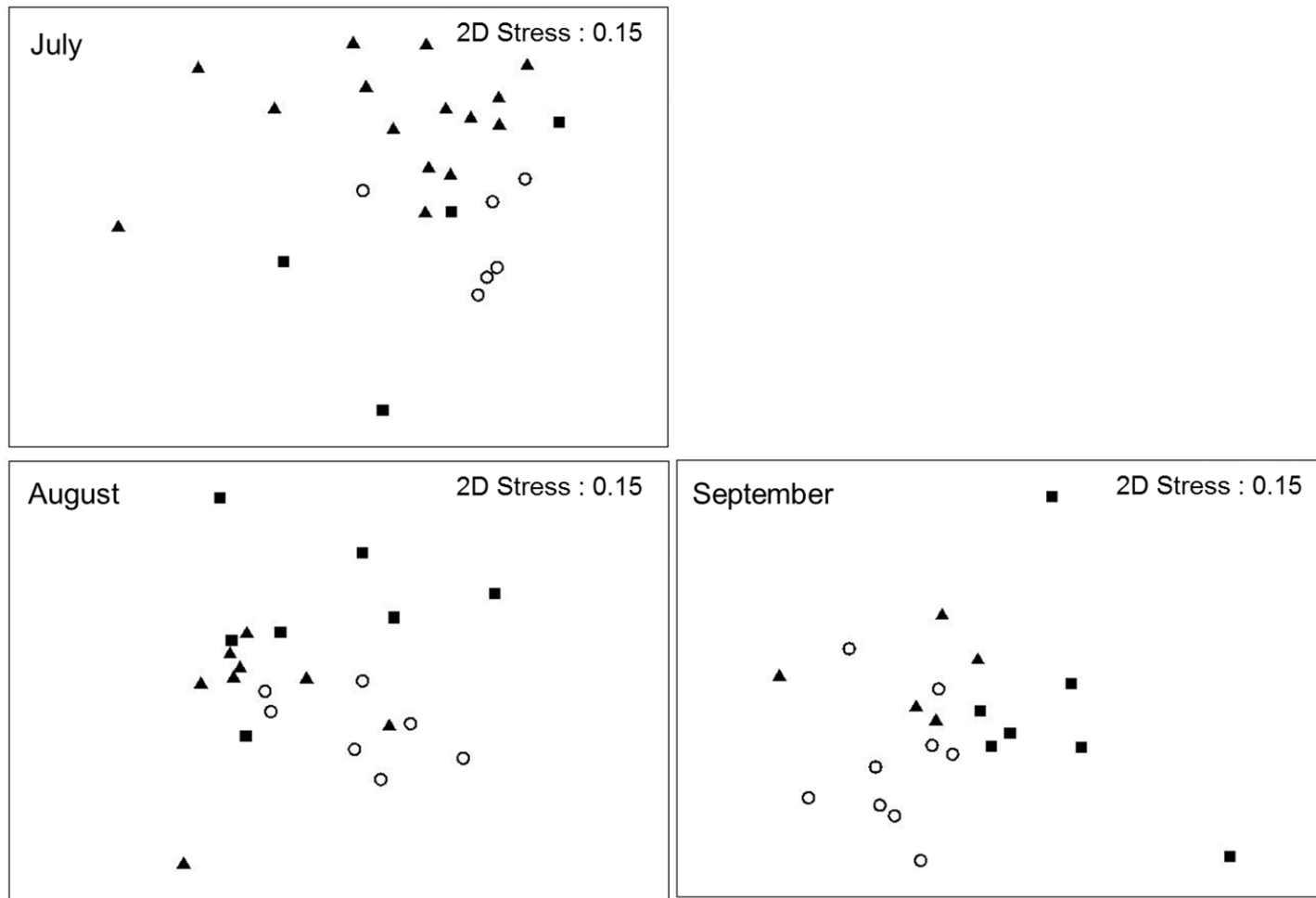


Figure 3. Non-metric multidimensional scaling (nMDS) ordinations, representing samples from July, August, and September from the Up habitat (triangles), the ETM habitat (circles) and the Down habitat (squares), based on Bray-Curtis resemblance matrix calculated on fourth-root ($\sqrt[4]{x}$) transformed abundance.

Table 7. Results of dissimilarity percentages (SIMPER) of June's pelagic assemblages based on Bray-Curtis resemblance matrix calculated on fourth-root ($\sqrt[4]{x}$) transformed abundance and biomass. Are shown, the average dissimilarity, the taxa contributing to 50% of dissimilarity (Taxon), their percent of contribution (%), the assemblage with their highest average abundance or biomass (Assemblage) and the cumulative percent of contribution to dissimilarity (Cumulative %).

		June					
		Abundance			Biomass		
		Up - ETM	Up - Down	ETM - Down	Up - ETM	Up - Down	ETM - Down
Average dissimilarity		47.11	70.2	70.98	56.01	74.6	74.95
%	Taxon	<i>Bosmina</i> sp.	Calanoida nauplii	<i>Bosmina</i> sp.	Diptera	Diptera	Gammaridae
	Assemblage	6.97 ETM	8.04 Down	9.62 ETM	10.44 Up	9.61 Down	8.61 ETM
		Bivalvia veliger	Calanoida C1-C3	Calanoida nauplii	Gammaridae	Hydracarina	Calanoida C1-C3
		6.29 Up	7 Down	8.12 Down	9.92 ETM	7.68 Up	5.14 Down
		<i>Diacyclops thomasi</i>	<i>Bosmina</i> sp.	Calanoida C1-C3	Hydracarina	Calanoida C1-C3	<i>Bosmina</i> sp.
		4.31 ETM	6.08 Up	6.41 Down	8.81 Up	5.19 Down	5.06 ETM
		<i>Eurytemora affinis</i>	Gastrotricha	Cyclopoida C1-C3	<i>Eurytemora affinis</i>	Calanoida nauplii	<i>Eurytemora affinis</i>
		3.98 ETM	4.96 Down	5.68 ETM	5.23 ETM	4.31 Down	5.01 ETM
		<i>Notholca</i> sp.	Cyclopoida C1-C3	Gastrotricha	Amphipoda	Cirripedia nauplii	Calanoida nauplii
		3.91 ETM	4.94 Up	5.46 Down	5.03 ETM	4.22 Down	4.54 Down
		Calanoida nauplii	Bivalvia veliger	Harpacticoida C6	<i>Diacyclops thomasi</i>	<i>Eurytemora affinis</i>	Cyclopoida C1-C3
		3.66 Up	4.83 Up	4.46 ETM	4.24 ETM	4.03 Up	4.34 ETM
		Cyclopoida C4-C5	Cirripedia nauplii	Cyclopoida C4-C5	Ephemeroptera	Cyclopoida C1-C3	<i>Daphnia</i> sp.
		3.66 ETM	4.41 Down	4.18 ETM	3.67 Up	3.53 Up	4.27 ETM
		Harpacticoida C4-C5	Harpacticoida C6	Cirripedia nauplii	Calanoida C4-C5	Calanoida C4-C5	<i>Diacyclops thomasi</i>
		3.55 ETM	4.02 Up	4.09 Down	3.49 ETM	3.49 Up	4.2 ETM
		Harpacticoida C6	Calanoida C4-C5	<i>Daphnia</i> sp.		Hemiptera	Amphipoda
		3.26 ETM	3.29 Down	4.06 ETM		3.46 Down	4.2 ETM
		Diplostraca	Cyclopoida C4-C5			<i>Acartia hudsonica</i>	Cirripedia nauplii
		3.18 Up	2.97 Up			3.35 Down	4.12 Down
		Cyclopoida C6				<i>Bosmina</i> sp.	Cyclopoida C4-C5
		3.11 ETM				3.13 Up	3.55 ETM
		<i>Kellicottia longispina</i>					
		3.04 Up					
		Ostracoda					
		3.04 ETM					
Cumulative %		51.95	50.54	52.07	50.82	52	53.05

Table 8. Results of dissimilarity percentages (SIMPER) of July, August, and September's littoral assemblages based on Bray-Curtis resemblance matrix calculated on fourth-root ($\sqrt[4]{x}$) transformed abundance. Are shown, the average dissimilarity, the taxa contributing to 50% of dissimilarity (Taxon), their percent of contribution (%), the assemblage with their highest average abundance (Assemblage) and the cumulative percent of contribution to dissimilarity (Cumulative %).

	July						August						September					
	Up - ETM		Up - Down		ETM - Down		Up - ETM		Up - Down		ETM - Down		Up - ETM		Up - Down		ETM - Down	
Average dissimilarity	65.68		70.42		64.89		58.76		63.43		64.89		62.43		71.66		74.75	
Taxon	Gammaridae		Gammaridae		<i>Bosmina</i> sp.		Hemiptera		Ostracoda		Ostracoda		Hemiptera		Gasteropoda		Hemiptera	
%	13.75	ETM	10.72	Down	10.99	ETM	11.66	ETM	15.82	Down	11.02	Down	19.46	ETM	8.1	Down	19.57	ETM
Assemblage	<i>Bosmina</i> sp.		<i>Neomysis americana</i>		Hemiptera		<i>Eurytemora affinis</i>		Hemiptera		<i>Eurytemora affinis</i>		Gammaridae		Diptera		Gammaridae	
	12.65	ETM	10.19	Down	10.97	ETM	11.28	ETM	9.93	Up	9.65	ETM	11.14	ETM	6.88	Up	10.04	ETM
	Hemiptera		<i>Mysis stenolepis</i>		<i>Neomysis americana</i>		Gammaridae		Gammaridae		Hemiptera		Diptera		Ostracoda		Gasteropoda	
	11.01	ETM	7.68	Down	7.77	Down	10.43	ETM	8.87	Down	9.28	ETM	7.22	Up	6.5	Up	6.92	Down
	Ostracoda		Hemiptera		Ostracoda		<i>Bosmina</i> sp.		Diptera		Gammaridae		Amphipoda		Hemiptera		Ostracoda	
	7.69	ETM	6.88	Up	6.76	ETM	6.64	ETM	6.57	Up	7.41	ETM	6.51	ETM	5.76	Up	6.68	ETM
	Amphipoda		Ostracoda		Gammaridae		Gasteropoda		Gasteropoda		<i>Bosmina</i> sp.		Gasteropoda		Gammaridae		Amphipoda	
	6.33	ETM	6.62	Down	6.61	ETM	5.55	Up	5.98	Up	6.02	ETM	5.98	Up	5.58	Up	6.31	ETM
			Diptera		Diptera		Amphipoda		<i>Neomysis americana</i>		Diptera				<i>Sida crystallina</i>		<i>Eurytemora affinis</i>	
			6.36	Up	5.82	ETM	5.13	ETM	4.99	Down	5.46	ETM			5.32	Up	4.85	ETM
			Hydracarina		<i>Mysis stenolepis</i>						Gasteropoda				Amphipoda			
			5.66	Down	5.35	Down					4.59	Down			5.25	Up		
															Hydracarina			
															5	Down		
															<i>Neomysis americana</i>			
															4.64	Down		
Cumulative %	51.43		54.12		54.26		50.7		52.16		53.44		50.32		53.04		54.37	

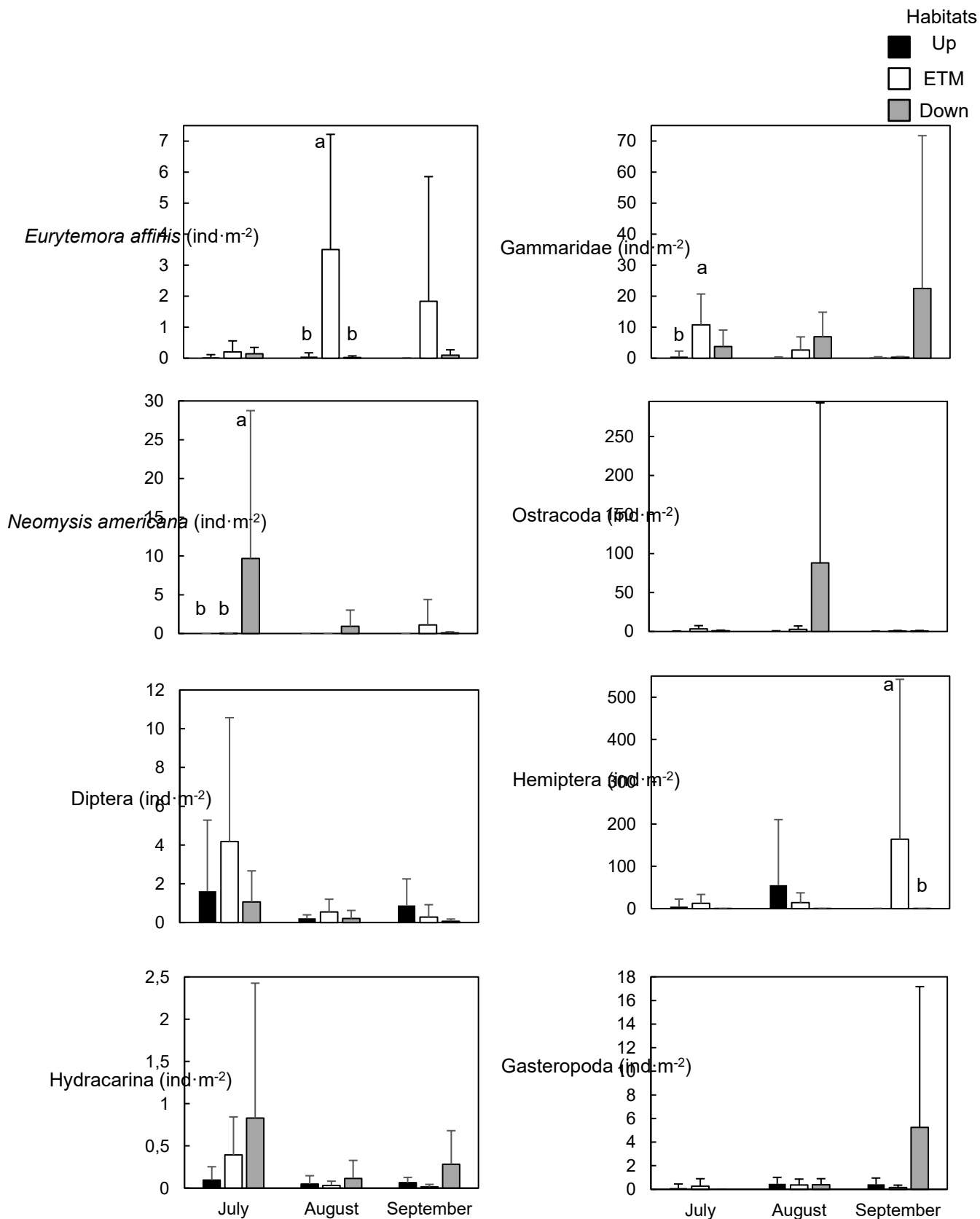


Figure 4. Kruskal-Wallis test followed by Dunn's test performed on mean abundance (ind·m⁻²) of taxa contributing to in-group similarity of littoral assemblages throughout the season among three habitats. Standard errors are represented by vertical lines. Significant differences are indicated with different letters (a and b).

1.4 DISCUSSION

This study aimed at describing the composition of the assemblage of pelagic and littoral invertebrates in the upper and middle SLE, along the salinity-turbidity gradient, from June to September 2014. It offered a first description of the abundance and distribution of planktonic and supra-benthic invertebrates along the intertidal environment of the estuarine transition zone littoral, an important feeding habitat for several fish species including the striped bass, and this during a full growing season.

1.4.1 Habitats

Three habitats, the Up, the ETM and the Down, have been distinguished based on salinity and turbidity, which were the most significant indicators of zooplankton composition and spatial distribution patterns in estuaries, both in the pelagic (Bousfield *et al.* 1975; Laprise and Dodson 1994; Winkler *et al.* 2003) and the littoral (Helenius *et al.* 2017) zones. In the pelagic zone, higher concentrations of chl-*a* were found in the Up and the ETM habitats. The high values upstream decreased as the transition gradient progressed, which was attributed to grazing, rather than dilution (Winkler *et al.* 2003). In the littoral zone, the highest mean chl-*a* concentration was found in the ETM. Salinity was higher in the brackish waters of the Down habitat in both the pelagic and the littoral zones. Temperatures were colder in the Down, in the pelagic zone. In the littoral zone, cooler waters in the Down habitat were only observed in July. Shallow waters of this zone warmed up in August and September, so that no temperature differences between habitats were detected

later in the summer. In the pelagic zone, turbidity peaked in the ETM due to hydrodynamic mechanisms, such as mixing currents, high particulate matter and suspended sediment input from adjacent shallow depth (Dodson *et al.* 1989; Laprise and Dodson 1994; Frenette *et al.* 1995). However, in the littoral zone, we recorded significantly higher turbidity measurements in the ETM and the Down compared to the Up habitat, for July and August. D'Anglejan and Smith (1973) provided evidence based on Neu's (1970) work that water in shallower area is well mixed upstream Isle-aux-Coudres and along the southern shore of the SLE.

1.4.2 Comparing the pelagic and littoral invertebrate assemblages along the estuarine gradient, through the striped bass growing season, from June to September

1.4.2.1 The pelagic zone

The similarity in composition within assemblages early in the season was partly due to the contribution of calanoid copepods, diplostracans and gammarids. The calanoid *Eurytemora affinis* contributed to the ETM assemblage in biomass, consistently with the maximum abundance reached in the estuarine turbidity maximum zone (Winkler *et al.* 2005; Favier and Winkler 2014). It constitutes an essential link in the transfer of energy from autotrophs to heterotrophs (Winkler *et al.* 2003; Cabrol *et al.* 2015). The diplostracan *Bosmina* sp. contributed to the Up assemblage in abundance and biomass, as well as in terms of biomass to the ETM assemblage. This is to be expected, since the sampling stations of the ETM habitat

in this study showed high turbidity, but almost no salinity at only 0.09 psu. Maximum abundance of *Bosmina* sp. typically occurs at the limit of saltwater intrusion (Laprise and Dodson 1994). In addition, the dynamics of the estuarine transition zone are highly dependent on tides, so salinity varies depending on the timing of sampling at a given station (Winkler *et al.* 2003). The Gammaridae contributed in biomass to the ETM assemblage. It is also worth mentioning that we identified the amphipod *Echinogammarus ischnus* in the ETM in June, confirming Cusson's (2012) first recording of the species in the SLE.

Diversity indices indicated that the Up is richer in species, more even and more diverse compared to the assemblage in the Down habitat. A strong overlap was revealed between the Up and the ETM assemblages, both in abundance and in biomass, while the Down assemblage remained distinct. These results contrast with previous descriptions in the estuarine transition zone, as richness increased seaward (Laprise and Dodson 1994) and three distinct assemblages were found (Laprise and Dodson 1994; Winkler *et al.* 2003). We attribute the lack of distinction between the Up and the ETM to the tidal freshwater we found in both habitats, which therefore support similar assemblages of taxa with low salinity tolerance. It could also be due to advection, stimulating the downstream dispersion of taxa typically associated with the upstream. For example, advection is responsible for transport of freshwater phytoplankton (Lapierre 2008) and zebra mussel larvae originating from upstream (Winkler *et al.* 2005) into to the St. Lawrence estuarine transition zone. Unlike Laprise and Dodson (1994), we did not calculate an index to account for the effect of advection. The Down assemblage corresponded to previous descriptions (Laprise and Dodson 1994; Winkler *et al.* 2003; Favier and Winkler 2014).

Larval striped bass, were concentrated in the pelagic ETM habitat early in the season. The high abundance of prey items, such as *E. affinis* and *Bosmina* sp. in the ETM habitat may provide better conditions for these larvae as compared to the Up or Down habitats. Vanalderweireldt *et al.* (2019b) confirmed the two species as main prey items of larval of striped bass, reinforcing the demonstration of the ETM as high-quality nursery and feeding habitat.

1.4.2.2 The littoral zone

We found higher overall zooplankton abundance in the ETM compared to the Up habitat in July and a similar trend in September. Our results further highlighted the wide variety of taxa contributing to the similarity in composition within assemblages of the littoral habitats, such as insects, amphipods, and ostracods. *E. affinis* contributed to the ETM assemblage in August and the mysid *Neomysis americana* to the Down assemblage in September.

Compared to the three main pelagic invertebrate assemblages previously found in the estuarine transition zone (Laprise and Dodson 1994; Winkler *et al.* 2003; Favier and Winkler 2014), the assemblages of the three habitats in the littoral zone of the same region showed very little differentiation. The shallow, potentially vegetated littoral zone is characterized by weaker currents and a longer residence time (Cusson 2012) compared to the deeper channels with strong currents in the pelagic zone (Simons *et al.* 2010).

We suggest that the Up and the ETM assemblages have not been differentiated because of the strong abundance of insects, namely Diptera and Hemiptera, which respectively contributed to both assemblages. As a matter of fact, Diptera contributed to all assemblages early in the season. The presence of these taxa typically associated with freshwater could be explained by the fact that salinity levels are not significantly different between these assemblages.

We attribute the non-differentiation of ETM and Down assemblages to the abundance of Gammaridae that dominate both assemblages in July and August and were distributed in the three habitats in September. Due to identification limitations, most individuals could not be assigned to the taxonomic resolution necessary to differentiate species, a significant factor allowing for assemblage discrimination. For instance, *Gammarus tigrinus* is typically associated with the Up habitat (Laprise and Dodson 1994), whereas *Gammarus oceanicus* and *Gammarus lawrencianus* are found in higher salinities of the middle estuary (Bourget 1997), which correspond to the Down habitat.

Unexpectedly, the Up and Down assemblages did not differ either. As mentioned before, this could be due to taxa distributed across all habitats, namely Diptera. Intrusions of freshwater insects in areas of higher salinity, well outside of their normal distribution, is unexpected, but possible and might be important in the Down habitat. As Merritt and Cummins (1996) described, some organisms typically from freshwater, can be transported to brackish water by runoff from tributaries, which could explain our observations of Diptera in all habitats. In addition, we also hypothesize that a longitudinal advection phenomenon would allow a passive

intrusion of littoral organisms further downstream (Modéran *et al.* 2012). Moreover, Gammaridae, also distributed across all habitats, and gastropods contributed strongly to the Up and the Down assemblages. A finer taxonomic resolution of these two taxa might have helped to distinguish the assemblages.

It should also be noted that we used a rectangle net, which allows for the sampling of the entire water column of the intertidal zone and could explain the significant presence of organisms associated with the supra-benthos, such as gastropods and Hydracarina. The latter is also known as water mites and its abundance declines drastically with depth (Modlin and Gannon 1973).

Abundances varied over from July to September, showing a peak for Gammaridae and *N. americana* in July, *E. affinis* in August, and Hemiptera in September. While these 4 taxa exhibited greater abundance in one habitat compared to the others at a given month, the remaining taxa did not vary significantly over the season. These elements indicate a stability in the distribution of taxa over the season in the littoral zone, as described in previous studies for the pelagic zone (Laprise and Dodson 1994; Winkler *et al.* 2003).

Young of the year striped bass encountered, in July, high abundances of Diptera pupa and Gammaridae in the Up and the ETM habitats, two important prey taxa (Vanalderweireldt *et al.* 2019b). The availability of potential larger prey items might explain how the upstream remains a favourable environment for juveniles in the early season. Throughout the summer, striped bass expanded their geographic range to the littoral habitats further downstream, thus encountering the invertebrate

assemblages therein. From August onwards, they came across gammarids and mysids, particularly *N. americana*, which were abundant taxa in the ETM and Down habitats respectively. The predation of early life stages on previous mentioned taxa has also been established (Vanalderweireldt *et al.* 2019b). Our results support that the composition of the prey field in the environment (dominant taxa of the assemblages) seem to have no influence on the feeding behaviour of the early stages of striped bass. They adopt an opportunistic feeding strategy as was found in the St. Lawrence (Vanalderweireldt *et al.* 2020), in the Miramichi River Estuary, in New Brunswick (Robichaud-LeBlanc *et al.* 1997) and in the Chesapeake Bay, in the United States (North and Houde 2003).

1.5 CONCLUSIONS

In summary, our study investigates invertebrate assemblages, in particular zooplankton, in the pelagic and the littoral habitats in the estuarine transition zone from tidal freshwater to mesohaline conditions. This study provide a first description of the littoral habitats in the SLE.

We described three habitats, Up, ETM and Down, revealing a distinct Down assemblage and strong similarity between the two upstream assemblages in the pelagic zone. The Up assemblage was the richest, most even and most diverse. However, highest striped bass larvae abundances were found in the ETM habitat, characterized by a zooplankton assemblage consisting mostly of Gammaridae, *Bosmina* sp., *Eurytemora affinis*.

Composition of assemblages of the littoral zone strongly overlapped throughout the season mostly due to high abundances of insects. We observed tidal freshwater in the ETM, making it a conducive habitat for taxa with low tolerance to salinity. As for the Down assemblage, we propose a strong influence of freshwater tributaries runoff into the brackish littoral waters, also allowing for passive downstream transport, explaining intrusions of freshwater associated organisms into the Down habitat. The gammarids were a major group in the littoral habitat, found in all assemblages. We expect these to be different species, but due to a lack of taxonomic resolution, we were not able to better distinguish the assemblages. Nevertheless, results indicated a stable distribution of major contributing taxa among the habitats of the littoral zone during the season. Furthermore, our results

highlighted the contribution of supra-benthic organisms in the shallow water of the littoral zone such as Ostracoda, Hydracarina and Gasteropoda.

In addition, interpretation of our results in light of recent publications (Vanalderweireldt *et al.* 2019a; 2020) highlight the ability of striped bass to adopt opportunistic feeding behaviour by exploiting the dominant taxa in their environment.

In perspective, we wish to encourage further studies to deepen the knowledge on estuarine littoral environments, as they remain poorly characterized and because this is necessary to improve management methods for aquatic species that are dependent on these specific habitats. Thus, including latest prey field dynamics improves the assessment of the carrying capacity of critical habitats, particularly nurseries and feeding habitats in estuarine environments. This approach aims to achieve re-establishment targets for species such as the reintroduced striped bass population in the St. Lawrence.

CONCLUSION GÉNÉRALE

La présente étude sur la variabilité spatio-temporelle des assemblages d'invertébrés dans l'estuaire du Saint-Laurent, largement utilisés par les jeunes stades de vie des poissons, s'inscrit dans une démarche d'acquisition de connaissances sur la disponibilité des proies des habitats estuariens. À travers les dernières décennies, de nombreuses études ont décrit la distribution spatio-temporelle du zooplancton en réponse aux interactions abiotiques et biotiques en milieu pélagique dans la zone de transition estuarienne du Saint-Laurent (Bousfield *et al.* 1975; Laprise et Dodson 1994; Winkler *et al.* 2003; Favier et Winkler 2014). Par ailleurs, les habitats littoraux demeurent peu connus pour la plupart des grands estuaires. À notre connaissance, nous présentons une première description de la composition de l'assemblage des invertébrés supra-benthiques et planctoniques des habitats littoraux intertidaux des estuaires fluvial et moyen du Saint-Laurent, et ce, pendant une saison complète de croissance d'une espèce de poisson estuarien. Cela revêt une importance toute particulière pour la nouvelle population de bar rayé du fleuve Saint-Laurent. Cette espèce est inscrite à la *Loi sur les espèces en péril* comme étant en voie de disparition et il incombe de planifier son rétablissement. La situation étroitement liée à la qualité des eaux peu profondes du littoral et le rôle écologique particulier du bar rayé en font une espèce exemplaire pour ce projet de recherche.

La zone de turbidité maximale (ZTM) de l'estuaire du Saint-Laurent (ESL) constitue une aire d'alevinage primordiale (Dodson *et al.* 1989; Vincent et Dodson 1999; Sirois et Dodson 2000a; Sirois et Dodson 2000b; Winkler *et al.* 2003) et tout

particulièrement pour le bar rayé (Pelletier *et al.* 2011; Morissette *et al.* 2016; Vanalderweireldt *et al.* 2019a; 2019b; 2020). Au moment de la résorption du sac vitellin et du passage à l'alimentation exogène, la survie des larves aux capacités natatoires restreintes dépend de la disponibilité des proies pélagiques (Kernehan *et al.* 1981). La ZTM leur offre un habitat de croissance idéale, entre autres grâce à sa forte abondance en zooplancton (Bousfield *et al.* 1975; Dodson *et al.* 1989). Nos observations en milieu pélagique corroborent l'abondance plus élevée des larves de bar rayé dans l'habitat ETM, liée à un assemblage caractérisé par une abondance de *Bosmina* sp. et par une biomasse de Gammaridae, *Bosmina* sp. et *Eurytemora affinis*. Cet assemblage semble chevaucher considérablement celui du Up, probablement dû aux eaux douces présentes dans ces deux habitats, rendant l'habitat ETM propice aux espèces peu tolérantes à la salinité. L'assemblage mésohalin de l'habitat Down se distingue de ceux en amont et se caractérise par son abondance et sa biomasse en calanoïdes de stades nauplie et copépodite C1-C3.

Lors du passage au stade juvénile, qui survient généralement au cours du mois de juillet, les bar rayés tolèrent mieux les variations des conditions environnementales et utilisent les milieux littoraux (Pêches et Océans Canada 2021). La zone intertidale, entre 0 et 5 m de profondeur, est alors essentielle à leur croissance (Pêches et Océans Canada 2017). Tout au long de la saison de croissance des juvéniles, c'est-à-dire jusqu'en septembre, nous observons un chevauchement dans la composition des assemblages littoraux. Comme en milieu pélagique, la présence d'eau douce dans l'habitat ETM littoral en fait un

environnement tout aussi convenable que l'habitat Up pour les taxons ayant une faible tolérance à la salinité. Ces habitats en amont sont entre autres caractérisés par leur abondance en insectes. L'assemblage Down, quant à lui, est probablement sous une forte influence du ruissellement des affluents d'eau douce dans ses eaux saumâtres littorales (Merritt et Cummins 1996), qui favoriserait aussi un transport longitudinal passif vers l'aval (Modéran *et al.* 2012), expliquant ainsi les intrusions des organismes associés à l'eau douce dans cet habitat. De plus, la distribution des taxons prédominants à travers les habitats littoraux est stable au cours de la saison. En outre, nos résultats mettent en évidence la contribution des organismes supra-benthiques aux assemblages de la zone littorale, en attestant de la présence d'ostracodes, d'hydracariens et de gastéropodes.

Vanalderweireldt *et al.* 2019b a démontré que les bars rayés juvéniles étendent leur aire de répartition aux habitats littoraux en aval, à mesure que la saison progresse. Nos résultats soutiennent les conclusions voulant que la composition des taxons prédominants des assemblages dans l'environnement semble être les proies privilégiées par les jeunes bars rayés, reflétant un comportement alimentaire opportuniste dans le Saint-Laurent (Vanalderweireldt *et al.* 2020), dans l'estuaire de la Rivière Miramichi, au Nouveau-Brunswick (Robichaud-LeBlanc *et al.* 1997) et dans la baie de Chesapeake, aux États-Unis (North et Houde 2003).

L'étude comporte certaines limites. Bien qu'elle ait impliqué un effort d'échantillonnage majeur et un travail méticuleux d'identification des organismes invertébrés présents à travers toute l'aire d'étude, une résolution plus précise au niveau des espèces pour certains taxons aurait été essentielle afin de distinguer les

assemblages. C'est particulièrement le cas des gammars qui constituent un groupe majeur des milieux littoraux et sont présents dans tous les habitats. Il s'agit vraisemblablement d'espèces différentes, mais nous n'avons pas été en mesure de le démontrer, car les structures anatomiques sur lesquels l'identification repose étaient endommagées. De plus, l'étude porte sur des échantillons de 2014 et la variabilité interannuelle n'a pas pu être évaluée. Nous n'avons pas d'indication à savoir si l'année 2014 est représentative des conditions moyennes dans le système, ou au contraire, s'il s'agit d'une année exceptionnelle.

Nos travaux fournissent une base à des études futures visant à décrire les habitats littoraux estuariens qui pourraient, par exemple, évaluer la variabilité interannuelle de la diversité et de l'abondance des organismes. Des indices d'état du système pourraient alors être développés et possiblement permettre de prédire le recrutement des poissons qui fréquentent ces milieux servant d'aires d'alevinage, d'alimentation et de croissance à des moments clés du cycle de vie. Il convient de promouvoir d'autres études visant à inclure la dynamique des niches alimentaires dans les évaluations de la capacité de support des milieux afin de soutenir les meilleures approches de gestion possible pour les espèces aquatiques qui en dépendent.

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Table 9. (continued)

Lowest taxonomic levels	Pelagic			Littoral								
	June			July			August			September		
	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down
Harpacticoida												
Copepodites C1-C3	X	X	X									
Copepodites C4-C5	X	X				X			X		X	X
Non-identified Harpacticoida C6	X	X	X	X		X		X	X		X	X
Diplostraca												
<i>Bosmina</i> sp.	X	X		X	X		X	X			X	
<i>Ceriodaphnia</i> sp.	X											
Chydoridae	X	X					X					
Chydorinae	X											
<i>Chydorus</i> sp.							X					
<i>Daphnia</i> sp.	X	X					X			X		
<i>Daphnia catawba</i>	X	X										
<i>Daphnia galeata mendotae</i>	X											
<i>Daphnia longiremis</i>	X											
<i>Daphnia longiremis</i> group ¹	X	X								X		
<i>Daphnia parvulata</i>								X				
<i>Daphnia pulex</i>	X	X										
<i>Daphnia pulex</i> group ²	X	X									X	
<i>Eurycerus</i> sp.	X			X								
<i>Ilyocryptus spinifer</i>								X		X	X	
<i>Monospilus dispar</i>	X											
<i>Polyphemus pediculus</i>	X			X								
<i>Sida crystallina</i>	X			X			X		X	X	X	
<i>Simocephalus vetulus</i>	X											
Non-identified Diplostraca	X	X						X				
Mysida												
<i>Mysis stenolepis</i>						X				X		X
<i>Neomysis americana</i>					X	X				X		X
Amphipoda												
Gammaridae												
<i>Echinogammarus ischnus</i>		X		X								
<i>Gammarus</i> sp.		X		X	X	X	X	X	X	X	X	X
Non-identified Gammaridae	X	X		X	X	X	X	X	X	X	X	X
<i>Hyalella azteca</i>				X	X	X		X	X			X
Non-identified Amphipoda	X	X		X	X	X	X	X	X	X	X	X

Table 9. (continued)

Lowest taxonomic levels	Pelagic			Littoral								
	June			July			August			September		
	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down
Crustacea												
Decapoda												
<i>Crangon septemspinosa</i>									X			X
Non-identified Decapoda larvae												X
Cirripedia Nauplii N1-N6			X									
Cumacea										X		
Isopoda						X				X		X
Maxillopoda Nauplii N1-N6			X									
Ostracoda	X	X	X	X	X	X	X	X	X	X	X	X
Non-identified Crustacea			X									X
Insecta												
Diptera												
Chironomidae larvae-pupae	X											
Non-identified Diptera larvae-pupae-adults	X		X	X	X	X	X	X	X	X	X	X
Hemiptera												
Corixidae nymphs-adults				X	X	X	X	X	X	X	X	X
Non-identified Hemiptera nymphs-adults	X		X	X	X	X	X	X	X	X	X	
Homoptera												
Aphidoidea nymphs-adults							X	X				
Cicadellidae nymphs-adults							X					
Membracidae nymphs-adults							X					
Psylloidea nymphs-adults									X		X	
Non-identified Homoptera nymphs-adults											X	X
Coleoptera larvae-pupae-adults	X		X	X	X	X				X	X	X
Ephemeroptera nymphs	X			X						X		
Forficulidae nymphs-adults				X								
Hymenoptera larvae-pupae-adults	X		X	X		X	X		X		X	X
Lepidoptera larvae										X		
Megaloptera larvae				X		X	X			X		
Odonata nymphs				X	X							
Plecoptera nymphs					X					X		
Thysanoptera larvae-pupae-adults			X	X			X		X			
Trichoptera larvae				X	X		X	X		X		
Non-identified Insecta				X	X		X	X	X	X		

Table 9. (continued)

Lowest taxonomic levels	Pelagic			Littoral								
	June			July			August			September		
	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down	Up	ETM	Down
Mollusca												
Gasteropoda												
<i>Patella</i> sp.										X		X
Non-identified Gasteropoda				X	X		X	X	X	X	X	X
Bivalvia veliger larvae	X											
Rotifera												
<i>Asplanchna</i> sp.	X	X										
<i>Asplanchna priodonta</i>	X	X		X								
<i>Asplanchna silvestrii</i>		X										
Bdelloidea	X											
<i>Brachionus</i> sp.	X	X	X									
<i>Brachionus bidentata</i>	X											
<i>Brachionus caliciflorus</i>		X										
<i>Brachionus quadrata</i>	X											
<i>Brachionus variabilis</i>	X	X										
<i>Euchlanis</i> sp.	X											
<i>Kellicottia longispina</i>	X	X										
<i>Keratella</i> sp.	X											
<i>Keratella quadrata</i>	X											
<i>Keratella taurocephala</i>	X											
<i>Notholca</i> sp.	X	X										
<i>Notholca acuminata</i>		X										
<i>Trichotria</i> sp.	X											
Non-identified Rotifera	X	X										
Others												
Arthropoda												
Acarina								X		X		X
Arachnida						X				X		
Araneae				X	X	X				X		X
Collembola	X			X	X	X	X			X	X	X
Hydracarina	X	X	X	X	X	X	X	X	X	X	X	X
Annelida	X							X	X	X		X
Gastrotricha	X		X									
Turbellaria	X											
Total number of taxa	67	43	34	32	25	21	30	28	29	26	27	32

¹ *Daphnia longiremis* group included *D. longiremis* and *D. galeata mendotae*

² *Daphnia pulex* group included *D. pulex* and *D. catawba*

ANNEXE 2

Table 10. Biomass conversion equations used for each of the lowest taxonomic levels and life stages identified in the St. Lawrence Estuary (SLE), from June to September 2014

Lowest taxonomic levels	Stages	Theoreticals equations	References
Copepoda			
Nauplii	N1-N6	$W=3.009*L^{1.706}$	Sirois and Dodson 2000a
Copepodites	C1-C5	$W=1.10*10^{-5}L^{1.89}$	Dumont <i>et al.</i> 1975
Calanoida			
Nauplii	N1-N6	$W=3.009*L^{1.706}$	Sirois and Dodson 2000a
Copepodites	C1-C5	$W=1.10*10^{-5}L^{1.89}$	Dumont <i>et al.</i> 1975
<i>Acartia hudsonica</i>	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
<i>Acartia longiremis</i>	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
<i>Epischura lacustris</i>	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
<i>Eurytemora</i> sp.	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
<i>Eurytemora affinis</i>	C4-C5	$\text{Log}W=2.441*\text{log}(L)-6.095$	Escaravage and Soetaert 1993
<i>Eurytemora affinis</i>	C6	$\text{Log}W=2.441*\text{log}(L)-6.095$	Escaravage and Soetaert 1993
<i>Eurytemora herdmani</i>	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
<i>Limnocalanus macrurus</i>	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
<i>Pseudocalanus minutus</i>	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
Non-identified Calanoida	C6	$W=0.0077*L^{2.33}$	Dumont <i>et al.</i> 1975
Cyclopoida			
Nauplii	N1-N6	$W=3.009*L^{1.706}$	Sirois and Dodson 2000a
Copepodites	C1-C5	$W=1.10*10^{-5}L^{1.89}$	Dumont <i>et al.</i> 1975
<i>Acanthocyclops</i> sp.	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Acanthocyclops robustus</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Acanthocyclops venustoides</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Acanthocyclops vernalis</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Cyclops</i> sp.	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Diacyclops nanus</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Diacyclops sicilis</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Diacyclops thomasi</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Ectocyclops phaleratus</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Eucyclops agilis</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Halicyclops</i> sp.	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Mesocyclops</i> sp.	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Orthocyclops modestus</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Tropocyclops</i> sp.	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
<i>Tropocyclops prasinus</i>	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
Non-identified Cyclopoida	C6	$W=4.9*10^{-8}*L^{2.75}$	Dumont <i>et al.</i> 1975
Harpacticoida			
Copepodites	C1-C5	$W=1.10*10^{-5}L^{1.89}$	Dumont <i>et al.</i> 1975
Non-identified Harpacticoida	C6	$W=12.51*L^{4.40}$	Dumont <i>et al.</i> 1975
Diplostraca			
<i>Bosmina</i> sp.	juveniles-adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Ceriodaphnia</i> sp.	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Chydoridae</i>	juveniles-adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Chydorinae</i>	juveniles	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Chydorus</i> sp.	juveniles	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia</i> sp.	juveniles	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia catawba</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia galeata mendotae</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia longiremis</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia longiremis</i> group ¹	juveniles	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia parvulata</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia pulex</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Daphnia pulex</i> group ²	juveniles	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Eurycercus</i> sp.	juveniles	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Ilyocryptus spinifer</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Monospilus dispar</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Polyphemus pediculus</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Sida crystallina</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
<i>Simocephalus vetulus</i>	adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976
Non-identified Diplostraca	juveniles-adults	$\text{Ln}W=\text{Ln}a+b\text{Ln}L$	Bottrell <i>et al.</i> 1976

Table 10. (continued)

Lowest taxonomic levels	Stages	Theoreticals equations	References
Mysida			
<i>Mysis stenolepis</i>		$DW=6.605*L^{2.57}$	Sirois and Dodson 2000a
<i>Neomysis americana</i>		$DW=6.605*L^{2.57}$	Sirois and Dodson 2000a
Amphipoda			
Gammaridae			
<i>Echinogammarus ischnus</i>		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
<i>Gammarus</i> sp		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non identified Gammaridae.		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
<i>Hyalella azteca</i>		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non-identified Amphipoda		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Crustacea			
Decapoda			
<i>Crangon septemspinosa</i>		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non-identified Decapoda	larvae	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Cirripedia Nauplii	N1-N6	$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Cumacea		$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Isopoda		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Maxillopoda Nauplii	N1-N6	$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Ostracoda		$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Non-identified Crustacea		$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Insecta			
Diptera			
Chironomidae	larvae-pupae	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non-identified Diptera	larvae-pupae-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Hemiptera			
Corixidae	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non-identified Hemiptera	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Homoptera			
Aphidoidea	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Cicadellidae	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Membracidae	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Psylloidea	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non-identified Homoptera	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Coleoptera	larvae-pupae-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Ephemeroptera	nymphs	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Forficulidae	nymphs-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Hymenoptera	larvae-pupae-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Lepidoptera	larvae	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Megaloptera	larvae	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Odonata	nymphs	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Plecoptera	nymphs	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Thysanoptera	larvae-pupae-adults	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Trichoptera	larvae	$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Non-identified Insecta		$LnW=Lna+bLnL$	Benke <i>et al.</i> 1999
Mollusca			
Gasteropoda			
<i>Patella</i> sp.		$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Non-identified Gasteropoda		$WW = 6.07(L^{2.59})$	Legendre and Michaud 1998
Bivalvia	Veliger larvae	$DW=0.5(37L^{2.59}-2.636L+0.058207)$	Sirois and Dodson 2000a

Table 10. (continued)

Lowest taxonomic levels	Stages	Theoreticals equations	References
Rotifera			
<i>Asplanchna</i> sp.		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Asplanchna priodonta</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Asplanchna silvestrii</i>		DW= 0.32 ug	Sirois and Dodson 2000a
Bdelloidea		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Brachionus</i> sp.		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Brachionus bidentata</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Brachionus caliciflorus</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Brachionus quadrata</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Brachionus variabilis</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Euchlanis</i> sp.		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Kellicottia longispina</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Keratella</i> sp.		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Keratella quadrata</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Keratella taurocephala</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Notholca</i> sp.		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Notholca acuminata</i>		DW= 0.32 ug	Sirois and Dodson 2000a
<i>Trichotria</i> sp.		DW= 0.32 ug	Sirois and Dodson 2000a
Non-identified Rotifera		DW= 0.32 ug	Sirois and Dodson 2000a
Others			
Arthropoda			
Acarina		$\text{LnDW} = a + bL + bL^2$	Sage 1982
Arachnida		$\text{LnDW} = a + bL + bL^2$	Sage 1982
Araneae		$\text{LnDW} = a + bL + bL^2$	Sage 1982
Collembola		$\text{WW} = 6.07(L^{2.59})$	Legendre and Michaud 1998
Hydracarina		$\text{DM} = a * L^b$	Baumgartner 2003
Annelida		$\text{WW} = 6.07(L^{2.59})$	Legendre and Michaud 1998
Gastrotricha		DW= 0.7 ug	Faubel 1982
Turbellaria		$M = aLb$	Benke <i>et al.</i> 1999

¹ *Daphnia longiremis* group included *D. longiremis* and *D. galeata mendotae*

² *Daphnia pulex* group included *D. pulex* and *D. catawba*