

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LE RETOUR DU BAR RAYÉ DANS L'ESTUAIRE DU SAINT-LAURENT :
ÉCOLOGIE DES JEUNES STADES DE VIE ET CARACTÉRISATION DES
HABITATS ESSENTIELS

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RÉSUMÉ

Dans l'estuaire du Saint-Laurent, la population ancestrale de bar rayé (*Morone saxatilis*) a disparu au cours des années 60 en raison d'une pression de pêche inadaptée et de l'altération de son habitat. Dès 2002, le Ministère des Forêts, de la Faune et des Parcs du Québec a entrepris la réintroduction d'une nouvelle population de bar rayé. Afin de favoriser son ré-établissement, cette étude de doctorat a pour objectif de documenter l'écologie des jeunes stades de vie du bar rayé et d'identifier son habitat essentiel.

De juin à septembre 2014, 162 stations pélagiques et 188 stations littorales ont été caractérisées en termes de physicochimie, de proies disponibles et d'assemblages ichtyologiques à l'aide d'un filet bongo, de seines de rivage et d'une sonde CTD. Dans la zone pélagique et littorale, quatre habitats estuariens ont été identifiés à partir des mesures de salinité et de turbidité : un habitat amont d'eau douce (UP), deux habitats localisés dans la zone de turbidité maximale de salinité oligohaline (O-ETM) et mésohaline (M-ETM), et un habitat aval polyhalin (DOWN). Les suivis se déroulant de juin à septembre 2014 ont permis l'échantillonnage de 765 bars rayés à partir desquels, un sous-échantillon de larves et de juvéniles a été utilisé pour l'analyse des contenus stomacaux, de la microstructure des otolithes et de la chimie des otolithes.

En juin, les larves de bar rayé étaient distribuées principalement dans l'habitat O-ETM où l'alimentation était composée de cladocères *Bosmina* sp. et de copépodes dont *Eurytemora affinis*. Dans une moindre mesure, une plus faible densité de larves fut identifiée dans l'habitat UP, où l'alimentation était composée de copépodes et diatomées. L'étude de l'alimentation, de la croissance et de la survie des larves suggèrent que les habitats UP et l'O-ETM sont des habitats d'alevinage essentiels et contribuent à parts égales au recrutement de la nouvelle population. Cependant, une plus forte pression sélective pourrait s'exercer dans l'habitat UP, et favoriserait la sélection de larves performantes aux croissances rapides. À l'inverse, l'habitat O-ETM présentait les meilleures conditions pour l'alimentation où les larves de bar rayé, plus abondantes, présentaient une mortalité réduite.

À partir de juillet, les bars rayés se sont dispersés le long du littoral dans tous les habitats estuariens et ont montré un changement drastique d'alimentation, composée

de proies plus énergétiques. En juillet, l'espèce était principalement distribuée dans l'UP, à proximité de sa frayère principale. Dans l'UP, les jeunes bars étaient caractérisés par une alimentation dominée par les pupes de diptère et une croissance plus rapide comparée aux habitats aval. En août et septembre, le bar rayé était concentré principalement dans les habitats O-ETM et M-ETM. Le long du littoral, l'alimentation du bar rayé était essentiellement composée de gammaridés dans l'O-ETM, de gammaridés et de mysidacés dans le M-ETM et de mysidacés dans le DOWN. En septembre, les bars rayés dispersés dans l'habitat DOWN présentaient certes des taux de croissance plus faibles, mais aussi un succès d'alimentation plus important comparé aux habitats amont.

De juin à septembre, les conditions les plus favorables au développement du bar rayé ont été identifiées dans l'habitat O-ETM en termes d'environnement physique et de disponibilité des proies. Les bars rayés issus de l'O-ETM présentaient des croissances rapides et une réduction des taux de mortalité-dispersion. Dès août, l'habitat M-ETM semble constituer un compromis écologique intéressant au développement du bar entre des conditions physiques plus coûteuses en énergie et l'accès à de nouvelles ressources. Nous suggérons que les migrations vers les habitats M-ETM et DOWN sont des comportements adaptatifs provoqués par des conditions sous-optimales et par une forte compétition des habitats amont. En élargissant leurs répartitions, les bars rayés juvéniles ont probablement réduit cette compétition en exploitant une nouvelle niche écologique, leur permettant d'accroître leur potentiel de survie. La coexistence de plusieurs patrons de migration divergents souligne les capacités adaptatives de cette nouvelle population, capable de rechercher et d'exploiter l'ensemble des habitats estuariens dont elle a besoin pour se ré-établir.

MOTS-CLÉS : jeunes stades de vie du bar rayé, ZTM, alimentation, croissance, mortalité

ABSTRACT

In the St. Lawrence estuary, striped bass (*Morone saxatilis*) was extirpated by the mid-1960, due to cumulative effects of overfishing and habitat destruction. To restore the biodiversity, the Minister of Forest, Wildlife and Parks of Québec initiated a reintroduction program of the species and it is now recognized that the population self-reproduced during the last decade. To promote the re-establishment of this new population, this study aims to document the ecology of striped bass early life stages and to identify critical habitats in terms of feeding ecology, growth and mortality.

From June to September 2014, 162 pelagic and 188 littoral stations were characterized in terms biophysical conditions, abundance of main prey, and fish assemblages using a bongo net, a beach seine, a seine net, and a CTD probe. In the pelagic and littoral zones, four estuarine habitats were characterized based on turbidity and salinity: an upstream freshwater section (UP), an oligohaline (O-ETM) and a mesohaline (M-ETM) estuarine turbidity maximum zone, and a downstream polyhaline section (DOWN). During the growing season, 765 striped bass larvae and juveniles were identified, and a subsample was analyzed for gut contents, otolith microstructures and otolith microchemistry.

During the larval stage, striped bass larvae were mainly distributed in the O-ETM where the diet was dominated by cladoceran *Bosmina* sp. and copepods such as *Eurytemora affinis*. In the UP, a lower density of faster-growth larvae was identified which mostly fed on copepods and diatoms. The O-ETM habitat had the best feeding conditions, possibly due to the presence of *Bosmina* sp. as a primary prey where more abundant larvae showed reduced mortality-dispersion. However, otolith microchemistry emphasized the fair contribution of the UP and O-ETM as main nursery habitats for the recruitment of the new population. Our results also suggested that a higher selective pressure may occur in the UP, selecting for individuals of faster growth.

From July, striped bass dispersed along the littoral zone in all estuarine habitats and shifted to larger preys, being generalist. In July, the species was primarily distributed in the UP, nearby the main spawning site and mainly fed on dipteran pupa. In the early summer, the UP provided a higher-quality nursery habitat where striped bass had a

higher feeding incidence and faster growth. In August and September, the species was concentrated in the ETM habitats where the diet was dominated by gammarids in the O-ETM and both gammarids and mysids in the M-ETM. In September, smaller striped bass dispersed in the DOWNS improved their feeding success by exploiting a new feeding niche, dominated by mysids.

Throughout the growing season, the O-ETM provided the most suitable conditions for the species, with optimal physical properties, important food resources where striped bass had fast-growth and lower mortality-dispersion rates. From August, the M-ETM appeared to provide a favorable trade-off for the species offering a less optimal physical environment although new feeding opportunities. We suggest that migrants adopted an adaptive migration behavior to avoid sub-optimal conditions and strong intraspecific competition in the upstream habitats. After July, striped bass dispersed further downstream, creating a spatial partitioning of estuarine habitats, potentially to reduce inter- and intra-specific competition and to search for new foraging opportunities. The potential advantage of a later season downstream migrations may be an ingenious tactic to promote the survival at early stages. The co-existence of distinct migratory pattern underlines the adaptive capacity of this new population, able to research and to exploit all the essential habitats to promote its re-establishment.

KEYWORDS : striped bass early life stages, ETM, feeding ecology, growth, mortality

INTRODUCTION GÉNÉRALE

0.1 Écosystèmes aquatiques : menaces et enjeux

Les écosystèmes aquatiques du monde entier connaissent aujourd'hui de profonds changements biologiques, et ce à une vitesse sans précédent (Butchart *et al.* 2010, Pereira *et al.* 2010). Cette crise écologique menace la biodiversité des écosystèmes aquatiques en altérant les interactions entre les espèces, la structure des réseaux trophiques et leurs dynamismes (Worm *et al.* 2006, Christensen *et al.* 2014). Depuis toujours, l'Homme a su tirer profit des écosystèmes aquatiques et de leurs ressources, et exerce aujourd'hui des pressions très fortes sur ses systèmes (Holmlund et Hammer 1999, Sarukhan *et al.* 2005, Collen *et al.* 2014, Llopiz *et al.* 2014). Les peuplements humains, en constante augmentation, sont principalement distribués autour des côtes et des cours d'eau; de ce fait, la perte ou la détérioration des services écosystémiques qu'ils procurent pourraient avoir des effets désastreux pour l'Homme (Adger *et al.* 2005). De plus récents travaux suggèrent que l'érosion de la biodiversité est non seulement responsable d'une perte de la stabilité des écosystèmes, mais aussi, de l'altération de ses services écosystémiques (Loreau *et al.* 2001, Hooper *et al.* 2005, Worm *et al.* 2006). La biodiversité des écosystèmes aquatiques est principalement menacée par son exploitation, la pollution des eaux, la dégradation des habitats aquatiques et la prolifération d'espèces envahissantes (Jackson *et al.* 2001, Dulvy *et al.* 2003, Lotze *et al.* 2006, Llopiz *et al.* 2014). Parmi ces menaces, la surpêche, observée dans presque toutes les pêcheries de la planète, exerce une pression très forte sur les écosystèmes aquatiques et entraîne le déclin des populations de poisson (Jackson *et al.*

2001, Watson *et al.* 2013). À travers le monde, la pêche est un moteur économique important qui procure nourriture et emploi. Pour de nombreux pays en voie de développement, le poisson est la principale source de protéines animales accessibles aux populations rurales (Mohan Dey *et al.* 2005). Au cours du siècle dernier, la pêche n'a cessé de s'intensifier, bien que ses rendements s'amenuisent, tant par l'effort de pêche que par l'argent investi. Plus les ressources s'épuisent, plus les pêcheurs s'exilent loin des ports à la recherche de nouvelles ressources. Cependant, peu d'actions sont mises en place par les gouvernements pour supporter une exploitation raisonnée et pérenne des ressources à travers le monde (Sumaila *et al.* 2010). La santé des populations de poisson est aussi fortement menacée par la perte, la détérioration et la fragmentation des habitats aquatiques, responsable d'une érosion drastique de la biodiversité (Hughes *et al.* 2002, Morita et Yamamoto 2002, Aarts *et al.* 2004, Fischer et Lindenmayer 2007, Collen *et al.* 2014). De par l'utilisation des habitats aquatiques et de leurs services écosystémiques, l'Homme a profondément transformé les paysages aquatiques. Dans les grands fleuves, la régularisation du débit a entraîné l'homogénéisation des habitats tandis que le développement de voies navigables et la construction de barrage hydroélectrique altèrent la connectivité entre les habitats (Vincent et Dodson 1999, Foubert 2017). Les perturbations anthropiques fragilisent la résilience et la stabilité des écosystèmes aquatiques, et sont responsables du déclin des populations de poisson (Thrush *et al.* 2008, Perkol-Finkel et Airoidi 2010). Dans l'estuaire du Saint-Laurent, les pressions exercées par la surpêche et l'altération des habitats menèrent à l'extinction de la population ancestrale du bar rayé (*Morone saxatilis*; Robitaille *et al.* 2011).

0.2 Recrutement des populations de poissons

Au cours des siècles précédents, les fluctuations démographiques des populations de poissons étaient perçues comme des processus de déplacement et de migration des poissons (Sinclair 1988). Cette perception ne fut réfutée qu'avec le développement des techniques d'estimation de l'âge et l'étude de la structure des classes d'âge, soulignant la variabilité du succès du recrutement chez les poissons (Dahl 1907, Lea 1910, Houde 2008). En science halieutique, le recrutement se définit par l'ajout d'une nouvelle cohorte de jeunes individus à la population, et qui contribueront eux-mêmes éventuellement à sa reproduction et donc, à son renouvellement. Très vite, un nouveau courant de pensée émergea attribuant le succès du recrutement à la survie des jeunes stades de vie (Hjort 1914, Lasker 1975, Cushing 1990). Lors de la première saison de croissance, les jeunes stades de vie des poissons sont caractérisés par de très fortes mortalités, très variables et pouvant atteindre des valeurs aussi élevées que 99,99% (Houde 1997). Chez les poissons, la survie des premiers stades de vie est principalement menacée par la prédation (Bailey et Houde 1989, Paradis *et al.* 1996), par le jeûne (Hjort 1914, Cushing 1990), et l'habitat physicochimique (Uphoff Jr 1989, Pepin 1991, Rutherford et Houde 1996, North et Houde 2003). Les premières hypothèses pour expliquer la variabilité du recrutement ont mis l'accent sur les conditions d'alimentation au commencement de l'alimentation exogène (hypothèses de la période critique, Hjort 1914 et du *match-mismatch*, Cushing 1990). Très vite, un nouveau paradigme émergea associant les croissances rapides avec la survie et le recrutement des populations de poisson (hypothèses de croissance-mortalité, Anderson 1988). Les individus aux croissances rapides sont enclins à un meilleur potentiel de survie, et ainsi, contribuent de manière plus importante au recrutement de l'espèce (1) par la réduction de la période de très forte mortalité lors des premiers stades de vie (hypothèse du *stage-duration*, Chambers et Leggett 1987, Houde 1987). De plus, les jeunes stades aux fortes croissances (2) sont moins vulnérables à la prédation que leurs conspécifiques (hypothèse du *bigger-is-better*,

Miller *et al.* 1988). De plus récentes études ont aussi mis en lien l'influence de la croissance des jeunes stades sur (3) les comportements et aptitudes d'évitement des prédateurs (hypothèse de *growth-selective predation*, Takasuka *et al.* 2003, 2007). Chez les poissons, la croissance est fortement reliée à la qualité de l'alimentation à travers l'abondance des proies disponibles et leurs valeurs énergétiques, les aptitudes de prédation des poissons et la sélectivité des proies (Wainright *et al.* 1996, Castonguay *et al.* 2008, Robert *et al.* 2009, 2014, Pepin *et al.* 2015). En outre, les propriétés de l'habitat physique sont susceptibles d'influencer la croissance lorsqu'ils induisent un coût physiologique important, comme cela a été souligné pour la salinité (Secor *et al.* 2000, Boeuf et Payan 2001) et la température (Cox et Coutant 1981, Anderson 1988, Clarke et Johnston 1999, Shoji *et al.* 2011, Kusakabe *et al.* 2017). Enfin, les processus spatiaux dont les mécanismes d'écoulement, de rétention et de connectivité entre les habitats estuariens sont susceptibles d'influencer la survie des jeunes stades et ainsi, le recrutement de l'espèce (Hjort 1914, Sinclair 1988, Houde 2008, North et Houde 2003). La présence de courants défavorables pourrait affecter le succès de recrutement de par la dispersion des jeunes stades de vie vers des habitats défavorables à partir desquels ils ne seraient plus en mesure de revenir (hypothèse de la dérive aberrante, Hjort 1914). En outre, le régime hydrologique d'un cours d'eau façonne les propriétés des habitats aquatiques et de leurs connectivités. De ce fait, la variation de ses caractéristiques hydrologiques peut profondément affecter la survie des jeunes stades et être à l'origine d'importantes fluctuations du recrutement (North et Houde 2003, 2006).

Malgré l'avancée des connaissances, prévoir les fluctuations du recrutement chez les populations de poisson demeure un véritable challenge. Les estuaires sont de véritables pouponnières à poisson; de ce fait, il est primordial de documenter les mécanismes sous-jacents qui contribuent au succès du recrutement des populations estuariennes.

0.3 Les estuaires, véritables pouponnières à poissons

À travers le monde, les estuaires fournissent d'importantes pouponnières à poissons où les larves et juvéniles vont pouvoir s'alimenter et croître dans des habitats répondant à leurs besoins (North et Houde 2003, Winkler *et al.* 2003, Able 2005, North et Houde 2006, Vasconcelos *et al.* 2011, Day *et al.* 2012). Une très grande diversité de poissons, dont de nombreuses espèces commerciales, utilise les estuaires pour compléter leur cycle de vie, particulièrement lors des premiers stades (Able 2005, Potter *et al.* 2015). Le long du gradient de salinité, les estuaires présentent de forts contrastes biophysiques, se répercutant directement sur les communautés d'invertébrés et de poissons qui l'habitent (Rakocinski *et al.* 1992, Laprise et Dodson 1994, Winkler *et al.* 2003, Selleslagh et Amara 2008, Potter *et al.* 2015). Dans la région aval du front salin, le contact entre l'eau douce et l'eau salée entraîne la mise en suspension d'une forte concentration de matière à l'origine d'une zone dite de turbidité maximale (ZTM). La ZTM est très largement utilisée par les espèces euryhalines et anadromes, où les jeunes stades de vie sont retenus et se maintiennent dans une région de forte turbidité. Chez les jeunes stades de vie, la turbidité joue un rôle très important dans la détection des proies, accentuant les contrastes visuels entre les proies colorées et l'environnement (Utne-Palm 2002, De Robertis *et al.* 2003). À l'inverse, les environnements turbides fournissent un refuge visuel pour les larves de poisson translucides contre les prédateurs (Miner et Stein 1996, Abrahams et Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003). Dans la ZTM, les jeunes stades de vie des poissons se maintiennent dans une région de forte production primaire et secondaire (Roman *et al.* 2001, North et Houde 2003, Winkler *et al.* 2003, Lapierre et Frenette 2008) et dans un environnement physique plus propice à la croissance et à la survie (Uphoff Jr 1989, Rutherford *et al.* 1997, Secor *et al.* 2000, Sirois et Dodson 2000-b). Dans l'estuaire du Saint-Laurent, la ZTM, de par sa forte abondance zooplanctonique et ses propriétés physiques, constitue une région favorable au développement des jeunes stades (Fig. 0.1, Bousfield *et al.* 1973, Winkler *et al.* 2003). La ZTM du Saint-

Laurent est utilisée comme pouponnière par de nombreuses espèces de poisson dont l'éperlan arc-en-ciel (*Osmerus mordax*), le poulamon atlantique (*Microgadus tomcod*) et le bar rayé (Laprise et Dodson 1990, 1994, Sirois et Dodson 2000-a, Valiquette *et al.* 2017).

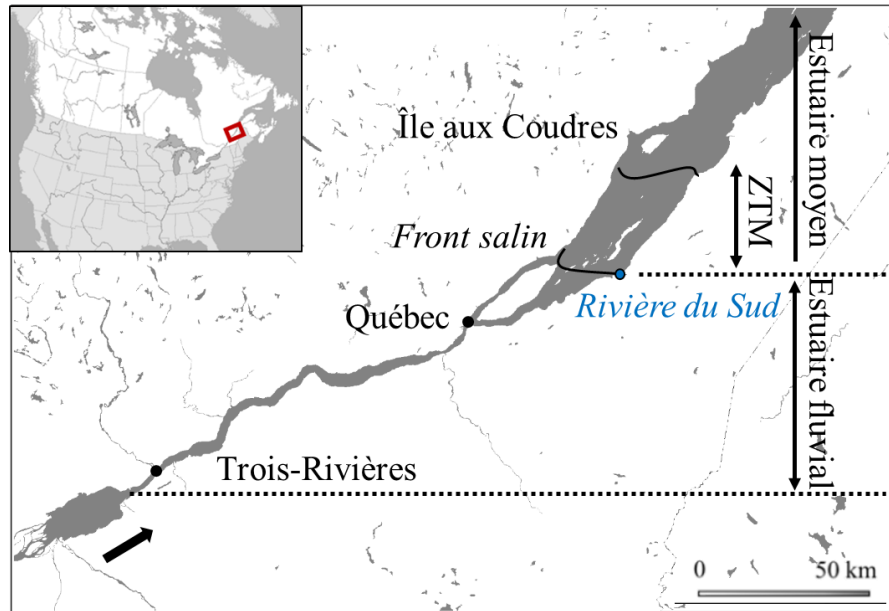


Figure 0.1 Localisation de la zone d'étude dans l'estuaire du Saint-Laurent comprenant l'estuaire fluvial et l'estuaire moyen et la zone de turbidité maximale (ZTM).

0.4 Le bar rayé (*Morone saxatilis*)

Le bar rayé est une espèce anadrome très présente sur la Côte-Nord Est américaine (Vladykov et Wallace 1938, Scott et Crossman 1974). Son aire de répartition s'étend de l'estuaire du Saint-Laurent jusqu'à la rivière Saint John en Floride, ainsi que dans les tributaires se jetant dans le golfe du Mexique. Il mesure en

moyenne entre 406 et 457 mm, même si l'espèce peut atteindre plus de 700 mm (Scott et Crossman 1974). Le bar rayé est une espèce prisée pour sa pêche récréative et commerciale puisqu'en 2015, son exploitation a été évaluée à plus de 10 000 tonnes aux États-Unis (National Marine Fisheries Service 2016). À la fin du printemps, le bar rayé effectue une migration annuelle à partir des eaux salées côtières et estuariennes vers l'eau douce et saumâtre où l'espèce se reproduit pendant trois à quatre semaines (Scott et Crossman 1974, Robitaille 2004, Valiquette *et al.* 2017). L'incubation des œufs très rapide, dure entre deux à trois jours à une température comprise entre 15 et 18°C. Le développement larvaire initial est associé à un milieu d'eau douce à légèrement saumâtre (Pearson 1938, Robitaille 2004, Wingate et Secor 2007). Les œufs qui mesurent entre 1,3 et 4,6 mm sont semi-pélagiques et utilisent les courants modérés ($> 0,3 \text{ m}\cdot\text{s}^{-1}$) pour maintenir un niveau d'oxygénation suffisant (Fahay 1983). Après une semaine de développement, les larves d'environ 6–7 mm ont totalement absorbé les réserves vitellines et commencent une alimentation exogène composée de petits crustacés, tels que des copépodes et des cladocères. Plusieurs études ont montré que les larves de bar rayé se nourrissent principalement du copépode *Eurytemora affinis* et des cladocères *Bosmina* sp. (Robichaud-LeBlanc *et al.* 1997, Shideler et Houde 2014). Après environ 30 à 50 jours, les bars rayés juvéniles vont rechercher des proies plus énergétiques comme les crangons, les gammarés, les mysidacés et les jeunes stades d'insecte (Robichaud-Leblanc *et al.* 1997, Jordan *et al.* 2003, Walter *et al.* 2003, Howe *et al.* 2008). À mesure que le bar rayé croît, il devient piscivore exclusif et se nourrit principalement de poissons-fourrages dont les clupéidés (alose sp.), les engraulidés (anchois sp.), les scianidés et les ammotydés (lançon sp.; Walter *et al.* 2003, Overton *et al.* 2008, 2009, Wuenschel *et al.* 2013).

0.5 Stratégies de migration du bar rayé

Chez les populations du bar rayé, on retrouve des regroupements d'individus, appelés contingent migratoire, qui se caractérisent par des patrons de migration communs entre leurs aires d'alimentation, d'hivernage et de reproduction (Clark 1968, Secor et Piccoli 1996, Jessop *et al.* 2002, Pautzke *et al.* 2010, Morissette *et al.* 2016). Les contingents migratoires se distinguent essentiellement par la coexistence de comportement de résidence à proximité des frayères et de comportement de migration (Zlokovitz *et al.* 2003, Chapman *et al.* 2012). Chez les poissons, l'expression des contingents migratoires évolue au cours du développement et peut être affectée par la physiologie des individus (Secor et Piccoli 2007, Conroy *et al.* 2015, Gahagan *et al.* 2015, Secor 2015). Initialement, les comportements de migration étaient perçus comme réservés au stade adulte, la proportion de migrants augmentant avec l'âge (Kohlenstein 1981, Dorazio *et al.* 1994). De plus récentes études ont souligné la mise en place des contingents migrateurs dès le stade juvénile (Jessop *et al.* 2002, Kerr et Secor 2009, Conroy *et al.* 2015, Morissette *et al.* 2016). Malgré l'avancée des connaissances, il demeure tout un consensus autour des mécanismes impliqués lors de la mise en place des comportements de migration :

Les migrations peuvent être influencées par le sexe. Cette première hypothèse est basée sur l'observation que les reproducteurs les plus performants arrivent en premier sur les sites de fraie de meilleure qualité (hypothèse du *arrival-time*, Chapman *et al.* 2011). L'occupation des sites de fraie par le contingent résident constituerait donc un avantage important en cas de forte compétition intrasexuelle, permettant aux reproducteurs d'accroître leurs succès de reproduction. En outre, plusieurs études ont mis en évidence des comportements de migration chez les femelles lorsque la reproduction induit un coût physiologique trop important (ex. : harcèlement, investissement énergétique, soin aux jeunes). Les femelles migrantes, en délaissant des sites de fraie sont capables de se soustraire des coûts associés à la reproduction (hypothèse du *sexual conflict*, Chapman *et al.* 2011).

Les comportements de migration sont réservés aux individus de meilleures conditions physiques. Dans cette deuxième hypothèse, seuls les individus aux plus fortes aptitudes phénotypiques sont capables de migrer à la recherche d'habitats plus productifs. Chez les poissons, la migration engendre des coûts énergétiques importants et une augmentation des risques de prédation que seuls les individus de meilleures conditions sont capables d'endosser (Werner *et al.* 1983, Kerr et Secor 2009, Chapman *et al.* 2011, Brodersen *et al.* 2014).

Au contraire, les migrations peuvent constituer une alternative viable pour les individus moins performants. Dans cette dernière hypothèse, les comportements de migration peuvent être le résultat de fortes compétitions inter- et intraspécifique pour les ressources de l'habitat source (MacCall 1990). De ce fait, seuls les individus les plus compétitifs sont ainsi capables de résider et d'exploiter les ressources locales. Les individus moins performants adopteraient des comportements de migration pour partir en quête de nouveaux habitats plus propices au développement et à la survie des individus (Hypothèse de *Competitive release*, Chapman *et al.* 2011, Brodersen *et al.* 2014, Secor 2015). Auquel cas, les comportements de migration constituent un compromis évolutif entre l'augmentation des risques et du coût énergétique associé à la migration et la découverte potentielle d'habitat plus optimal au développement des migrants.

Le concept des contingents migratoires soulève de nombreuses questions quant à leurs fonctions écologiques chez les populations de poisson (Sinclair 1988, MacCall 1990, Chapman *et al.* 2011, Secor 2015). Le développement des migrants est-il un indice de bonne santé de la population source, capable de s'étendre et de coloniser de nouveaux habitats ? À l'inverse, faut-il considérer les comportements de migration comme des signaux de détresse de la population ? Auquel cas, on parlerait plutôt d'une recherche par les migrants de nouveaux habitats alternatifs, capables de soutenir la

population actuelle. Secor et Piccoli (1996) argumentent le maintien de telle structure comme un compromis écologique entre la découverte d'habitats favorables à l'expansion et à la productivité de la population et d'habitats peu propices à la survie. Lors de l'exploration de nouveaux habitats, les individus migrants s'exposent à un risque nouveau de ne pas trouver de conditions favorables à la survie, à la reproduction et au développement des jeunes stades. À l'inverse, le contingent des résidents, moins productif, assure la restauration de la population et permet donc d'en accroître sa stabilité (Fig. 0.2, Kerr *et al.* 2009, Secor 2015). En écologie, la stabilité d'un système se définit comme la capacité d'une population à maintenir son intégrité et à persister tandis que sa résilience désigne la capacité d'une population à retrouver son état de référence après une perturbation. La coexistence et le maintien des comportements de résidence et d'exploration contribuent aux mécanismes de régulation de la population, et assurent sa stabilité, sa résilience et sa productivité (Fig. 0.2, Kerr *et al.* 2009, Secor 2015). Lors de perturbations, la diversité des mécanismes de réponse exhibée par les différents contingents migratoires permet d'accroître la résilience des populations de poisson (Fig. 0.2, Kerr *et al.* 2009).

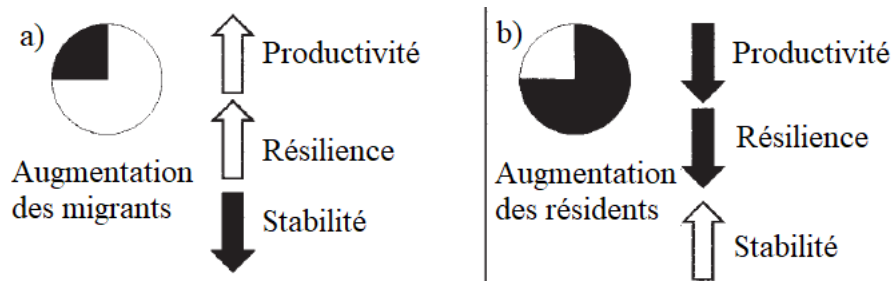


Figure 0.2 Mécanisme de régulation d'une population de poisson suite (a) à l'augmentation du contingent migrateur et (b) l'augmentation du contingent résident. Figure adaptée de Kerr *et al.* 2009.

Les migrations sont des stratégies d'adaptation conditionnelles à un environnement donné (Dodson 1988, Secor 2015). Dans l'estuaire du Saint-Laurent, la

coexistence de contingents migratoires distincts souligne chez la nouvelle population de bar rayé ses importantes aptitudes d'adaptation (Morissette *et al.* 2016).

0.6 La nouvelle population de bar rayé de l'estuaire du Saint-Laurent

Les populations du bar rayé Atlantique ont connu d'importants déclin (Goodyear *et al.* 1985, Richards et Rago 1999), menant plusieurs stocks jusqu'au bord de l'extinction (Robitaille *et al.* 2011). Dans l'estuaire du Saint-Laurent, la forte pression exercée par les pêches et les modifications importantes de son habitat, dont la construction du chenal de navigation, conduisirent la population ancestrale à s'éteindre au milieu des années 1960 (Robitaille *et al.* 1988). Au cours des années 1990, l'amélioration de la qualité des eaux du Saint-Laurent et la réduction des activités de dragage ont laissé entendre une diminution des pressions à l'origine de sa disparition, et donc, que la réintroduction de l'espèce était possible (Centre du Saint-Laurent 1996, Environnement Canada 2016). À la suite de tentatives fructueuses débutées en 1999, desensemencements réguliers ont été réalisés à partir de 2002 à l'initiative du Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP). Dans ce but, lesensemencements ont été effectués à partir de progénitures d'individus reproducteurs issus de la rivière Miramichi (Nouveau-Brunswick), soit la population la plus proche géographiquement. Entre 2002 et 2013, plus de 34,5 millions de larves et de juvéniles ont été ensemencés dans l'estuaire fluvial et moyen du Saint-Laurent (Fig. 0.1, Fisheries and Oceans Canada 2017). Très vite, l'espèce a donné des signes positifs de rétablissement ce qui a permis la mise en place, dès 2004, d'un premier réseau de suivi documenté par les captures accidentelles des pêcheurs commerciaux et sportifs. En 2008, les captures de jeunes de l'année, alors que l'espèce n'avait pas été ensemencée cette année-là, ont été les premiers indices d'une reproduction naturelle dans le

système. Dans l'estuaire du Saint-Laurent, on retrouve aujourd'hui la présence d'une nouvelle population de bar rayé engagée dans un processus de ré-établissement (Pelletier *et al.* 2011, Morissette *et al.* 2016, Valiquette *et al.* 2017). Cependant, la population de bar rayé du Saint-Laurent est toujours considérée comme disparue d'après la loi canadienne sur les espèces en péril (LEP). Afin de favoriser son rétablissement, il est essentiel de documenter la niche écologique occupée par le bar rayé de l'estuaire du Saint-Laurent. En écologie, la niche écologique se définit à la fois par (1) la somme des conditions nécessaires à la viabilité de l'organisme, mais aussi par (2) la position occupée par l'organisme, la population ou l'espèce dans l'écosystème (Soberón et Nakamura 2009). En outre, l'identification des habitats essentiels, particulièrement lors de la première saison de croissance, a été fixée comme l'un des objectifs prioritaires du plan de rétablissement de l'espèce (Robitaille 2004). D'après la LEP, l'habitat essentiel d'une espèce aquatique en péril est défini comme « *...les frayères, aires d'alevinage, de croissance et d'alimentation et routes migratoires dont sa survie dépend, directement ou indirectement, ou aire où elle s'est déjà trouvée et où il est possible de la réintroduire* » (Robitaille *et al.* 2011). Hall *et al.* (1997), élargit la définition de l'habitat comme étant « *les ressources et conditions présentes à un endroit qui permettent l'occupation – incluant la survie et la reproduction – par un organisme donné* ». Depuis 2013, le bar rayé fait l'objet d'un suivi standardisé de l'abondance des jeunes de l'année. Toutefois, de nombreuses lacunes demeurent quant à la caractérisation de la niche écologique utilisée par la nouvelle population et de son utilisation des habitats selon les divers stades de développement (Fisheries and Oceans Canada 2017).

0.7 Utilisation des habitats estuariens de la nouvelle population de bar rayé

Dans l'estuaire du Saint-Laurent, une frayère principale a été identifiée à

l'embouchure de la rivière du Sud, en frontière du front salin (Pelletier *et al.* 2013, Valiquette *et al.* 2017). Dans une moindre mesure, de récents travaux ont montré l'existence d'une frayère secondaire dans l'estuaire fluvial, à proximité du port de Québec (Fig. 0.1, Valiquette *et al.* 2017). Contrairement aux larves qui sont pélagiques, les bars rayés juvéniles recherchent des eaux peu profondes et abritées le long des berges (Robichaud-Leblanc *et al.* 1998, Robitaille 2004). Dans l'estuaire du Saint-Laurent, les suivis annuels de la zone littorale ont montré que les jeunes de l'année sont distribués principalement dans le secteur de la ZTM (Pelletier *et al.* 2011, Fisheries and Oceans Canada 2017, Valiquette *et al.* 2017). Durant l'été 2012, des migrations vers l'aval ont été observées dans l'estuaire moyen, et ce dès la première saison de croissance (Pelletier 2013, Morissette *et al.* 2016, Valiquette *et al.* 2017). À l'automne, les bars rayés juvéniles et adultes migrent en eau douce pour se soustraire aux basses températures de l'eau salée et y passer l'hiver (Pelletier 2013, Valiquette *et al.* 2017). Dès le stade juvénile, la nouvelle population de bar rayé se caractérise par la coexistence de trois contingents migratoires : (1) un premier contingent résident en eau douce ainsi que deux contingents migrants des eaux (2) oligohalines et (3) mésohalines (Morissette *et al.* 2016). La présence de différentes stratégies de migration souligne les capacités de colonisation et d'adaptation du bar rayé à un nouvel environnement. Néanmoins, l'écologie des jeunes stades et l'utilisation des habitats estuariens restent à ce jour très peu documentées. Par conséquent, la présente étude doctorale porte sur l'écologie des jeunes stades de vie du bar rayé et sur l'identification des habitats essentiels au recrutement de la nouvelle population.

0.8 Objectifs

Cette étude de doctorat a pour objectif de documenter l'écologie et l'habitat essentiel des jeunes stades de vie du bar rayé dans l'estuaire du Saint-Laurent à travers l'étude de l'alimentation, de la croissance et de la survie. Dans ce but, plusieurs sous-objectifs ont été fixés :

Chapitre I : Étude de l'utilisation des habitats pélagiques et littoraux par les larves et les juvéniles du bar rayé dans l'estuaire du Saint-Laurent

Sous-objectif 1 : Utilisation des habitats estuariens par les larves et les juvéniles de bar rayé

H1 : Dans la zone pélagique, les larves de bar rayé seront principalement distribuées à proximité du front salin, dans l'estuaire fluvial aval et l'estuaire moyen amont (Robichaud-LeBlanc *et al.* 1996, Shideler et Houde 2014). À partir de juillet, les juvéniles seront distribués dans la zone littorale (Robichaud-Leblanc *et al.* 1998). Plus tard dans la saison, les bars rayés se disperseront dans l'estuaire moyen (Pelletier *et al.* 2014, Morrissette *et al.* 2016).

Sous-objectif 2 : Caractérisation des habitats estuariens le long du gradient de salinité-turbidité

H2 : Dans la région étudiée de l'estuaire du Saint-Laurent, les variables d'habitat permettront de mettre en évidence quatre habitats estuariens (Fig. 0.3; Laprise et Dodson 1994, St. Lawrence Centre 1996, Vincent *et al.* 1996, Winkler *et al.* 2003) :

(1) l'estuaire fluvial amont situé entre Trois-Rivières et Québec

(2) l'estuaire fluvial aval situé entre Québec en la pointe Est de l'île d'Orléans

(3) l'estuaire moyen amont situé entre la pointe est de l'île d'Orléans et l'île-aux-Coudres,

(4) l'estuaire moyen aval situé entre l'île aux Coudres et Rivière-du-Loup (c.-à-d. limite aval de l'aire d'étude).

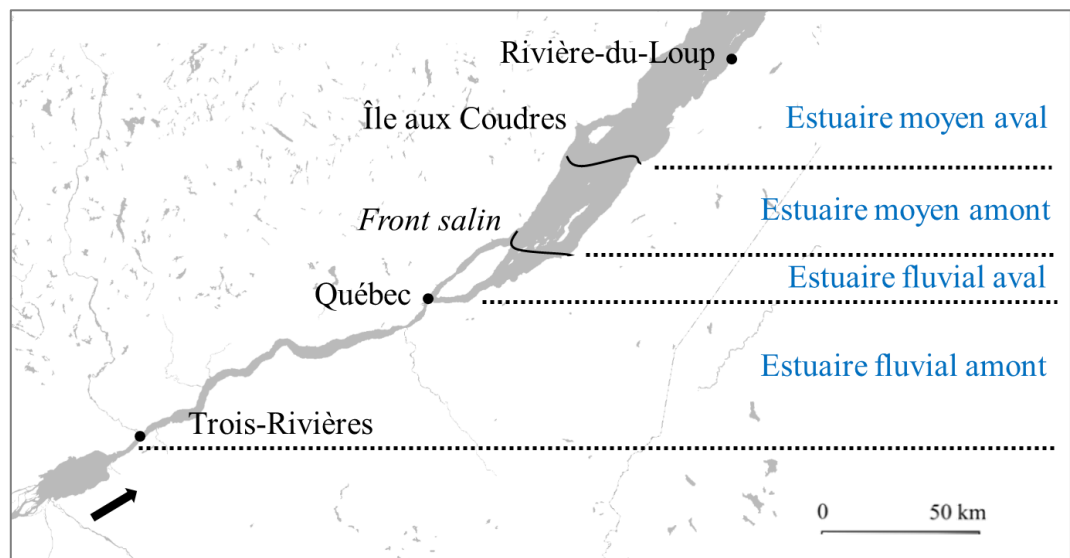


Figure 0.3 Représentation des habitats estuariens suggérés dans le secteur d'étude, entre les villes de Trois-Rivières et Rivière-du-Loup.

Sous-objectif 3 : Caractérisation physique des habitats estuariens des zones pélagique et littorale

H3 : Dans les zones pélagique et littorale :

(1) l'estuaire fluvial amont sera caractérisé par une eau douce peu turbide aux températures supérieures, et par une oxygénation de ses eaux plus faibles comparées aux habitats en aval.

(2) l'estuaire fluvial aval sera caractérisé par une eau peu turbide aux températures légèrement inférieures à la section amont, et par une oxygénation de ses eaux supérieure à la section amont.

(3) l'estuaire moyen amont sera caractérisé par les plus fortes valeurs de turbidité, une salinité oligohaline, une diminution de la température et un accroissement de l'oxygénation de ses eaux.

(4) l'estuaire moyen aval sera caractérisé par une eau turbide mésohaline, par la diminution importante de sa température et l'accroissement de son oxygénation.

Sous-objectif 4 : Caractérisation biologique des habitats estuariens dans les zones pélagique et littorale. Dans ce but, les habitats estuariens ont été étudiés en termes de concentration en chlorophylle *a*, d'abondance de proies et de communautés ichthyologiques.

- **Concentration en chl-*a***

H4 : Dans les zones pélagique et littorale, de fortes concentrations de chl-*a* seront observées dans l'estuaire fluvial (Vincent *et al.* 1996, Vincent et Dodson, 1999). L'estuaire moyen amont sera caractérisé par les plus fortes concentrations de chl-*a* induites par une importante production primaire dans cet habitat (Vincent *et al.* 1996, Winkler *et al.* 2003). Dans la section aval de l'estuaire moyen, la pression exercée par les brouteurs contribueront à une diminution significative de la chl-*a* (Vincent *et al.* 1996).

- **Abondance des proies :**

L'étude de l'abondance des proies disponibles à l'alimentation des larves de bar rayé se concentrera sur l'étude des petits crustacés dont les copépodes *E. affinis*, les

calanoides, les cyclopoïdes et cladocères *Bosmina* sp. (Robichaud-LeBlanc *et al.* 1997, Shideler et Houde 2014).

H4 : Dans la zone pélagique, le cladocère d'eau douce *Bosmina* sp. sera uniquement distribué dans l'estuaire fluvial et sera très abondant dans la région avoisinante au front salin (Winkler *et al.* 2003). Le copépode *E. affinis* sera très abondant dans les eaux oligohaline de l'estuaire moyen amont. Les copépodes cyclopoïdes seront principalement distribués dans l'estuaire fluvial tandis que les copépodes calanoides seront plus abondants dans les eaux mésohalines de l'estuaire moyen (Winkler *et al.* 2007, Cusson 2011, Favier et Winkler 2014).

L'étude des proies disponibles à l'alimentation des bars rayés juvéniles se concentrera sur les jeunes stades d'insecte, les gammaridés et les mysidacés (Robichaud-Leblanc *et al.* 1997, Jordan *et al.* 2003, Walter *et al.* 2003, Howe *et al.* 2008).

H4 : Dans la zone littorale, l'estuaire fluvial sera caractérisé par la présence de pupes de diptère et de gammaridés tandis que les mysidacés seront dominants dans l'estuaire moyen (Winkler *et al.* 2003).

- Communautés ichthyologiques

H4 : Dans la zone pélagique, l'abondance de ichthyoplancton sera plus importante dans l'estuaire moyen, et sera principalement dominée par l'éperlan arc-en-ciel. Dans l'estuaire fluvial, la communauté ichthyologique sera constituée de taxons d'eau douce et saumâtre tels que l'aloise savoureuse (*Alosa sapidissima*), le baret (*Morone americana*) et les catostomidés (Able, 1978, Robitaille *et al.* 2008).

Le long du littoral, l'abondance des larves et juvéniles de poissons sera plus importante dans l'estuaire fluvial où le fondule barré *Fundulus diaphanus* et les cyprinidés seront dominants (Pelletier *et al.* 2014). L'estuaire moyen amont sera dominé par le baret

tandis que l'estuaire moyen aval sera caractérisé par la présence des gasterosteidés (épinuche sp.), de l'éperlan arc-en-ciel et des ammodytidés (lançon sp.; Pelletier *et al.* 2014).

Chapitre II : Étude de l'alimentation des larves et des juvéniles de bar rayé dans l'estuaire du Saint-Laurent

Sous-objectif 1 : Étude de la composition de l'alimentation des larves et des juvéniles de bar rayé le long du gradient de salinité

H1 : L'alimentation des larves de bar rayé sera dominée par le copépode calanoïde estuarien *Eurytemora affinis* et dans une plus faible mesure, par le cladocère d'eau douce *Bosmina sp.*. De récentes études dans la baie de Chesapeake ont déjà montré que ces deux taxons étaient des proies communes dans l'alimentation des larves de bar rayé. La présence de *Bosmina sp.* dans l'alimentation du bar rayé sera favorisée en amont du front salin (Robichaud-LeBlanc *et al.* 1997, Shideler et Houde 2014). Lorsque les juvéniles auront atteint une longueur totale supérieure à 25 mm, l'alimentation sera composée majoritairement de gammaridés dans l'estuaire fluvial et de mysidacés dans l'estuaire moyen, dont les espèces *Neomysis americana* et *Mysis stenolepis* (Robichaud-Leblanc *et al.* 1997, Jordan *et al.* 2003, Walter *et al.* 2003).

Sous-objectif 2 : Comparaison de l'incidence et du succès d'alimentation des bars rayés entre les différents habitats estuariens

H2 : Les incidences d'alimentation et les succès d'alimentation des larves seront plus importants dans la région du front salin où l'abondance des proies préférentielles du bar rayé sera supérieure (Winkler *et al.* 2003, Favier et Winkler 2014). Dans la zone littorale, les juvéniles seront caractérisés par des incidences d'alimentation et des succès d'alimentation plus importants dans l'estuaire moyen où les gammaridés et les mysidés seront très abondants (Winkler *et al.* 2003).

Sous-objectif 3 : Étude du chevauchement des niches écologiques du bar rayé entre les habitats estuariens

H3 : Dans l'estuaire du Saint-Laurent, le front salin forme une barrière importante entre les espèces d'eau douce peu tolérantes à l'augmentation de la salinité et les espèces estuariennes. De ce fait, la niche écologique du bar rayé sera vraisemblablement très distincte entre l'estuaire fluvial et l'estuaire moyen.

Chapitre III : Étude de la mortalité-dispersion et de la croissance des larves et des juvéniles de bar rayé dans les habitats estuariens

Sous-objectif 1 : Comparaison des estimations de mortalité-dispersion des larves et des juvéniles de bar rayé entre les habitats estuariens. L'estimation des taux de mortalité-dispersion sera réalisée à partir de courbes de capture de la zone pélagique et littorale.

H1 : Dans les zones pélagique et littorale, nous émettons l'hypothèse que les taux de mortalité et de dispersion seront supérieurs dans l'estuaire fluvial comparé à l'estuaire moyen. Dans l'estuaire moyen, la très forte turbidité des eaux de la ZTM fournira un refuge visuel permettant la réduction de la mortalité associée à la prédation, comme cela a déjà été observé en laboratoire (Utne-Palm 2002, De Robertis *et al.* 2003). À l'inverse, le risque de prédation et ainsi, la mortalité seront vraisemblablement supérieurs dans les eaux moins turbides de l'estuaire fluvial. En outre, nous suggérons que la dispersion des jeunes stades est un processus important dans l'estuaire du Saint-Laurent. Chez la nouvelle population de bar rayé, plusieurs études ont mis en évidence la présence de comportements de migration vers l'estuaire moyen au cours de la première saison de croissance (Morissette *et al.* 2016, Valiquette *et al.* 2017).

Sous-objectif 2 : Comparaison de la croissance des larves et des juvéniles de bar rayé entre les différents habitats estuariens. Les estimations d'âge et de croissance seront réalisées à l'aide de l'otolithométrie.

H2 : En milieu pélagique, les larves de bar rayé auront une croissance plus importante dans la région du front salin. L'estuaire moyen amont forme une aire d'alevinage propice au développement où les larves du bar rayé se maintiendront dans un habitat riche en zooplancton (Sirois et Dodson 2000-a, Winkler *et al.* 2003, Martino et Houde 2010). Plus tard dans la saison, la forte productivité de l'estuaire moyen aval favorisera la croissance des bars rayés juvéniles.

Sous-objectif 3 : Caractérisation des contingents migratoires. Afin d'étudier l'utilisation passée des habitats estuariens, nous utiliserons la chimie des otolithes.

H3 : La nouvelle population de bar rayé du Saint-Laurent sera caractérisée par la présence de trois contingents migratoires. Une précédente étude réalisée sur des bars rayés juvéniles échantillonnés entre 2011 et 2012 a révélé la présence de trois contingents migratoires : des individus résidents en eau douce, des migrants des eaux oligohalines et des migrants des eaux mésohalines (Morissette *et al.* 2016).

Sous-objectif 4 : Comparaison de la croissance et de la morphologie du bar rayé entre les contingents migratoires

H4 : La croissance sera favorisée chez les contingents migrateurs contrairement au contingent résident. Les déplacements des jeunes de l'année seront propices à la découverte de nouveaux milieux très productifs et riches en ressources (Kerr et Secor 2009, Chapman *et al.* 2011, Brodersen *et al.* 2014).

CHAPITRE I

IS THE NEWLY REINTRODUCED POPULATION OF STRIPED BASS (*MORONE SAXATILIS*) IN THE ST. LAWRENCE ESTUARY USING THE FULL POTENTIAL OF ITS DIVERSE HABITATS?

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Mingelbier, Pascal Sirois

1.1 Abstract

After being extirpated from the St. Lawrence estuary (SLE) in the 1960s, striped bass (*Morone saxatilis*) was reintroduced in 2002. By 2008, they were naturally reproducing in the estuary. To document the early life history of this new population, we characterized a wide gradient of estuarine habitats and their use by striped bass. From June to September 2014, 162 pelagic and 188 littoral stations were characterized in terms of biophysical conditions (turbidity, salinity, temperature, dissolved oxygen and chlorophyll-a concentration), abundance of main prey, and fish assemblages. In the pelagic and littoral zones, four estuarine habitats were defined based on turbidity and salinity: an upstream freshwater section (UP), an oligohaline (O-ETM) and a mesohaline (M-ETM) estuarine turbidity maximum zone, and a downstream polyhaline section (DOWN). Our study revealed that the re-established population of striped bass of the St. Lawrence River is using the wide spectrum of contrasting habitats available along the estuary. At the onset of striped bass development, the O-ETM and

the UP were the main nursery habitats. The O-ETM provided the most suitable conditions for the species with optimal physical properties and abundant food resources. Later in the season, the M-ETM provided a favourable trade-off habitat for striped bass offering a less optimal physical environment although new feeding opportunities. After July, striped bass dispersed further downstream, creating a spatial partitioning of estuarine habitats, potentially to reduce inter- and intra-specific competition and to search for new foraging opportunities.

Keywords: Striped bass • Estuarine habitats • Pelagic zone • Littoral zone • Fish assemblage

1.2 Introduction

Characterized by a salinity gradient, estuaries are composed of unique habitats, each having specific biophysical features and each inhabited by species having varying levels of physical tolerance and needs (Martino and Able 2003, McLusky and Elliott 2004, Elliott *et al.* 2007, Potter *et al.* 2015). Determining the appropriate factors and, therefore, boundaries that define fish habitats remains, however, under standardized and uncertain (Peters and Cross 1992, Able 1999, Peterson *et al.* 2000). According to Hall *et al.* (1997), a habitat is defined as “the resources and conditions present in an area that produce occupancy-including survival and reproduction by a given organism.” At the population level, the concept of habitat encompasses functional requirements, such as spawning activities, nursery sites, feeding sites, overwintering areas, and migration corridors; thus, a strong knowledge of fish community needs and dynamics is essential for conservation efforts (Hall *et al.* 1997, Dennis *et al.* 2003). The distribution of a fish species among estuarine habitats is affected by its suitability in terms of physical environment, predation pressure, food availability, and

competition (Holbrook and Schmitt 1989, Lankford and Targett 1994, Robertson 1996, Johnson *et al.* 2012).

The estuarine turbidity maximum (ETM) is recognized as an important nursery habitat for many fish species (Sirois and Dodson 2000-a, North and Houde 2003, Winkler *et al.* 2003). Early life stages of fishes retained in the ETM region take advantage of (1) an effective visual refuge from predators due to the marked turbidity (Miner and Stein 1996, Abrahams and Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003), (2) a high zooplankton biomass and productivity (North and Houde 2003, Winkler *et al.* 2003, Lapierre and Frenette 2008), and (3) optimal salinity and temperature conditions for development (Uphoff Jr 1989, Rutherford *et al.* 1997, Secor *et al.* 2000). In the St. Lawrence estuary, the high zooplankton biomass of the ETM (Bousfield *et al.* 1973, Winkler *et al.* 2003) supports the early life stages of estuarine species, including striped bass (Morissette *et al.* 2016, Valiquette *et al.* 2017).

Striped bass disappeared from the St. Lawrence estuary in the 1960s due to overfishing, environmental pollution, and habitat destruction (Robitaille *et al.* 2011). Since 2002, the Quebec Ministry of Forests, Wildlife, and Parks conducted a reintroduction program of this species by stocking more than 34.5 million striped bass larvae and juveniles in the St. Lawrence estuary (Valiquette *et al.* 2017, Fisheries and Oceans Canada 2017). This new population has shown signs of a prompt re-establishment, and natural reproduction was confirmed in 2008 (Valiquette *et al.* 2017). Presently, the re-established population of striped bass is known to spawn at the mouth of Rivière du Sud and possibly near to the harbour of the city of Québec (Fisheries and Oceans Canada 2017, Valiquette *et al.* 2017). During the first growing season, striped bass early life stages gradually migrate from the pelagic zone to littoral habitats a few weeks after hatching (Robichaud-Leblanc *et al.* 1998). As early as the middle of their first growing season, striped bass exhibit a second downstream migration in the St.

Lawrence estuary (Morrisette *et al.* 2017). In the St. Lawrence estuary, the pelagic zone used by striped bass larvae has been well described (Laprise and Dodson 1994, Winkler *et al.* 2003, Favier and Winkler 2014, Cabrol *et al.* 2015), whereas the littoral habitats remain uncharacterized along the salinity gradient. Improving baseline knowledge of the use of pelagic and littoral habitats by striped bass larvae and juveniles in the St. Lawrence estuary will provide insights into the most favourable conditions for early life survival and recruitment, factors that are essential for ensuring a successful re-establishment of the population (Robitaille *et al.* 2011, COSEWIC 2012, Fisheries and Oceans Canada 2017).

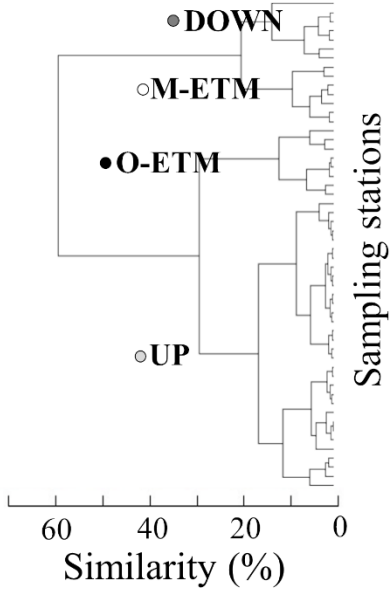
This present study aims to describe the pelagic and littoral habitats in the St. Lawrence estuary and to document their use by striped bass larvae and juveniles. We have placed particular emphasis on describing littoral habitats in the estuary, which have never been documented in the literature. From June to September 2014, we investigated the spatio-temporal distribution of striped bass across the estuary. Fish habitats were characterized in terms of biophysical conditions (turbidity, salinity, temperature, dissolved oxygen and chlorophyll-a concentration), abundances of main preys and fish assemblages (early life stages). We analyzed all these characteristics in order to geographically delineate the most contrasting habitats and to evaluate their potential for fish survival and recruitment.

1.3 Methods

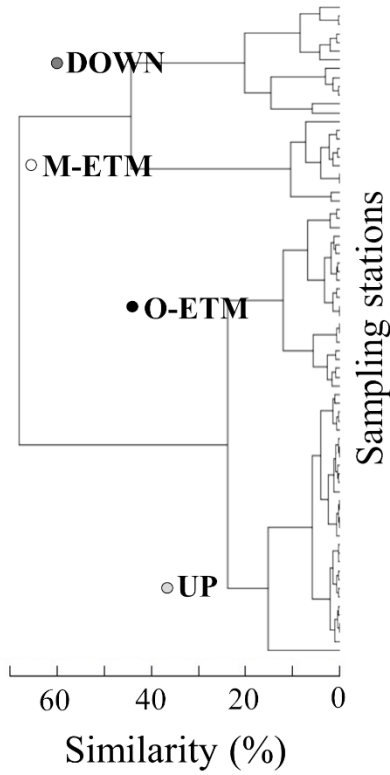
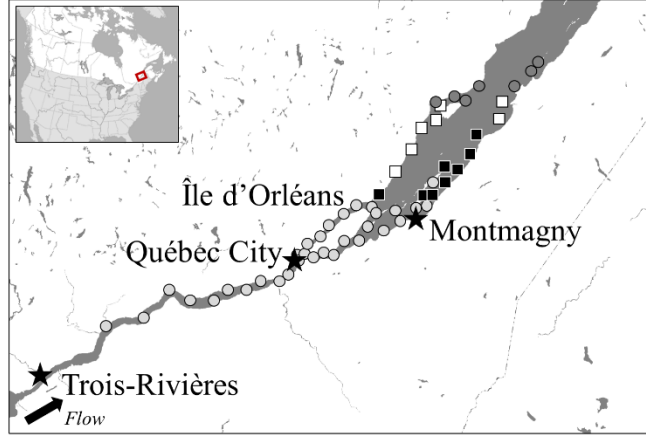
1.3.1 Study site

The fluvial (freshwater) and middle (brackish) sections of the St. Lawrence estuary stretch from Trois-Rivières (130 -km upstream of the Quebec City) to Tadoussac (230 -km downstream of Quebec City, Fig. 1.1). These two sections of the estuary

encompass a wide salinity range of 0–25 PSU. Mean annual water discharge is on the order of $12\,600\text{ m}^3\cdot\text{s}^{-1}$ (St. Lawrence Centre 1996). The estuarine circulation is primarily controlled by semi-diurnal tides with a range of 3–5 m in amplitude, and secondarily by neap and spring tide (semi lunar 14 d; Simons *et al.* 2010). The saline front is located at the eastern tip of Île d’Orléans and marks the upstream limit of the ETM. Shallow bathymetry, estuarine circulation, tides, and the contact of fresh and salt water produce high concentrations of suspended matter in the water column. Depending on river discharge, the ETM can vary 70–120 km in length (Silverberg and Sundby 1979). Large variations in salinity and turbidity result in a vast range of physicochemical conditions that support various planktonic and nektonic communities (Laprise and Dodson 1994, Winkler *et al.* 2003).



(a) June



(b) September

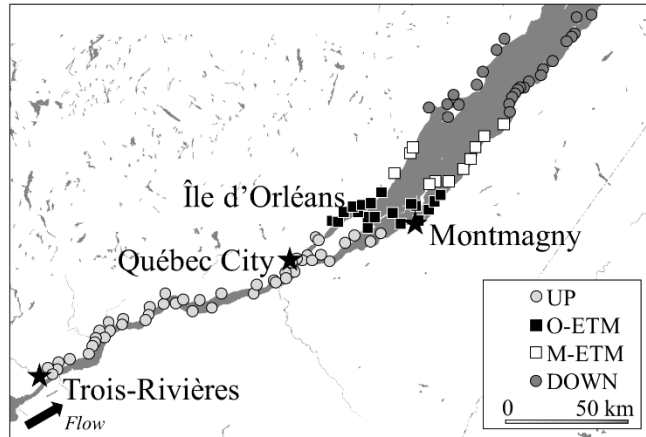


Figure 1.1 Cluster analysis dendrogram, based on measured turbidity and salinity, and locations of stations for (a) the first 54 stations sampled in June and (b) the 101 stations sampled in September 2014. In July and August, the littoral stations were similar to the September stations, except that only half of them were sampled.

1.3.2 Field surveys

In 2014, striped bass larvae and juveniles were collected in the fluvial and middle estuary portions of the St. Lawrence estuary over the course of three pelagic surveys (4–8 June, 12–17 June, and 21–28 June) and three littoral surveys (7–16 July, 8–12 August, and 8–22 September). In June 2014, we used bongo nets having a 0.5 m diameter opening during the pelagic surveys. The bongo frame was equipped with two different mesh size nets: a 333 μm and a 158 μm mesh size to collect fish larvae and zooplankton, respectively. We undertook oblique tows lasting 10 min in the surface layer (0–5 m). General Oceanics flowmeters registered the filtered water volume, on average $371.2 \pm 5.0 \cdot \text{m}^3$. During the pelagic survey, 54 shallow stations were sampled three times at a 5 m depth from the upstream (freshwater) to the downstream (mesohaline) sections of the estuary (Fig. 1.1, Table 1.1). Collected samples were immediately fixed in 95% ethanol that was changed after 24 h to avoid dilution.

A few weeks after hatching, pelagic striped bass larvae migrate to littoral habitats (Robichaud-Leblanc *et al.* 1998). Therefore, in July, August, and September 2014, only littoral surveys were carried out to sample fish and invertebrate communities (Table 1.1). In July, we sampled 43 stations using a beach seine measuring 12.5 m long, 4 m deep, and having a mesh size of 3.2 mm. In August and September, the surveys relied on a second beach seine that was 15 m long, 1.8 m deep, and having a mesh size of 9.5 mm for the wings and 6.3 mm for the central pocket. In August, we sampled 44 littoral

stations, and in September, we sampled 101 littoral stations (Table 1.1, Fig. 1.1). To collect invertebrates, we used a seine net—4 m long, 1 m deep, having a 500 μm mesh and equipped with a bucket (Table 1.1). Invertebrates were sampled by standardized 15 m transects running against the current. All littoral samples were immediately frozen in the field on dry ice and then transferred into containers filled with 95% ethanol in the lab. The ethanol in the containers was changed after 24 h. For pelagic and littoral surveys, a CTD probe (SBE19, Sea-Bird Electronics, Inc.) recorded the turbidity, salinity, temperature, dissolved oxygen, and fluorescence. In addition, we collected 55 water samples in brown Nalgene bottles at 0.5 m to quantify chlorophyll-a concentrations for calibrating the CTD fluorescence measurements. During the littoral surveys, the vegetation cover of each station was visually classified into one of five categories: 1: absent, 2: < 25%, 3: 25–50%, 4: 51–75%, 5: > 75% coverage. Similarly, the granulometry was categorized as clay and silt (< 0.125 mm), sand (0.125–5 mm), gravel (6–40 mm), or pebbles and rock (> 40 mm) by visual inspections on the field.

Table 1.1 Summary of the pelagic and littoral surveys carried out in the St. Lawrence estuary from June to September 2014

	June	July	August	September
Zone	Pelagic	Littoral	Littoral	Littoral
Fish surveys				
Dates	4–28	7–16	8–12	8–22
Number of stations	162	43	44	101
-Sampling gear	Bongo net	Beach seine	Beach seine	Beach seine
-Mesh size	333 μm	3.2 mm	9.5 mm	9.5 mm
Invertebrate surveys				
Dates	4–8	7–16	8–12	8–22
Number of stations	20	25	22	22
-Sampling gear	Bongo net	Seine net	Seine net	Seine net
-Mesh size	158 μm	500 μm	500 μm	500 μm
CTD probe surveys				
Dates	4–28	7–16	8–12	8–18
Number of stations	161	42	44	77

1.3.3 Laboratory analyses

1.3.3.1 Fish identification

All larvae and juvenile fish were sorted from the pelagic ($n = 13,857$ fish) and littoral sites ($n = 15,609$ fish). Individuals were firstly identified using morphological criteria and measured under a stereomicroscope Leica, MZ 12.5 (Pearson, 1938, Auer 1982, Waldman *et al.* 1999). To ensure accurate identifications, we performed genetic analyses on striped bass larvae because they co-occurred with white perch (*Morone americana*), a congener species which is morphologically very similar during early life stages. We used mitochondrial DNA sequence data from 216 striped bass larvae and 48 white perch (total of 264 fish). To discriminate the two species, we selected the cytochrome oxidase b gene (CYTb). DNA was extracted from muscle tissues and then stored in 95% ethanol using the DNEasy Tissue kit (Qiagen) protocol. We amplified ~350 pb through polymerase chain reaction (PCR) using the primers Morocytb836r and Morocytb484f (Kearse *et al.* 2012). Amplification success was verified by electrophoresis on a 1.5 % agarose gel with GelRed solution and loading blue dye. PCR products were sent to the Genome Sequencing and Genotyping Platform in Quebec City for sequencing. Sequences were verified and aligned using MEGA5 (Tamura *et al.* 2011) and BIOEDIT v. 7.2.5 (Hall 1999). Sequences were then compared to those of the GenBank database using BLAST procedures to assign these to either striped bass or white perch (Orrell *et al.* 2002). Of the 264 fish selected for genotyping, 118 striped bass larvae were confirmed via genetic analysis from which 100 were correctly identified only using morphological characteristics, while the other 18 samples corresponded to misidentified white perch larvae.

1.3.3.2 Invertebrate identification

From June to September 2014, we identified invertebrates within a subsample of 91 stations (Table 1.1). Invertebrate samples were divided into size classes using a 6.3 mm sieve for the largest size fraction, a 1000 μm sieve retaining the middle-sized fraction, and a small size fraction (158–1000 μm for pelagic habitats, 500–1000 μm for littoral habitats). The entire large fraction was analysed. The middle and small size fractions were subsampled to identify at least a hundred individuals. Invertebrates were then identified to the lowest taxonomic level using several identification keys. We used a Leica MZ 12.5 stereomicroscope for observing the samples (Edmondson 1959, Préfontaine and Brunel 1962, Vidal 1971, Pennak 1978, Smith and Fernando 1978, Merritt and Cummins 1996, Brunel *et al.* 1998).

1.3.3.3 Chlorophyll-*a* concentration

Chlorophyll-*a* (chl-*a*) concentrations provide an effective measurement of the algal biomass (Steinman *et al.* 1996). For 55 stations, 250 mL surface water samples (0.5 m depth) were filtered into two technical replicates through GF/F filters (47 mm diameter), immediately frozen on dry ice in the field, and then stored at -60 °C until analysis. Chl-*a* was extracted following Musch (1980) and Jeffrey and Welschmeyer (1997). We measured chl-*a* by fluorescence with a mass spectrophotometer coupled to Cary Win UV software. These measurements of chl-*a* were used to calculate a calibration curve ($n = 55$, $R^2 = 0.73$) and to estimate chl-*a* for each station from the CTD fluorescence probe data:

$$\log(\text{chl-}a) = 0.6405 \times \ln(\text{Fluo}) + 0.7019$$

where chl-*a* is the chlorophyll-*a* concentration in $\mu\text{g}\cdot\text{L}^{-1}$ and Fluo is the fluorescence measurements in $\mu\text{g}\cdot\text{L}^{-1}$.

1.3.4 Data analysis

1.3.4.1 Habitat identification

For each survey, we conducted cluster analyses in order to group the sampling stations in distinct and geographically types of habitats. The analyses were based on a log-10 transformed salinity, the square root of turbidity, and by using the average linkage method with Euclidean distance coefficients (McGarigal *et al.* 2000, Borcard *et al.* 2011). Results enabled assigning each sampling station to one specific habitats. For stations with missing or outlier data, a habitat was designated according to a geographical consistency (McGarigal *et al.* 2000, Borcard *et al.* 2011). Cluster analyses were performed using R software v.3.5.0 (R Core Team 2018) running the vegan (Oksanen *et al.* 2018), the cluster (Maechler *et al.* 2018), and the glcus (Hurley 2012) packages.

1.3.4.2 Fish abundance

In the pelagic zone, the density of fish larvae at each station was expressed as $\text{ind}\cdot\text{m}^{-3}$ as the number of larvae per volume of water filtered. To estimate the density of striped bass larvae, we used rates of accurate striped bass and white perch identification using morphological criteria and confirmed through genetic analysis. The density of striped bass was expressed as $\text{ind}\cdot\text{m}^{-3}$ using:

$$\frac{(Nbr_{genetic}) + (Nbr_{striped\ bass,morpho} \times Success) + (Nbr_{white\ perch,morpho} \times (1 - Success))}{Vol}$$

where $Nbr_{genetic}$ is the number of striped bass larvae identified through genetic analysis, Nbr_{morpho} is the number of larvae identified exclusively using morphological criteria, $Success$ is the rate of accurate striped bass identification, $(1-Success)$ represents the rate of misidentification of white perch, and Vol is the volume of water filtered. $Success$ and $(1-Success)$ were estimated for each estuarine habitat. In the littoral zone, the abundance of fish was expressed as the number of individuals sampled per beach seine effort (catch per unit effort: CPUE).

1.3.4.3 Invertebrate abundance

In the pelagic and littoral zones, the abundance of invertebrates was expressed as density in $\text{ind}\cdot\text{m}^{-3}$ and abundance in $\text{ind}\cdot\text{m}^{-2}$, respectively. In the pelagic zone, we specifically examined the distribution of the cladoceran *Bosmina* sp., the calanoid copepod *Eurytemora affinis*, other calanoid copepods, and cyclopoid copepods, all of which are major components of the diet of striped bass larvae. (Robichaud-Leblanc *et al.* 1997, Shideler and Houde 2014). In the littoral zone, we examined the distribution of gammarids, mysids, and dipteran pupa, all important components of the diet of striped bass juveniles (Robichaud-Leblanc *et al.* 1997, Jordan *et al.* 2003, Walter *et al.* 2003, Howe *et al.* 2008).

1.3.4.4 Habitat comparisons

Once the habitats were clustered, biophysical features of habitats were compared between them using either analysis of variance (ANOVA test) followed by Tukey's HSD post-hoc tests or Kruskal-Wallis ANOVA of ranks, followed by a non-parametric multiple post-hoc tests (Dunn 1964); the choice depended on the normality of the

residuals (Quinn and Keough 2002). We used Pearson's Chi-squared tests to compare vegetation cover and granulometry between habitats. To compare fish assemblages among habitats, we used permutational analysis of variance separately for each month (i.e. one-way PERMANOVA) followed by pairwise multiple comparison tests. PERMANOVA was based on Bray-Curtis dissimilarities (Bray and Curtis 1957) and was performed using 999 permutations. The homogeneity of dispersion was verified following Anderson (2001). To document fish assemblages, we performed similarity percentage analyses (SIMPER) and identified the main taxa responsible for the dissimilarities between habitats (Clarke 1993). All statistical comparisons were performed using R software v.3.5.0 (R Core Team 2018) running the *vegan* package (Oksanen *et al.* 2018).

1.4 Results

1.4.1 Habitat clustering

For each survey, clustered analyses identified four groups of stations in the pelagic and littoral zones as four distinct habitats. They corresponded to: (1) the fluvial estuary in the upstream freshwater section (UP), (2) the oligohaline ETM habitat (O-ETM), (3) the mesohaline-ETM habitat (M-ETM), and (4) the downstream polyhaline section (DOWN; Fig 1). These four estuarine habitats, geographical consistend along the salinity-turbidity gradient, were systematically used for comparisons of physical and biological characteristics.

1.4.2 Striped bass distribution among the four habitats

In June, pelagic larvae were found primarily in the O-ETM habitat (0.214 ± 0.074 ind·m⁻³; mean \pm SE; note that for all results, we present the mean \pm SE; Fig. 1.2a). Densities were low in the UP (0.004 ± 0.003 ind·m⁻³) and the M-ETM habitat (0.0003 ± 0.0003 ind·m⁻³), and no larvae were captured in the DOWN habitat. In July, the abundance of striped bass in the littoral zone was similar among all habitats, due to the high variability of abundance within the habitats (Fig. 1.2b). However, there was a decreasing trend in the mean abundance of striped bass, being more than 6 \times higher in the UP (20.48 ± 19.71 CPUE) compared to further downstream (Fig. 1.2b). In August, the abundance of striped bass was lower in the UP (0.43 ± 0.23 CPUE) compared to the O-ETM (3.00 ± 1.47 CPUE) and the M-ETM (3.56 ± 1.84 CPUE; Fig. 1.2b). No striped bass were captured in the DOWN habitat. In September, most striped bass were found in the O-ETM (1.16 ± 0.28 CPUE) and M-ETM (1.36 ± 0.51 CPUE); the UP (0.09 ± 0.04 CPUE) and DOWN habitats (0.68 ± 0.56 CPUE; Fig. 1.2b) had a marked lower abundance.

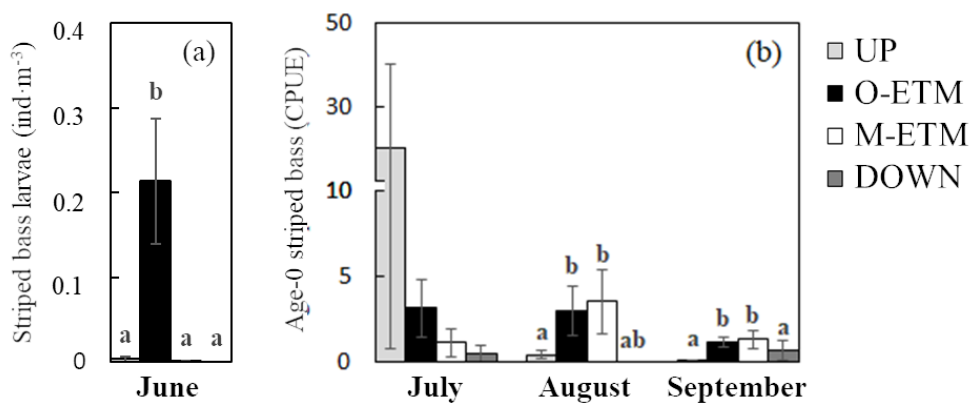


Figure 1.2 Abundance of striped bass among the four estuarine habitats (a) in the pelagic zone in June (ind·m⁻³), (b) in the littoral zone from July to September (CPUE).

Vertical lines represent standard errors. Different letters indicate significantly different mean values (Kruskal-Wallis ANOVA, followed by Dunn's test, $p < 0.025$)

Table 1.2 Statistical summary comparing striped bass distribution and abundance, biophysical features, and prey items between the four estuarine habitats from June to September 2014

Tested variable	Test	June				July				August				September			
		df	n	F	p	df	n	F	p	df	n	F	p	df	n	F	p
Striped bass	Kruskal-Wallis	3	162	112.32	<0.001	3	43	1.16	0.762	3	44	8.59	0.035	3	101	29.44	<0.001
Temperature	ANOVA	3	162	150.00	<0.001	3	43	51.07	<0.001	3	44	11.80	<0.001	3	79	27.57	<0.001
Dissolved oxygen	ANOVA	3	162	39.46	<0.001	3	43	4.66	0.007	3	44	13.24	<0.001	3	79	17.52	<0.001
Chl- <i>a</i>	ANOVA	3	162	1.47	0.225	3	43	9.51	<0.001	3	44	9.87	<0.001	3	79	10.52	<0.001
<i>Bosmina</i> sp.	Kruskal-Wallis	3	20	16.57	<0.001												
<i>E. affinis</i>	Kruskal-Wallis	3	20	5.42	0.143												
Other calanoids	Kruskal-Wallis	3	20	10.68	0.014												
Cyclopoids	Kruskal-Wallis	3	20	14.50	0.002												
Dipteran pupa	Kruskal-Wallis					2	23	0.81	0.667	2	20	5.27	0.072	3	19	8.97	0.030
Gammarids	Kruskal-Wallis					2	23	8.19	0.017	2	20	4.07	0.131	3	19	3.03	0.387
Mysids	Kruskal-Wallis					2	23	17.92	<0.001	2	20	7.76	0.021	3	19	14.81	0.002
Fish abundance	Kruskal-Wallis	3	162	47.97	<0.001	3	43	7.51	0.057	3	44	5.39	0.145	3	101	6.84	0.077
Composition of fish assemblage	PERMANOVA	3	162	15.01	<0.001	3	42	3.49	0.001	2	42	2.81	0.001	3	83	3.86	0.001

From July to September, vegetation cover in the littoral zone was not related to the distribution of striped bass (Table 1.3); however, striped bass inhabited more frequently stations having sand, gravel, pebbles, and rocks than stations having clay and silt substrate (Table 1.3).

Table 1.3 Comparison of (a) vegetation cover and stations having striped bass and (b) granulometry of littoral stations and striped bass presence. Chi-squared statistics are provided

Littoral zone	Number of stations	Stations with striped bass
(a) Vegetation cover		
Absent	114	37
<25%	48	18
25–50%	15	2
51–75%	7	2
>75%	4	0
Total	188	59
Chi-squared tests		
Chi-squared χ^2	5.0195	
Degrees of freedom (df)	4	
<i>p</i>	0.2853	
(b) Granulometry		
Clay and silt	58	27
Sand	72	53
Gravel	32	23
Pebble and rock	26	19
Total	188	122
Chi-squared tests		
Chi-squared χ^2	12.4156	
Degrees of freedom (df)	3	
<i>p</i>	0.0061	

1.4.3 Physical characteristics of the four habitats

In the pelagic zone, the UP habitat was characterized by low turbidity (12.52 ± 2.00 NTU) and freshwater conditions (Fig. 1.3a–b). In the UP, the temperature (18.11 ± 0.11 °C) was higher and the oxygen levels of the water were lower (8.19 ± 0.06 mg·L⁻¹) relative to the M-ETM and DOWN (Table 1.2; Fig. 1.3c–d). The O-ETM was marked

by having the highest turbidity values among the estuarine habitats (45.57 ± 4.08 NTU, Fig. 1.3a). In the O-ETM, values for salinity, temperature, and oxygen content were like those of the UP (Table 1.2; Fig. 1.3b–d). The M-ETM was characterized by a very high turbidity (26.04 ± 3.37 NTU) and by an increasing salinity (8.56 ± 0.99 PSU, Fig. 1.3a–b). In the M-ETM, temperature and the water oxygen levels were transitional between the upstream habitats and the DOWNS (Table 1.2; Fig. 1.3c–d). The DOWNS habitat was characterized by low turbidity water, similar to that of the UP, and the highest salinity values among the estuarine habitats (14.57 ± 0.99 PSU, Fig. 1.3a–b). In the DOWNS, the temperature dropped significantly by ca. 7°C , and the oxygen levels increased sharply (Table 1.2; Fig. 1.3d).

In the littoral zone, the UP was characterized by freshwater having a low turbidity, ranging from 5.20 to 13.17 NTU (Fig. 1.3a–b). This zone also had the highest recorded temperatures, ranging $19.45\text{--}24.24^\circ\text{C}$ (Table 1.2; Fig. 1.3c). The oxygen levels were low relative to habitats further downstream, ranging from $5.57\text{--}7.95\text{ mg}\cdot\text{L}^{-1}$ (Table 1.2; Fig. 1.3d). The O-ETM was characterized by high turbidity, $35.28\text{--}57.26$ NTU (Fig. 1.3a), whereas salinity, temperature and the oxygen levels were similar to the UP yet distinct from the more downstream habitats (Table 1.2; Fig. 1.3b–d). The M-ETM was marked by the highest turbidity values of the littoral habitats at > 57.01 NTU (Fig. 1.3a) and an increased salinity of $6.01\text{--}8.88$ PSU (Fig. 1.3b). The temperature and the dissolved oxygen values in the M-ETM were transitional between the higher temperature and lower oxygen waters of the upstream habitats and the colder, more oxygenated waters of the DOWNS (Fig. 1.3c). The DOWNS was distinguished from the other zones by its cold ($6\text{--}9^\circ\text{C}$), saline, well-oxygenated, and low turbidity waters (Fig. 1.3c-d).

In the littoral zone, vegetation cover was not related to the distribution of striped bass (Table 1.3); however, striped bass inhabited more frequently stations having sand, gravel, pebbles, and rocks than stations having clay and silt substrate (Table 1.3).

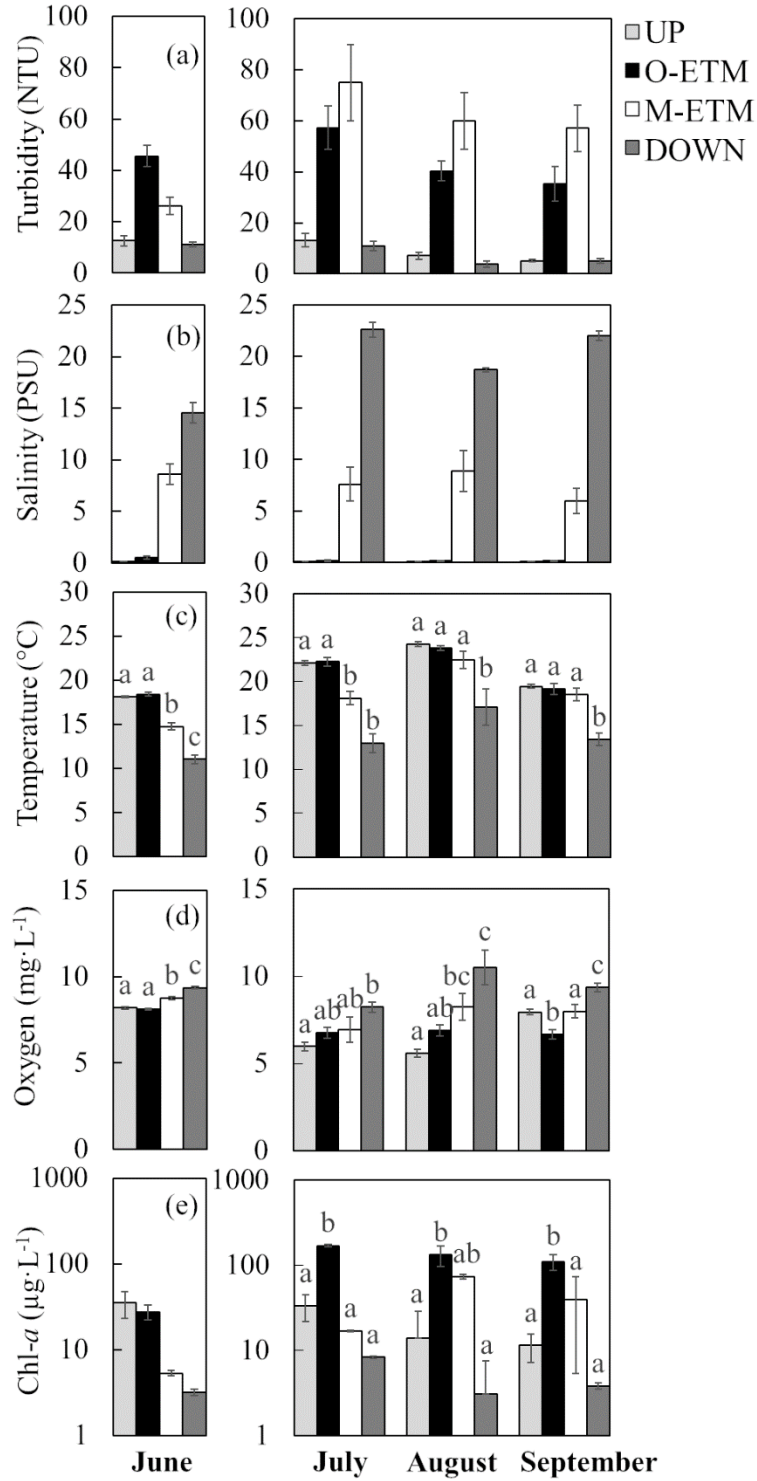


Figure 1.3 Habitat characteristics showing the mean values and standard errors of (a) turbidity, (b) salinity, (c) temperature, (d) dissolved oxygen, and (e) chl-*a* in June (pelagic zone), July, August, and September 2014 (littoral zone) in the St. Lawrence estuary. Different letters indicate mean values are significantly different (one-way ANOVA, followed by Tukey's HSD post-hoc tests). No statistical tests were performed for turbidity and salinity as they were used to determine the habitats in the cluster analysis

1.4.4 Biological characteristics of the four habitats

1.4.4.1 Distribution of chl-*a* and main prey items

In the pelagic zone habitats, chl-*a* fluctuated from 3.17 to 35.06 $\mu\text{g}\cdot\text{L}^{-1}$, exhibiting the highest values upstream in the UP and O-ETM and decreasing downstream, although the differences were not significant (Table 1.2; Fig. 1.3e). In June, *Bosmina* sp. were only found in the UP ($167.69 \pm 152.53 \text{ ind}\cdot\text{m}^{-3}$) and in the O-ETM ($480.08 \pm 287.70 \text{ ind}\cdot\text{m}^{-3}$, Table 1.2; Fig. 1.4a). *E. affinis* densities ranged from 0.40 to 16 $\text{ind}\cdot\text{m}^{-3}$ with a density 40× higher in the UP relative to the DOWN (Table 1.2; Fig. 1.4b). The opposite pattern was observed for calanoid copepods where their density was about 70× lower in the UP ($54.25 \pm 34.84 \text{ ind}\cdot\text{m}^{-3}$) compared to the DOWN ($3960.19 \pm 2451.01 \text{ ind}\cdot\text{m}^{-3}$; Table 1.2; Fig. 1.4c). The density of cyclopoids, 9.01–293.91 $\text{ind}\cdot\text{m}^{-3}$, was lowest in the DOWN with more similar levels found in the more upstream habitats (Table 1.2; Fig. 1.4d).

In the littoral zone, the O-ETM had the highest chl-*a* concentrations, 109.79–170.13 $\mu\text{g}\cdot\text{L}^{-1}$, whereas the chl-*a* did not exceed 33.51 $\mu\text{g}\cdot\text{L}^{-1}$ in either the UP or the DOWN (Table 1.2; Fig. 1.3e). The abundance of dipteran pupa did not exceed 0.75 $\text{ind}\cdot\text{m}^{-2}$ and

remained similar between habitats early in the season, then became greater in the M-ETM in September (Table 1.2; Fig. 1.4e). The abundance of gammarids, 0.14–20.26 ind·m⁻², was highest in the O-ETM, although the differences were only significant in July (Table 1.2; Fig. 1.4f). The abundance of mysids fluctuated from 0–14.12 ind.m⁻² and was highest in the M-ETM (Table 1.2; Fig.1.4g).

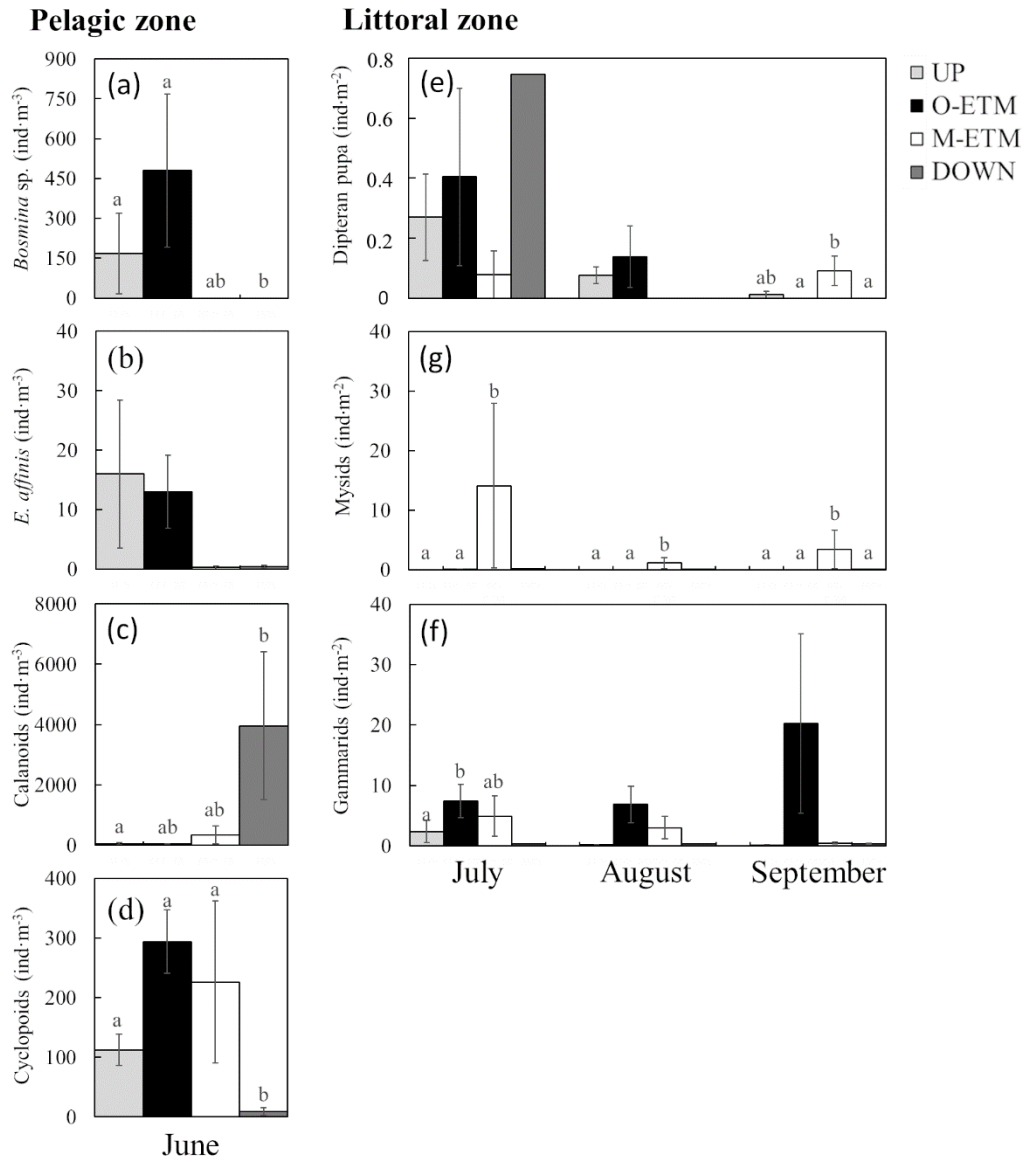


Figure 1.4 Abundance of invertebrates (ind·m⁻³ and ind·m⁻²) among the four estuarine habitats over the sampling season. Pelagic habitat mean abundance in June for (a) *Bosmina* sp., (b) *Eurytemora affinis*, (c) other calanoid copepods, and (d) cyclopoid copepods. Mean abundance in littoral habitats in July, August, and September for (g) dipteran pupa, (e) gammarids, and (f) mysids. Vertical lines represent standard errors.

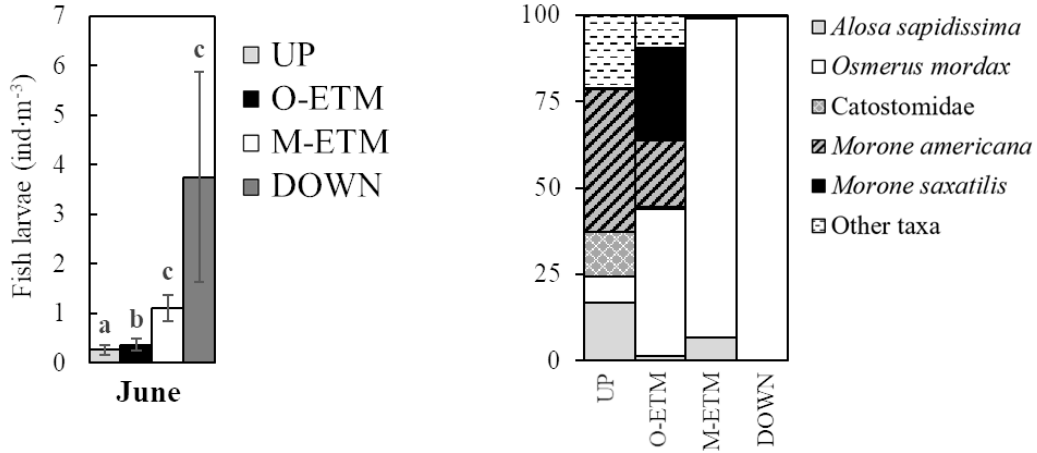
Different letters indicate mean values being significantly different (Kruskal-Wallis ANOVA, followed by Dunn's test, $p < 0.025$)

1.4.4.2 Early life stage assemblages of fishes of the four habitats

In the pelagic zone, the density of ichthyoplankton increased moving downstream from the UP (Table 1.2; Fig. 1.5a). In June, fish assemblages differed between habitats; white perch dominated the UP, rainbow smelt (*Osmerus mordax*), striped bass, and white perch dominated the O-ETM driven, and rainbow smelt dominated the fish assemblages at the two furthest downstream habitats (Tables 1.2 and 1.4, Fig. 1.4a).

In the littoral zone, the abundance of early life stage fish was similar between habitats (Table 1.2; Fig. 1.4b). In July, the UP and the O-ETM again had similar freshwater assemblages having a high abundance of yellow perch, American shad (*Alosa sapidissima*), and Catostomidae, although they also differed due to the presence of white perch (Tables 1.2 and 1.4, Fig. 1.4b). Both ETM habitats had a high abundance of white perch, and rainbow smelt was dominant in the DOWN (Table 1.4, Fig. 1.4b). In August, UP fish assemblages, composed mainly of American shad and Cataostomidae, differed from the O-ETM and M-ETM fish assemblages marked by more white perch (Tables 1.2 and 1.4; Fig. 1.4b). In September, we observed three distinct fish assemblages: (1) in the UP, driven by banded killifish (*Fundulus diaphanus*) and yellow perch, (2) in the O-ETM explained by high abundances of white perch and striped bass, and (3) in the DOWN dominated by rainbow smelt and blackspotted stickleback (*Gasterosteus wheatlandi*; Tables 1.2 and 1.4; Fig. 1.4b).

Pelagic zone (a)



Littoral zone (b)

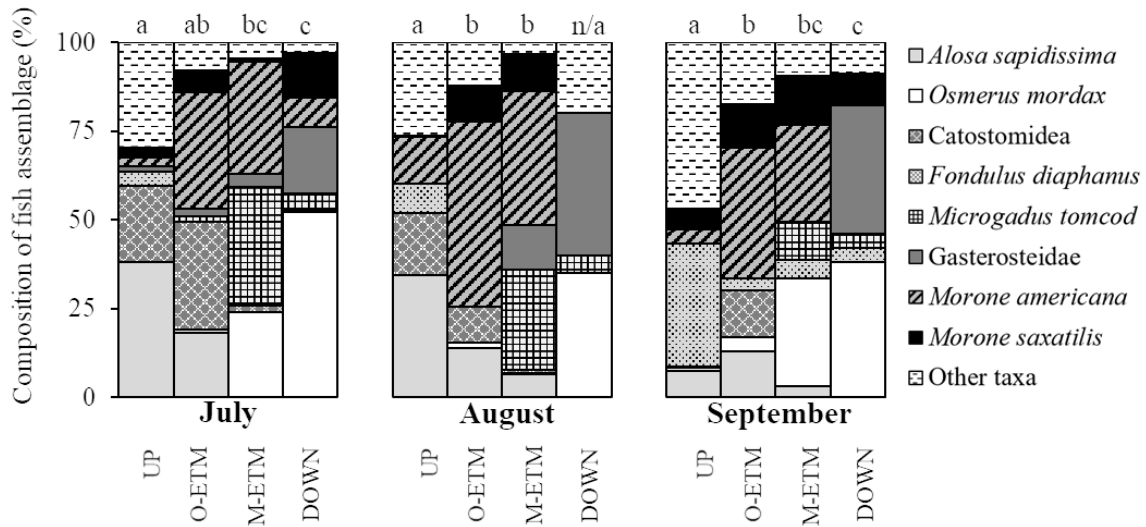
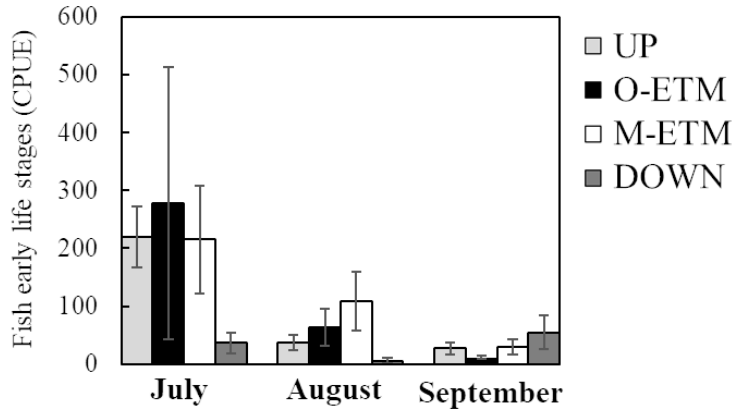


Figure 1.5 Abundances ($\text{ind}\cdot\text{m}^{-3}$ and CPUE) and assemblage composition of early life stage fish between the four estuarine habitats (a) in the pelagic and (b) littoral zones. Vertical lines represent standard errors. Different letters indicate significant differences in abundance (Kruskal-Wallis ANOVA, followed by Dunn's test, $p < 0.025$) and fish assemblage composition (PERMANOVA, followed by pairwise multiple comparison tests)

Table 1.4 Results of SIMPER analysis. Most important taxa contributing to the between-habitat dissimilarity from June to September 2014 as expressed in %. The taxa contributing > 50% of the total dissimilarity are shown in bold.

		Fish taxon									
		Clupeidae	Osmeridae	Cyprinidae	Catostomidae	Fundulidae	Gadidae	Atherinidae	Gasterosteidae	Moronidae	Percidae
		<i>P. aqj.</i>	<i>A. sapidissima</i>	<i>O. mordax</i>	<i>F. diaphanus</i>	<i>M. tomcod</i>	<i>G. aculeatus</i>	<i>G. wheatlandi</i>	<i>M. americana</i>	<i>M. saxatilis</i>	<i>P. flavescens</i>
Pelagic zone											
June											
UFS	O-ETM	0.006	33						23	23	
UFS	M-ETM	0.006	78								
UFS	DPS	0.006	82								
O-ETM	M-ETM	0.006	70							14	
O-ETM	DPS	0.006	73								
	M-ETM	DPS	1								
Littoral zone											
July											
UFS	O-ETM	0.03				11			19		10
UFS	M-ETM	0.006	24								13
UFS	DPS	0.006	31		13						
O-ETM	M-ETM	0.012									
O-ETM	DPS	0.006	12		14				21		
	M-ETM	DPS	0.846								
August											
UFS	O-ETM	0.006	16		15				40		
UFS	M-ETM	0.003	16	7	11	17			24		
	O-ETM	M-ETM	0.027								
September											
UFS	O-ETM	0.006	7		5		4		22	6	4
UFS	M-ETM	0.006	24		20	6			13	7	4
UFS	DPS	0.006	21		21		3		17	5	4
O-ETM	M-ETM	0.594									
O-ETM	DPS	0.006	23						17	21	9
	M-ETM	DPS	0.090								

1.5.1 Pelagic habitat characteristics

The biophysical characterization of estuarine habitats in the pelagic zone matched findings from the existing literature (Laprise and Dodson 1994, Centre du Saint-Laurent 1996, Winkler *et al.* 2003). The UP was characterized by freshwater having low turbidity, higher temperatures, and reduced oxygen levels compared to habitats further downstream habitats. The O-ETM was comparable to the UP, differentiated from it by the very turbid water conditions in the O-ETM. The M-ETM was also marked by a high turbidity; however, it differed from the upstream habitats by colder and more oxygenated mesohaline waters. The DOWN was marked by clearer, polyhaline waters of having lower temperatures and a higher dissolved oxygen content. Elevated chl-*a* concentrations in the UP and O-ETM reflect a probability that high-quality food may be more available to selective grazers, such as the cladoceran *Bosmina* sp. (DeMott 1982) and the copepod *E. affinis* (Peitsch 1995, Tackx *et al.* 1995, 2003) than in downstream habitats. Our results agree with previous studies showing that the high phytoplankton biomass occurred in the well-mixed, low salinity region upstream of the salt front, i.e., the O-ETM as defined in our study (Winkler *et al.* 2003, Martineau *et al.* 2004, Favier and Winkler, 2014, Cabrol *et al.* 2015). In the St. Lawrence estuary, the decline of chlorophyll *a* at the leading edge of the ETM is likely to be caused by zooplankton grazers (Vincent *et al.* 1996) as phytoplankton is a more nutritious food compared to detritus and bacteria (Mauchline 1996, Lehman 2000). The UP and the O-ETM supported high densities of cladocerans *Bosmina* sp., calanoids, *E. affinis*, and cyclopoids, whereas only cyclopoids were found in the M-ETM, and a very high density of calanoids was observed in the DOWN. Winkler *et al.* (2003) had observed a comparable abundance for *Bosmina* sp. and cyclopoids in late June; however, they noted a much greater abundance of *E. affinis*—about 1000 times higher

than our observations—in the O-ETM habitat. We suspect that in early June 2014, at the time of zooplankton sampling, the bloom of *E. affinis* in the O-ETM had not (yet) occurred. In contrast, ichthyoplankton density was lower in the UP and O-ETM, habitats where the fish assemblages were dominated by white perch and striped bass, respectively. In further downstream habitats, rainbow smelt was the most abundant species of the larval fish assemblages. In the St. Lawrence estuary, only a single study has reported white perch in the O-ETM (Dodson *et al.* 1989). Until recently, white perch was known to occur in the estuary, but its contribution to fish assemblages was insignificant. Our results suggest, however, that the population of white perch has expanded, and that the UP and the O-ETM may provide a nursery habitat for white perch larvae. In the pelagic zone, rainbow smelt largely dominated the ichthyoplankton community (Dodson *et al.* 1989, Marquis 2013). The main spawning grounds of rainbow smelt are located in the DOWN habitat (Lecomte and Dodson 2004), again agreeing with our results, as we also found the highest density of smelt larvae in this habitat. In the pelagic zone, variable compositions of the ichthyoplankton assemblages among the different habitats may be viewed as a means of partitioning the estuary to minimize competition between species.

1.5.2 Littoral habitat characteristics

This study offers the first description of littoral habitats along the St. Lawrence estuary. The littoral patterns were similar to those of the pelagic habitats along the salinity gradient. The littoral UP was distinguished by its warm, low oxygen, low turbidity freshwater. The littoral O-ETM habitat is very similar to the UP in terms of salinity, temperature, and dissolved oxygen; however, the O-ETM is marked by very turbid water. In the M-ETM, we observed a sharp increase in salinity and dissolved oxygen content, whereas temperatures decreased. In contrast to the pelagic zone, the M-ETM the most turbid habitat for the littoral zones and more comparable to upstream habitats

for temperature and dissolved oxygen features. Finally, the DOWNS was distinguished from the other zones by the highest salinity values, low turbidity, cold, and much oxygenated waters. In the littoral zone, elevated chl-*a* concentrations were primarily measured in the O-ETM and secondarily in the M-ETM. Along the littoral, both phytoplankton, benthic macroalgae and periphyton may contribute to the total chl-*a* concentration (Martineau *et al.* 2014), explaining differences with the pelagic zone.

In the littoral zone, the UP contained a low abundance of food resources, comprised mainly of gammarids and dipteran pupa. In contrast, the ETM habitats supported a higher abundance of prey items, represented by gammarids in the O-ETM and by both gammarids and mysids in the M-ETM. Prey abundance in the DOWNS littoral zone was lower than that of the littoral ETM.

Similar abundances of dipteran pupa were found across all habitats, although there was a distinct abundance peak in September in the M-ETM. These results are unexpected; insects are often associated with freshwater environments and avoid more saline waters (Merritt and Cummins 1996). We hypothesize that high-foraging pressure might have significantly reduced the abundance of dipteran pupa, especially in freshwater. We also suggest that freshwater flow may have dispersed dipteran pupa to more saline habitats along the littoral zones, explaining its distribution across all habitats.

Gammarids were mostly concentrated in the littoral O-ETM. In the pelagic zone, four species of gammarids co-occur in the middle estuary, known to be associated with the ETM (Dodson *et al.* 1989, Winkler *et al.* 2003). In the littoral zone, our results emphasized that, mysids, represented by *Neomysis americana* and *Mysis stenolepis*, were more abundant in the M-ETM habitat. Previous studies in the pelagic zone highlighted that mysids are more abundant downstream of the saline front, in weakly stratified waters having salinities from 0.5–6 PSU (Dodson *et al.* 1989, Winkler *et al.* 2003).

From July to September, the abundance of early life stage fish in the littoral zone was comparable between estuarine habitats. However, variability in the composition of fish assemblages may be a mechanism to partition the estuary and minimize interspecific competition. In July and August, two distinct fish assemblages co-occurred along the salinity gradient: (1) a freshwater assemblage driven by American shad, Catostomidae, and yellow perch, and (2) a more saline fish assemblage driven by white perch and rainbow smelt. In September, three different fish assemblages partitioned the estuary: (1) a freshwater assemblage driven by banded killifish and yellow perch, (2) an O-ETM–M-ETM fish assemblage dominated by striped bass and white perch, and a (3) M-ETM–DOWN fish assemblage mainly composed of rainbow smelt and blackspotted stickleback. Along the littoral zone, American shad is a dominant species of the UP (Robitaille *et al.* 2008, Maltais *et al.* 2010). A survey in July 2006, revealed the presence of two coastal areas having elevated concentrations of American shad juveniles in the fluvial estuary: (1) in the UP, about 150 km upstream of the salt front and (2) in the UP, upstream of the salt front (Robitaille *et al.* 2008, Maltais *et al.* 2010). In the littoral zone, the presence of white perch has been reported in recent years, suggesting that its population may be expanding (Valiquette *et al.* 2017). Our results emphasize the main contribution of white perch within the ETM fish assemblages and its important association with the distribution of striped bass. In more saline waters, fish assemblages were dominated by rainbow smelt. Along the southern shore, two large and coastal bays—St. Anne Bay (M-ETM) and nearby the city of Rivière-du-Loup (downstream of our study)—contribute to the passive retention of fish (D'Anglejan *et al.* 1981, St-Onge-Drouin *et al.* 2014). Concordant with our results, these two major retention areas are known to be used by early life stages of rainbow smelt (Lecomte 2005, Dodson *et al.* 2012).

1.5.3 Habitat use by striped bass larvae

In the pelagic zone, striped bass larvae were mostly found in the O-ETM. A lower density of larvae was found in the UP, and a very low amount was observed in the M-ETM, 60× and 330× lower, respectively, compared to the O-ETM. Currently, the re-established population of striped bass is known to spawn at the mouth of Rivière du Sud (O-ETM) and possibly near to the harbour of Quebec City (UP) (Fisheries and Oceans Canada 2017, Valiquette *et al.* 2017). In June, the distribution of striped bass reflected the location of the spawning grounds, despite larvae not having the swimming capacity to be retained in vicinity of the spawning grounds (Beamish 1978).

We hypothesized that the distribution of pelagic larvae is affected by the biophysical properties of habitats, such as turbidity. As turbid environments accentuate the visual contrast between coloured prey and the background environment, foraging conditions are improved for fish larvae feeding on highly pigmented preys (Boehlert and Morgan 1985, De Robertis *et al.* 2003). Higher turbidity may provide a visual shelter for translucent larvae of striped bass, reducing the risk from predation (Miner and Stein 1996, Abrahams and Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003), as we suspect occurs in the O-ETM. Sirois and Dodson (2000-b) suggested that larvae allocate more energy for growth in highly turbid conditions.

The salinity increases between the M-ETM and the DOWN may also negatively influence the distribution of striped bass by entailing significant physiological costs that are harmful to the development of larvae (Winger and Lasier 1994, Peterson *et al.* 1996). Temperature differences along the estuarine salinity gradient may also influence the distribution of striped bass; the temperature drop from 3.5 to 7°C in the M-ETM and DOWN habitats relative to the more upstream zones can also result in important physiological costs. East Coast populations of striped bass have an optimum temperature for development at 15–19 °C, while yolk sac larvae exposed to temperatures below 12 °C suffer high mortality (Dey 1981, Secor and Houde 1995,

Rutherford and Houde 1996, Limburg *et al.* 1999). Striped bass larvae are also quite sensitive to low-oxygen levels with a high mortality below $2.4 \text{ mg}\cdot\text{L}^{-1}$ (Hall 1991, cited in Secor and Houde 1995, Millet *et al.* 2002). However, dissolved oxygen levels within all estuarine habitats were never not restrictive for striped bass larvae.

As observed in other estuaries, the distribution of striped bass larvae appeared to be associated with the distribution of *Bosmina* sp. and *E. affinis*, taxa concentrated in the salt front and within the ETM (i.e., the UP and the O-ETM habitats) (Robichaud-Leblanc *et al.* 1997, Limburg *et al.* 1999, North and Houde 2006, Martino and Houde 2010, Campfield and Houde 2011, Shideler and Houde 2014). In the UP and O-ETM, striped bass larvae co-occur with white perch in habitats having a lower density of ichthyoplankton, and where interspecific competition may be reduced. Along the salinity gradient, we hypothesized that the specific use of estuarine habitats by striped bass is related to environmental preferences, prey item distribution, and reduced competition with other fish species.

1.5.4 Habitat use by striped bass juveniles

In July, striped bass larvae and juveniles dispersed along the estuary, becoming distributed among all littoral habitats. They were mainly concentrated at a single station located in the UP—at the mouth of Rivière du Sud, the major spawning ground of the species (Robitaille *et al.* 2011, Valiquette *et al.* 2017). Later in the season, striped bass occupied primarily the littoral O-ETM and M-ETM habitats. In the littoral zone, dispersal of striped bass may impact less the distribution of the species than for striped bass larvae in the pelagic zone, as the retention potential increases for older-stage fish due to their greater swimming capacity (Beamish 1978). As suspected in the pelagic zone, the distribution of striped bass within the littoral zone is likely related to the marked turbidity that reduces the risk of predation (Miner and Stein 1996, Abrahams and Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003) and improves energy

allocation to growth (Sirois and Dodson 2000-b). In the littoral zone, the UP and O-ETM provided more optimal conditions for development in terms of salinity (Secor *et al.* 2000, Hurst and Conover 2002) and temperature (Cox and Coutant 1981, Cech *et al.* 1984, Secor *et al.* 2000, Duston *et al.* 2004, Cook *et al.* 2010).

Several studies have also highlighted the important role of low-oxygen levels (below 4 mg·L⁻¹) on predatory activity and the escape behaviour of prey of striped bass juveniles (Breitburg *et al.* 1997, Brandt *et al.* 2009). Juveniles likely avoid low-oxygen waters below 3 mg·L⁻¹ (Coutant 1985, Miller *et al.* 2002). From July to September, oxygen levels being > 5.58 mg·L⁻¹ likely did not restrict striped bass distribution. In the littoral zone, striped bass distribution was not related to vegetation cover, dominated by Juncacea in the upstream part of the UFS, and by Gramineae and Cyperaceae further downstream. Our results suggested that the distribution of striped bass was associated with granulometry, avoiding stations having clay and silt substrates. However, at present we do not know if substrate has a direct effect on the distribution of striped bass or whether the effect is indirect via biological processes, such as prey availability or the presence/absence of other fish taxa.

In July, striped bass were concentrated in the UP habitat where food resources, composed mainly of gammarids and dipteran pupa, were at lower densities than found in the downstream habitats. From August, striped bass were mainly distributed in the O-ETM and M-ETM where they had access to greater amounts of food, composed primarily of gammarids in the O-ETM and mysids in the M-ETM. In the littoral zone, few striped bass were found in the DOWN where the abundance of prey was very low. Here, striped bass initially co-occurred within a freshwater fish assemblage, whereas later in the season, striped bass was found in a fish assemblage mainly composed of white perch and rainbow smelt. We hypothesized that striped bass, capable of exploiting all estuarine habitats, minimized interspecific competition by dispersing

throughout the estuary. Nonetheless, the distribution of white perch was strongly related to that of striped bass. White perch is a congener species used to share very comparable feeding niches to striped bass, and these two species may be competing for the same resources (Limburg *et al.* 1997, St-Hilaire *et al.* 2002). The increase in spatial coherence between the two species suggest potential for interspecific competition within the two ETM habitats.

1.6 Conclusion

Our study revealed that the re-established population of striped bass of the St. Lawrence River is using the wide spectrum of contrasting habitats available along the estuary. At the onset of striped bass development, the O-ETM and the UP were the main nursery habitats. Those habitats, located nearby the spawning grounds, exhibit optimal biophysical conditions, where pelagic larvae can find two main prey items, the cladoceran *Bosmina* sp. and the copepod *E. affinis*. As the growing season progressed, striped bass first inhabited the littoral habitats near the spawning grounds, where there were elevated abundances of gammarids. Thereafter, in August, striped bass dispersed further downstream and, by being distributed throughout the estuary, potentially reduced competition and favoured the discovery of new foraging opportunities. In the littoral zone, the O-ETM remained the most suitable habitat with optimal conditions for striped bass development. Later in the season, the M-ETM represented a favourable trade-off for striped bass to select new feeding opportunities, such as preying on mysids, although at an increased physiological cost due to mesohaline salinity and the colder temperatures. We hypothesized that intraspecific competition leads some juvenile striped bass to disperse toward the DOWN, in search of new feeding opportunities even though this habitat seems suboptimal for species development. In the coming decades, it is likely that climate changes will induce important changes in estuarine habitat features. With warming, the distribution of aquatic ecosystems will

change as species follow the shifting climate, especially in upper latitudes where the distribution of species is mainly related to temperature. For the new population of striped bass, the climate change may probably promote the advantage of downstream migration. Further investigations should be conducted on feeding ecology, growth, and mortality of striped bass along the salinity gradient of the St. Lawrence estuary, as these elements represent essential knowledge for ensuring the continued re-establishment of the striped bass population.

1.7 Acknowledgements

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CHAPITRE II

FEEDING ECOLOGY OF EARLY LIFE STAGES OF STRIPED BASS (*MORONE SAXATILIS*) ALONG AN ESTUARINE SALINITY-TURBIDITY GRADIENT, ST. LAWRENCE ESTUARY, CANADA

Lucie Vanalderweireldt, Pascal Sirois, Marc Mingelbier, Gesche Winkler

2.1 Abstract

After being extirpated from the St. Lawrence River in the 1960s, striped bass (*Morone saxatilis*) were reintroduced to the estuary in 2002 and by 2008, they were naturally reproducing. To document the habitat use and feeding ecology of this reintroduced population, we examined the gut contents of 332 larvae and juveniles. Samples were collected in four estuarine habitats in 2014: the upstream freshwater section (UP), the oligohaline (O-ETM) and the mesohaline (M-ETM) estuarine turbidity maximum zones, and the downstream polyhaline section (DOWN). In June, pelagic larvae developed in the UP and the O-ETM, feeding mainly on copepods such as *Eurytemora affinis*. The O-ETM exhibited better suitable feeding conditions compared to the UP, likely due to the presence of *Bosmina* sp. as a primary prey. After July, striped bass shifted to larger prey items, consuming mainly dipteran pupa in upstream littoral habitats and gammarids and mysids in downstream habitats. In the early summer, the UP provided a high-quality nursery habitat and as the season progressed, the smallest juveniles dispersed downstream and improved their feeding success by exploiting a

new feeding niche. This observation suggests that being distributed throughout the estuary may increase the potential survival of striped bass early life stages.

Keywords: Early life stages • *Morone saxatilis* • Habitat • Diet composition • Feeding success

2.2 Introduction

In fishery science, the main recruitment hypotheses assume that variability of year-class strength is controlled by early life history (Hjort 1914, Anderson 1988, Cushing, 1990). Among the mechanisms underlying recruitment, the physical and biological properties of a fish habitats affect the survival of early life stages. This influence occurs through feeding ecology (Hjort 1914, Chesney 1989, Cushing 1990, Shideler and Houde 2014), growth (Anderson 1988, Miller *et al.* 1988), and dispersion processes between habitats (North and Houde 2003, 2006, Martino and Houde 2010). Initial research centred on the critical period at the onset of larval feeding and its match-mismatch with zooplankton production (Hjort 1914, Cushing 1990). Other proposed hypotheses related to the feeding ecology of young stages relate generally to their indirect survival mediated through growth (Anderson 1988, Uphoff Jr, 1989, Martino *et al.* 2012) and size-dependent predation (Miller *et al.* 1988, Takasuka *et al.* 2003, 2007).

During early life history of fishes, the feeding ecology is exposed to wide spatio-temporal variation with shifts between different prey categories and sizes (Dower *et al.* 2008, Leclerc *et al.* 2011, Robert *et al.* 2014, Shideler and Houde 2014). Ontogenic changes in diet occur during early life stages, especially from the planktivorous larval stages to the juvenile stages (Robichaud-Leblanc *et al.* 1997, Scharf *et al.* 2000, Jordan *et al.* 2003). Feeding shifts directly relate to fish size and its biological environment, such as prey resource availability. In estuaries, prey community composition is influenced by dynamic environmental conditions marked

by high spatial and temporal fluctuations. Thus, food availability for early life stages is highly variable.

The St. Lawrence River (Canada), which connects the Great Lakes to the Atlantic Ocean, ends in a dynamical tidal freshwater estuary, followed by a brackish water section characterized by an estuarine turbidity maximum (ETM) and a strong salinity gradient. In general, ETMs provide an excellent nursery habitat for the early life stages of several fish species (Sirois and Dodson 2000-b, North and Houde 2003, Winkler *et al.* 2003). Early-staged fish within the ETM encounter a high zooplankton biomass and productivity (Roman *et al.* 2001, North and Houde 2003, Winkler *et al.* 2003, Lapierre and Frenette 2008) as well as optimal physical conditions for development (Uphoff Jr, 1989, Miner and Stein 1996, Abrahams and Kattenfeld 1997, Rutherford *et al.* 1997, Secor *et al.* 2000, Sirois and Dodson 2000-b). Along the St. Lawrence estuary, the coexistence of contrasting habitats having specific physical attributes shapes the distribution of invertebrates and fish early life stages (Laprise and Dodson 1994, Winkler *et al.* 2003, Vanalderweireldt *et al.* in prep-a). In the St. Lawrence fluvial and middle estuaries, four habitats were defined using salinity, turbidity and temperature as following: (1) the fluvial estuary in the upstream freshwater section (UP), with low turbidity, freshwater and the highest water temperatures; (2) the oligohaline ETM habitat (O-ETM) with high turbidity, low salinity and water temperatures still high; (3) the mesohaline-ETM habitat (M-ETM) with turbid, brackish, and colder temperature waters; and (4) the downstream polyhaline section (DOWN) with low turbidity, increasing salinity and the lowest temperatures (Vanalderweireldt *et al.* in prep-a). The St. Lawrence ETM supports a nursery habitat for estuarine species such as rainbow smelt (*Osmerus mordax*), Atlantic tomcod (*Microgadus tomcod*), white perch (*Morone americana*), and striped bass (*Morone saxatilis*; Laprise and Dodson 1990, 1994, Sirois and Dodson 2000-a, Winkler *et al.* 2003, Morissette *et al.* 2016, Vanalderweireldt *et al.* in prep-a).

Striped Bass is an anadromous species, widely distributed in North America from the Gulf of Mexico to the estuary and Gulf of the St. Lawrence (Vladykov and Wallace 1938, Scott and Crossman 1974). The St. Lawrence estuary sustains one of the most northern populations of striped bass along the eastern coast of North America. During the 1960s, the population disappeared due to overfishing, environmental pollution, and habitat destruction (Robitaille *et al.* 2011). Since 2002, a reintroduction program has led to the re-establishment of a new striped bass population able to reproduce since 2008 in the estuary (Fisheries and Oceans Canada 2017).

At the onset of striped bass development, semi-buoyant eggs and pelagic larvae are distributed near to the salt front in the upper ETM (North and Houde 2003, Valiquette *et al.* 2017). As the first growing season progresses, juvenile striped bass are found in littoral habitats. Several of these juvenile bass then move toward downstream estuarine habitats (Morissette *et al.* 2016, Valiquette *et al.* 2017, Vanalderweireldt *et al.* in prep-a). Even if the striped bass was previously present in the St. Lawrence estuary, its re-introduction raises questions in regard to its feeding ecology and habitat use (Fisheries and Oceans Canada 2017).

Given the interest for this recreational fish species and the contrasts found in fish habitats along the salinity-turbidity gradient of the St. Lawrence estuary, we examined several components of the feeding ecology of striped bass larvae and juveniles. Between June and September 2014, we sampled young striped bass in the four estuarine habitats to document the relationship between fish size and feeding characteristics. We then compared these estuarine habitats in terms of striped bass diet composition, feeding incidence, and feeding success. Finally, we characterized the feeding niches of striped bass larvae and juveniles and their overlap between the four estuarine habitats.

2.3 Methods

2.3.1 Study site

The fluvial (freshwater) and middle (brackish) sections of the St. Lawrence estuary stretch from Trois-Rivières (130 -km upstream of Quebec City) to Tadoussac (230 -km downstream of Quebec City, Fig. 2.1). These two sections of the estuary encompass a wide salinity range of 0–25 PSU. Mean annual water discharge is on the order of $12\,600\text{ m}^3\cdot\text{s}^{-1}$ (St. Lawrence Centre 1996). The estuarine circulation is primarily controlled by semi-diurnal tides with a range of 3–5 m in amplitude, and secondarily by neap and spring tide (semi lunar 14 d; Simons *et al.* 2010). The saline front is located at the eastern tip of Ile d’Orléans and marks the upstream limit of the ETM. Shallow bathymetry, estuarine circulation, tides, and the contact of fresh and salt water produce high concentrations of suspended matter in the water column. Depending on river discharge, the ETM can vary 70–120 km in length (Silverberg and Sundby 1979). Large variations in salinity and turbidity result in a vast range of physicochemical conditions that support various planktonic and nektonic communities (Laprise and Dodson 1994, Winkler *et al.* 2003, Vanalderweireldt *et al.* in prep-a).

2.3.2 Field survey

In 2014, early life stages of striped bass were collected across the salinity-turbidity gradient in the fluvial and middle portions of the St. Lawrence estuary during three pelagic surveys (4–8 June, 12–17 June, 21–28 June 2014) and three littoral surveys (7–16 July, 8–12 August, and 8–22 September 2014). In June, we sampled ichthyoplankton using bongo nets having a 0.5-m-diameter opening and a 333- μm mesh size. We conducted oblique tows of 10 min in the surface layer (0–5 m). General Oceanics flowmeters registered the filtered water volume, averaging $400.9 \pm 7.1\text{ m}^3$. During pelagic surveys, 54 stations located on the 5 m isobaths were sampled on three

occasions from the upstream freshwater to the downstream mesohaline section of the estuary (Fig 1). All sampled larvae were anesthetized using a clove solution mixed with 95% ethanol and water collected from the estuary (to prevent gut regurgitation). After collection, samples were immediately fixed in 95% ethanol. From July to September, we carried out three littoral surveys as striped bass undertake shoreward migration from pelagic to littoral habitats (Robichaud-Leblanc *et al.* 1998). In July, we used a beach seine (12.5-m-long, 3.2-mm mesh, towed at depths up to 4 m) at 43 stations. In August and September, the surveys used a beach seine (15-m-long, 9.5-mm mesh for the wings, 6.3-mm mesh in the central pocket, towed at depths up to 1.8 m). In total, 44 and 101 stations were sampled in August and September, respectively (Fig 1). In the field, all samples were immediately frozen with dry ice and then transferred into 95% ethanol. For pelagic and littoral surveys, a CTD probe (SBE19, Sea-Bird Electronics, Inc.) measured abiotic variables such as salinity, temperature and turbidity.

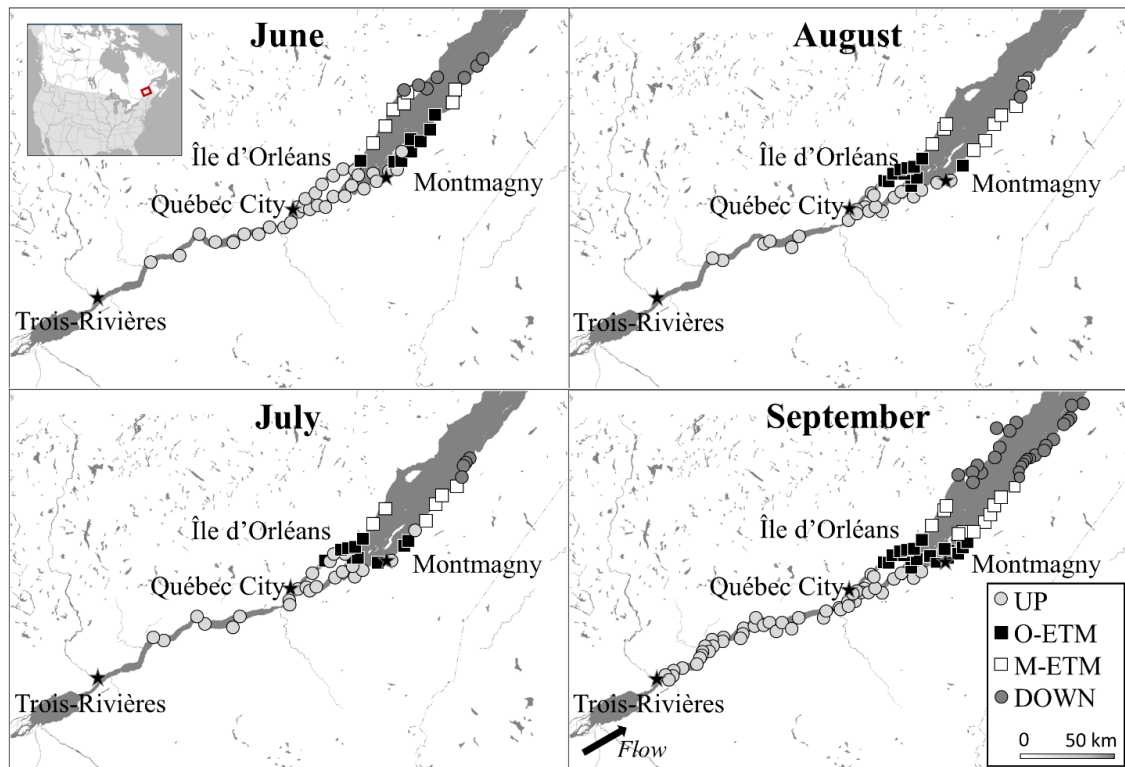


Figure 2.1 Stations for the pelagic (4–8 June) and littoral surveys (7–16 July, 8–12 August, and 8–22 September 2014). The four estuarine habitats correspond to light grey circles in the upstream freshwater section (UP), black squares in the oligohaline estuarine turbidity maximum habitat (O-ETM), white squares in the mesohaline-ETM (M-ETM), and dark-grey circles in the downstream polyhaline section (DOWN)

2.3.3 Laboratory analyses

2.3.3.1 Striped bass identification

All larvae and juvenile fish were sorted from the pelagic ($n = 13,857$ fish) and littoral sites ($n = 15,609$ fish). Individuals were firstly identified using morphological criteria and measured under a stereomicroscope Leica, MZ 12.5 (Pearson 1938, Auer 1982, Waldman *et al.* 1999). To ensure accurate identifications, we performed genetic analyses on striped bass larvae because they co-occurred with white perch (*Morone americana*), a congener species which is morphologically very similar during early life stages. We used mitochondrial DNA sequence data from 216 striped bass larvae and 48 white perch (total of 264 fish). To discriminate the two species, we selected the cytochrome oxidase b gene (CYTb). DNA was extracted from muscle tissues and then stored in 95% ethanol using the DNEasy Tissue kit (Qiagen) protocol. We amplified ~350 pb through polymerase chain reaction (PCR) using the primers Morocytb836r and Morocytb484f (Kearse *et al.* 2012). Amplification success was verified by electrophoresis on a 1.5 % agarose gel with GelRed solution and loading blue dye. PCR products were sent to the Genome Sequencing and Genotyping Platform in Quebec City for sequencing. Sequences were verified and aligned using MEGA5 (Tamura *et*

al. 2011) and BIOEDIT v. 7.2.5 (Hall 1999). Sequences were then compared to those of the GenBank database using BLAST procedures to assign these to either striped bass or white perch (Orrell *et al.* 2002). Of the 264 fish selected for genotyping, 118 striped bass larvae were confirmed via genetic analysis from which 100 were correctly identified only using morphological characteristics, while the other 18 samples corresponded to misidentified white perch larvae.

For pelagic surveys, the density of striped bass larvae at each station was estimated as:

$$\frac{(Nbr_{genetic}) + (Nbr_{morpho} \times Success) + (Nbr_{white\ perch,morpho} \times (1 - Success))}{Vol}$$

where density is expressed as ind·1000 m⁻³, $Nbr_{genetic}$ is the number of striped bass identified through genetic analysis, Nbr_{morpho} is the number of larvae identified exclusively using morphological criteria, $Success$ is the rate of accurate striped bass identification, $(1-Success)$ represents the rate of misidentification of white perch, and Vol is the volume of water filtered. $Success$ and $(1-Success)$ were estimated for each estuarine habitat. From July to September 2014, 647 striped bass were identified in the estuarine littoral habitat. For littoral surveys, the abundance of striped bass was expressed as the number of striped bass sampled per beach seine effort (catch per unit effort: CPUE).

2.3.3.2 Dietary composition of striped bass

To characterize diet composition, we dissected striped bass larvae and juveniles. Prey items collected from the digestive track in larvae or from the stomach in juveniles were identified, counted, dried, and weighed. When mass measurements were impossible, we estimated dry weights of prey (DW) using length–weight relationships found in the

literature (Table 2.1). We analysed a total of 332 gut contents (118 for June, 80 for July, 77 for August, and 57 for September 2014). For pelagic surveys, gut contents were only analysed for striped bass larvae confirmed by genetic analyses. For the July samples, we selected a subsample of 80 of 512 striped bass based on the proportion of length frequency. For the August and September samples, all identified striped bass were dissected for gut contents.

Table 2.1 Size range and biomass conversion equations for prey items measured in the gut contents of striped bass

Taxon	Size range (mm)	Biomass conversion (μg)	Source
<i>Bosmina</i> sp.	0.20 – 0.48	$DW = 10^{4.849 \text{ Log}(L) - 3.857} \times 10^5$	Rosen 1981
<i>Chydoridae</i>	2.42	$DW = 89.43 L^{3.93}$	Dumont <i>et al.</i> 1975
Copepod	0.36 – 0.64	$DW = 7.047 L^{2.399}$	Bottrell <i>et al.</i> 1976
Copepod		Mean DW = 1.51	This study
<i>Diacyclops thomasi</i>	1.21	$DW = 7.047 L^{2.399}$	Copepod conversion, Bottrell <i>et al.</i> 1976
<i>Bacillariophyta</i>	0.20	$DW = 0.47 V^{0.99}$	Reynolds 2006
<i>Eurytemora affinis</i> eggs		DW = 0.13	Heinle and Flemer 1975
<i>Eurytemora affinis</i>	0.54 – 0.72	$DW = 10^{2.088 L - 0.859}$	Burkill and Kendall 1982
<i>Eurytemora affinis</i>		Mean DW = 3.58	This study
Harpacticoid	0.39	$DW = 12.51 L^{4.40}$	Dumont <i>et al.</i> 1975

2.3.4 Data analyses

2.3.4.1 Diet characterization

We investigated feeding ecology using diet composition, feeding incidence, and feeding success, and we also assessed the overlap of feeding niches between habitats. To describe the diet of striped bass larvae and juveniles, we used the dry weights of prey and summarized our results by estimating the percent mass of each prey taxon. As such, percent mass is defined as the ratio between the dry weight of prey *i* and the total dry weight measured for all prey contained in the gut contents of each fish. Feeding incidence (FI) was calculated as the percentage of striped bass having at least one prey item in their gut contents. Feeding success (FS) was defined as the residual values of the linear regression of the dry weight of ingested prey ($\ln(DW+1)$) and striped bass

standard length (SL in mm) (modified from Michaud *et al.* 1996). As such, the estimated FS was calculated using a single regression equation that included all examined gut contents (Fig. 2.2):

$$\ln(DW + 1) = 0.039 \times SL + 0.2483$$

where DW is the dry weight of ingested prey (in mg) and SL is the standard length of striped bass (in mm).

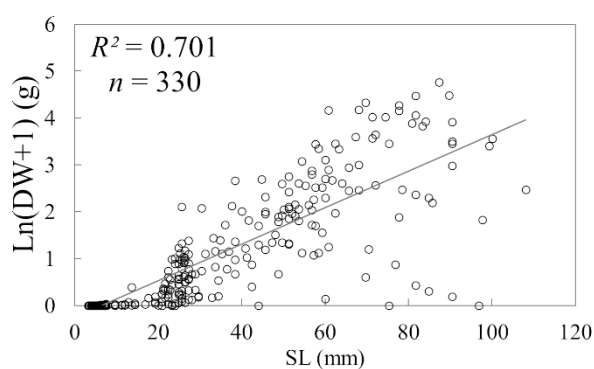


Figure 2.2 Relationship between the dry weight of ingested prey (DW) and the standard length (SL) of larvae and juveniles of striped bass

In addition, we assessed the overlap of the striped bass feeding niches between habitats using Schoener's index (D) (Schoener 1968):

$$D = 1 - 0.5(\sum | p_{ij} - p_{ik} |)$$

where p_{ij} and p_{ik} are the dry weight proportions of the prey i in the diet of striped bass from the habitat j and k , respectively. The Schoener's index range from 0 (no observed overlap) to 1 (complete overlap).

2.3.4.2 Statistical analyses

To compare striped bass diet between habitats, we used permutational analysis of variance, separately for each month (i.e. one-way PERMANOVA). PERMANOVA analyses were based on Bray-Curtis dissimilarities (Bray and Curtis 1957) and were performed using 999 permutations. The homogeneity of dispersion was verified following Anderson (2001) prior to each PERMANOVA. In the case of significant PERMANOVA results, pairwise multiple comparison tests identified the differences between habitats. To document these contrasts of diet composition between habitats, we performed similarity percentage analyses (SIMPER), and we identified the main taxa responsible for the dissimilarities (Clarke 1993). FI was compared among the four habitats using Pearson's Chi-square tests. We applied analyses of variance (one-way ANOVA tests) to test for differences of FS between habitats, followed by Tukey's HSD post-hoc tests. To comply ANOVA's requirements, residuals were inspected visually (Quinn and Keough 2002). All statistical analyses were performed with R software v.3.5.0 (R Core Team 2018) running the *vegan* package (Oksanen *et al.* 2018).

2.4 Results

2.4.1 Density and size distribution of striped bass

In June, striped bass larvae were mainly found in the O-ETM (0.214 ± 0.074 larvae $\cdot 1000 \text{ m}^{-3}$; mean \pm SE; note that for all density and CPUE results, we present the

mean \pm SE). Lowest densities were found in the UP (0.004 ± 0.003 larvae \cdot 1000 m⁻³) and the M-ETM (0.0003 ± 0.0003 larvae \cdot 1000 m⁻³). Most striped bass were 5–9 mm in length (Fig. 2.3).

In July, the highest abundance of striped bass at early life stages was in the UP (20.48 ± 19.71 CPUE). Abundance decreased toward the downstream habitats: the O-ETM (3.20 ± 1.69 CPUE), followed by the M-ETM (1.17 ± 0.83 CPUE), and finally the DOWN (0.5 ± 0.5 CPUE). Early life stages were larger in the UP (median size = 25–29 mm) and shorter in habitats further downstream (median size of 20–24 mm, and 10–14 mm in the O-ETM and M-ETM respectively; Fig. 2.3). Two large striped bass were also sampled in the DOWN (median size = 25–29 mm).

In August, the abundance of striped bass increased moving from the UP (0.43 ± 0.23 CPUE), to the O-ETM (3.00 ± 1.47 CPUE), and then the M-ETM (3.56 ± 1.84 CPUE). Striped bass were, however, larger in the UP (median size = 50–59 mm) than further downstream (median size of 45–49 mm and 40–44 mm in the O-ETM and M-ETM, respectively; Fig. 2.3).

In September, most striped bass were found in the O-ETM (1.16 ± 0.29 CPUE) and M-ETM (1.36 ± 0.51 CPUE), rather than the UP (0.09 ± 0.04 CPUE) and DOWN (0.68 ± 0.56 CPUE). Striped bass length was 20–109 mm in the O-ETM (median size = 80–84 mm), while being 25–99 mm in the UP (median size = 65–74 mm), 25–79 mm in the M-ETM (median size = 65–69 mm), and 50–89 mm in the DOWN (median size = 65–74 mm; Fig. 2.3).

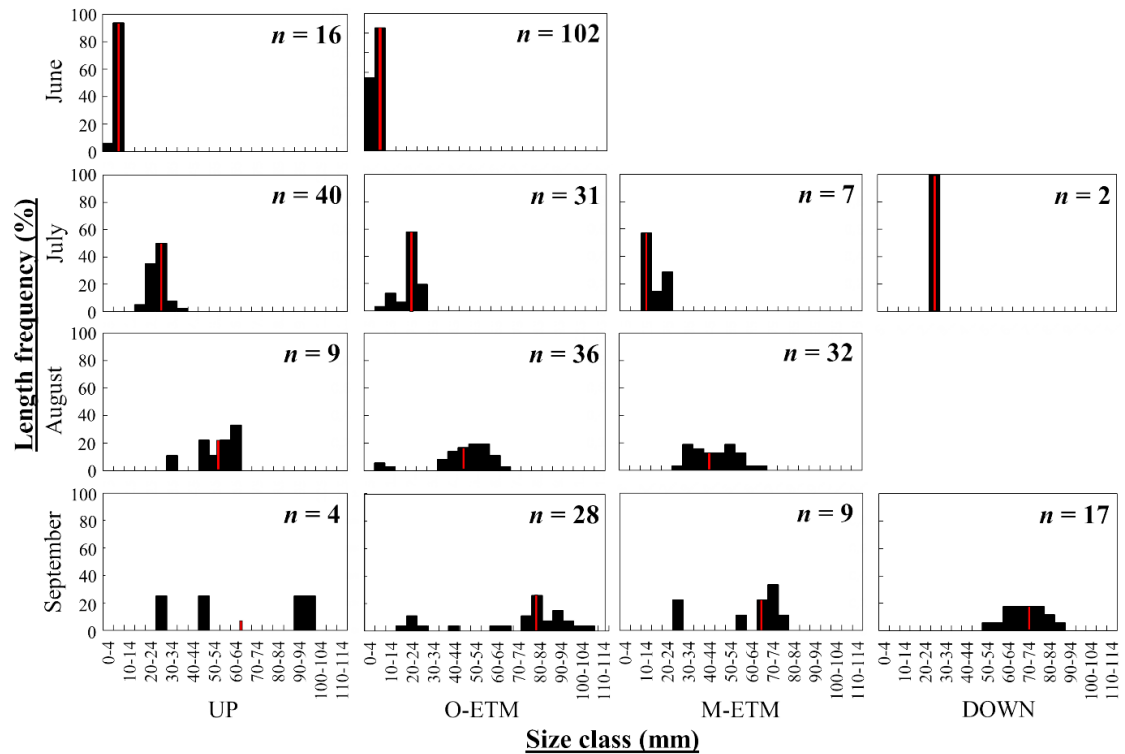


Figure 2.3 Percent length frequency distribution of striped bass larvae and juveniles in June, July, August, and September 2014, in each estuarine habitats. Striped bass standard length is described using 5-mm size class. Red bars represent median values

2.4.2 Characterization of striped bass larvae and juvenile diets between estuarine habitats

In June, the diet of striped bass larvae was mostly composed of diatoms and copepods in the UP, while in the O-ETM the diet was mostly composed of the cladoceran *Bosmina* sp., copepod eggs, and the calanoid *Eurytemora affinis* (Table 2.2). The feeding incidence of striped bass larvae was two times lower in the UP (FI = 13.0 %)

compared to the O-ETM (FI = 26.0 %), although this difference was not significant ($\chi^2 = 1.456$; $df = 1$; $p = 0.228$; Table 2.2).

In July, striped bass diet was similar in the O-ETM and M-ETM, and significantly different for the UP (one-way PERMANOVA: $F_{2,71} = 6.312$, $p = 0.001$; Table 2.3). This difference in diet resulted from a higher ingestion of dipteran pupa in the UP, while striped bass in the O-ETM and M-ETM mostly fed on *Gammarus* sp. (SIMPER: 73.8–80.4 % diet dissimilarities; Tables 2.2 and 2.3). The FI of early life stages was statistically superior for striped bass from the UP (FI = 97.5 %) and O-ETM (FI = 90.3 %) compared to the M-ETM (FI = 57.1 %), and significantly higher in the UP compared to the DOWN (FI = 50.0 %; $\chi^2 = 14.456$; $df = 3$; $p = 0.002$; Table 2.2).

In August, striped bass diets differed significantly between the UP and M-ETM (one-way PERMANOVA: $F_{2,69} = 3.712$, $p = 0.001$; Table 2.3). Diet differed in terms of the consumed proportions of *E. affinis*, *Gammarus* sp., *Neomysis americana*, dipteran pupa, and fish larvae (SIMPER: 71.8–76.9 % diet dissimilarities). In the M-ETM, striped bass consumed a greater proportion of *Gammarus* sp. and *N. americana* compared to diets of striped bass from the UP and O-ETM, where their diet was mainly *E. affinis* and dipteran pupa (Tables 2.2 and 2.3). The feeding incidence was similar for striped bass distributed in the UP (FI = 100.0%), the O-ETM (FI = 88.9%), and M-ETM (FI = 90.6 %; $\chi^2 = 1.081$; $df = 2$; $p = 0.583$; Table 2.2).

In September, the diet of striped bass differed significantly between the ETM and DOWN (one-way PERMANOVA: $F_{2,44} = 6.899$, $p = 0.001$; Table 2.3). Three taxa explained from 93.6%–95.6% of the dissimilarity of diet observed between the ETM habitats and DOWN (SIMPER). Striped bass from O-ETM and M-ETM fed essentially on *Gammarus* sp., while early life stages caught in the DOWN ingested marked proportions of *N. americana* and *Mysis stenolepis* (Tables 2.2 and 2.3). All striped bass caught in the UP, M-ETM and DOWN had full guts (FI = 100.0%), contrasting with

striped bass from the O-ETM (FI = 75.0%; Table 2.2). Indeed, the FI of striped bass caught in the O-ETM was significantly lower than for the M-ETM ($\chi^2 = 8.529$; $df = 3$; $p = 0.036$; Table 2.2).

Table 2.2 Diet of striped bass larvae and juveniles (expressed as dry weight percent contribution of the different prey taxa) for each estuarine habitat, sampled from June to September 2014. Feeding statistics are also provided

Prey items	June			July			August			September		
	UP	O-ETM	DOWN	UP	O-ETM	DOWN	UP	O-ETM	DOWN	UP	O-ETM	DOWN
<i>Bacillariophyta</i>	50	4	-	-	-	-	-	-	-	-	-	-
Crustacean												
Cladoceran												
<i>Bosmina</i> sp.	-	41	<1	3	-	-	<1	<1	-	-	1	-
<i>Chydoridae</i>	-	3	-	-	-	-	-	-	-	-	-	-
Copepod												
Calanoid	-	11	3	6	24	-	16	7	<1	-	7	-
Harpacticoid	-	4	-	-	-	24	-	-	-	-	-	-
Cyclopoid	-	-	-	-	-	-	<1	-	-	-	-	-
<i>Halicyclopid</i> sp.	-	-	3	<1	-	-	-	-	-	-	-	-
<i>Diacyclops thomasi</i>	-	4	-	-	-	-	-	-	-	-	-	-
Copepod eggs	-	26	-	-	-	-	-	-	-	-	-	-
Non identified Copepod	50	8	<1	-	-	-	1	1	-	-	3	-
Amphipod												
<i>Gammarus</i> sp.	-	-	12	22	3	-	13	18	34	13	60	6
Non identified Amphipod	-	-	-	6	-	-	2	8	2	4	-	<1
Mysid												
<i>Neomysis americana</i>	-	-	-	-	-	-	-	1	13	-	-	11
<i>Mysis stenolepis</i>	-	-	-	-	-	-	-	-	-	5	-	30
Non identified Mysid	-	-	-	-	8	-	-	2	8	9	3	7
Insect												
Dipteran pupa	-	-	58	17	3	-	42	19	3	30	6	1
Hemipteran	-	-	-	-	-	-	3	1	4	1	<1	1
Ephemeropteran	-	-	-	-	-	-	1	-	-	-	-	-
<i>Polychaeta</i>	-	-	-	-	-	-	-	-	3	-	-	6
<i>Bivalvia</i>	-	-	-	-	-	-	7	-	-	-	-	<1
Fish larvae	-	-	5	21	-	-	<1	9	10	45	3	-
Non identified residues	-	-	20	26	62	76	14	33	23	11	14	13
Feeding statistics												
Number of fish examined	16	102	40	31	7	2	9	36	32	4	28	17
Mean SL of fish with ≥ 1 prey (mm)	5.7	6.0	25.5	22.1	18.2	25.6	53.6	51.7	45.2	67.9	79.9	70.8
Feeding incidence (%)	13	26	98	90	57	50	100	89	91	100	75	100
Mean number of prey	<1	1	56	12	2	22	423	136	20	7	35	16

Table 2.3 Most important ingested prey of striped bass that contribute to the dissimilarities in diet between habitats (as determined via SIMPER analyses). Data are from striped bass sampled from July to September 2014 and are expressed in %. Comparisons in bold represent significant differences according to one-way PERMANOVA tests followed by multiple pairwise tests

		<i>P. adj</i>	Copepod <i>E. affinis</i>	Amphipod <i>Gammarus</i> sp.	Mysid <i>M. stenolepis</i>	<i>N. americana</i>	dipteran pupa	Fish
<u>July</u>								
	UP O-ETM	0.003		19.6			54.2	
	UP M-ETM	0.003		14.6			65.8	
	O-ETM M-ETM	0.120						
<u>August</u>								
	UP O-ETM	1.000						
	UP M-ETM	0.006	9.3	25.2		11.8	30.6	
	O-ETM M-ETM	0.003		32.8			18.6	20.4
<u>September</u>								
	O-ETM M-ETM	0.636						
	O-ETM M-ETM DOWN	0.003		31.7	26.5	35.4		
	M-ETM DOWN	0.009			30.0	45.6		

2.4.3 Feeding success across habitats

In June, feeding success was similar for larvae in the UP (FS = 0.033 ± 0.003) and O-ETM (FS = 0.043 ± 0.005 ; Fig. 2.4). In July, FS remained low, i.e. below mean values, and decreased from the UP (FS = -0.018 ± 0.070), to the O-ETM (FS = -0.185 ± 0.058), followed by the M-ETM (FS = -0.324 ± 0.069), although these differences were not significant. In August, feeding success was similar for the UP (FS = 0.117 ± 0.205), O-ETM (FS = 0.013 ± 0.090), and M-ETM (FS = 0.179 ± 0.124 ; Fig. 2.4). In contrast, the FS for striped bass sampled in September was similar for the O-ETM (FS = -0.660)

± 0.275) and M-ETM ($FS = -0.410 \pm 0.317$). FS was significantly higher in the DOWN ($FS = 1.193 \pm 0.121$; one-way ANOVA: $F_{2,53} = 14.570$, $p < 0.001$, Fig. 2.4).

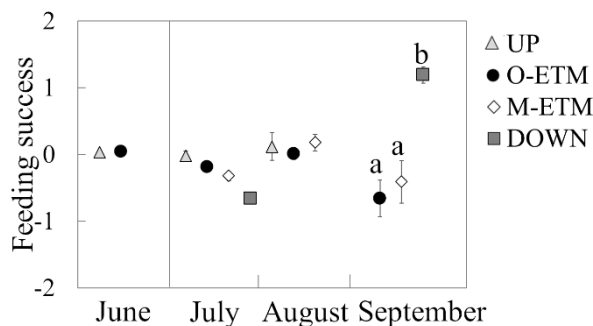


Figure 2.4 Feeding success of striped bass larvae and juveniles within the different estuarine habitats, as sampled from June (larvae) to July-September (juveniles) 2014. A feeding success value of 0 represents the mean value of feeding success as estimated for all striped bass larvae and juveniles. Vertical lines represent standard errors and letters indicate groups having significantly different mean values (one-way ANOVA followed by Tukey post-hoc tests)

2.4.4 Diet niche overlap

Estimates of diet overlap emphasized the similarity of striped bass niches in the O-ETM and M-ETM in both August ($D = 0.622$) and September ($D = 0.814$). Moderate values of niche overlap suggested that striped bass distributed in the UP and O-ETM fed on similar prey items in July ($D = 0.451$) and August ($D = 0.515$). In contrast, our results highlighted that striped bass distributed in the DOWN had a distinct diet having a low niche overlap ($D < 0.2$; Table 2.4).

Table 2.4 Comparison of striped bass dietary niche overlap between habitats, for striped bass sampled between July and September 2014. Habitats having a niche overlap > 0.40 are highlighted in bold

	July		August		September	
	UP	O-ETM	UP	O-ETM	O-ETM	M-ETM
O-ETM	0.45	-	0.52	-	n/a	n/a
M-ETM	0.14	0.20	0.38	0.62	0.81	-
DOWN	n/a	n/a	n/a	n/a	0.19	0.04

2.5 Discussion

In the St. Lawrence estuary, striped bass larvae and juveniles exhibited a generalist feeding behavior, foraging on a wide range of prey. During the first three months of development, the feeding ecology of striped bass appears mainly influenced by ontogeny and its distribution along the salinity-turbidity gradient.

2.5.1 Feeding ecology of striped bass larvae and juveniles

The pelagic larvae of striped bass, which were sometimes still carrying a yolk sac, were mainly distributed in the UP and the O-ETM, near their known spawning sites. At the onset of feeding, their diet was similar between the UP and O-ETM, feeding mostly on copepods. Striped bass larvae had more suitable feeding conditions in the O-ETM relative to the UP, possibly due to the presence of *Bosmina* sp. as a primary prey.

However, a previous study suggested a positive selection for the copepod *E. affinis* and a negative preference for *Bosmina* sp. may occur (Robichaud-Leblanc *et al.* 1997, Shideler and Houde 2014), probably induced by differences in calorific values (Vijverberg and Franck 1976) and catchability (Drenner *et al.* 1978). Although not statistically significant, striped bass larvae in the O-ETM were more abundant and displayed higher FI than those in the UP. In the O-ETM, striped bass larvae were characterized by lower growth and a reduced mortality-dispersal rates compared to larvae within the UP (Vanalderweireldt *et al.* in prep-c). The O-ETM is particularly turbid, which can benefit larval fish feeding. As turbid environments accentuate the visual contrast between coloured prey and the background environment, energy investment into foraging may be decreased (Sirois and Dodson 2000-b). However, the influence of turbidity on FS remains uncertain (Chesney 1989, Sirois and Dodson 2000-b). Turbid waters also provide a visual shelter from predators (Abrahams and Kattenfeld 1997). Turbidity affects differentially the various early life stages, especially as mobility and foraging skills change greatly. We had hypothesized that limited prey within the UP—the prey mainly represented by copepods—was responsible for a strong intraspecific competition and a selection toward fast-growing individuals. In contrast, the O-ETM, marked more abundant prey items—in particular, *Bosmina* sp. at its highest density in the estuary—provided a nursery habitat for a larger portion of the striped bass population (Vanalderweireldt *et al.* in prep-a).

As the young stages developed, we observed a gap in both the fish size and its feeding characteristics between pelagic and littoral habitats. Increasing size in young striped bass were associated with an important shift in diet, progressively including larger prey such as dipteran pupa, gammarids, and mysids. Within the littoral estuarine habitats, the UP was more favourable for feeding relative to the more downstream habitats. Striped bass in the UP were more abundant, larger, had a higher FI and the fastest growth compared to the O-ETM and M-ETM (Vanalderweireldt *et al.* in prep-c). These results suggest that striped bass in the UP likely found abundant food, appropriate prey

in terms of size, energetic values, and catchability, reflected the higher ingestion of high-energy dipteran pupa (Wissing and Hasler 1971).

Niche overlap was relatively high between the O-ETM and M-ETM, suggesting that these two habitats offered some similar food sources, albeit in different abiotic conditions. In these two habitats, the diet of striped bass was mainly composed by gammarids. Although amphipods are less calorific value compared to dipteran pupa (Cummins and Wuycheck 1971), gammarids were the most abundant potential prey in the ETM (Vanalderweireldt *et al.* in prep-a). Our results emphasized that feeding conditions provided in the UP and O-ETM are associated with larger striped bass than those found in the M-ETM and DOWN. However, dispersal of striped bass occurred throughout the different estuarine habitats with smaller striped bass migrating to the M-ETM and the DOWN in late summer to exploit a new feeding niche, dominated by mysid prey. The abundance of striped bass was low in the DOWN and FS was significantly higher there than in the other habitats. An elevated FS and a distinct trophic niche, in comparison with the other habitats, were due primarily to the ingestion of large and high-energy prey, such as mysids (Tyler 1973). Thus, small striped bass may be advantaged in migrating to and feeding in the DOWN habitat in late summer, a habitat that was not used during their earlier development stages.

This confirms that the O-ETM represents a transition habitat between two distinct feeding niches, dominated by dipteran pupa prey in the UP and mysids in the M-ETM and DOWN. In addition, we observed a marked variability in the feeding characteristics of striped bass, mediated by size-dependent requirements. In the early summer, the upstream habitats appeared more suitable for larger sized striped bass. The slower growth of striped bass distributed in the M-ETM and DOWN may suggest that downstream migrations are adaptative behaviours related to suboptimal conditions in upstream habitats marked by strong intraspecific competition. In upstream habitats, smaller and larger sized striped bass might have competed for limited resources, favouring the feeding of larger-sized individuals. As such, the lack of sufficient resources in upstream habitats may encourage the colonization of new estuarine

habitats, pushing smaller striped bass to forage further downstream. In the late summer, smaller striped bass improved their FS by exploiting a new downstream feeding niche, suggesting that being distributed throughout the estuary may increase their potential survival.

2.5.2 Early life feeding in the St. Lawrence versus other North American populations

Previous studies in other estuarine environments have revealed the importance of the copepod *E. affinis* and the cladoceran *Bosmina* sp. in the diet of striped bass larvae (Robichaud-Leblanc *et al.* 1997, Limburg *et al.* 1999, North and Houde 2006, Martino and Houde 2010, Campfield and Houde 2011, Shideler and Houde 2014). The distribution of striped bass larvae is associated with the distribution of *E. affinis* and *Bosmina* sp., species that are often more abundant within the salt front and the ETM zones (North and Houde 2006, Martino and Houde 2010, Campfield and Houde 2011). As striped bass develop, the pelagic larvae migrate to littoral habitats and shift their diets to more highly nutritious prey (Robichaud-Leblanc *et al.* 1996, 1997, 1998). In contrast to the St. Lawrence population, however, diets of age-0 striped bass in the Miramichi River (i.e. the geographically closest population to the St. Lawrence population) were dominated by mysids (*N. americana*) and sand shrimp (*Crangon septemspinosa*) in the upper, middle, and lower estuary portions (Robichaud-Leblanc *et al.* 1997). Diets of striped bass from the mid-Hudson estuary were less comparable to our results, being composed by invertebrate generalists (Gardinier and Hoff 1982, Jordan *et al.* 2003, Howe *et al.* 2008). However, the striped bass in the Hudson estuary also fed selectively on gammarids, shrimp (*Crangon* sp.) and dipteran larvae (Howe *et al.* 2008). In Chesapeake Bay, the diet of young striped bass was highly variable between years and was dominated by polychaetes, gammarids, mysids, and insect larvae (Markle and Grant 1970, Boynton *et al.* 1981, Hartman and Brandt 1995). In

North Carolina, mysid shrimp were the primary prey of striped bass and were consumed in the more saline waters.

As in the St. Lawrence River, important contrasts in feeding ecology have been observed along a salinity-turbidity gradient (Wainwright *et al.* 1996, Cooper *et al.* 1998). For American coastal striped bass populations, the salt front and the ETM regions provide a high-quality nursery habitat for feeding and growth, favouring recruitment (North and Houde 2006, Martino *et al.* 2007, Shideler and Houde 2014). However, only a few previous studies (Robichaud-Leblanc *et al.* 1998, Mohan *et al.* 2015) have shown the potential advantage of a later-season downstream migration, through the partitioning of the estuary in several feeding niches, and the searching for more optimal habitat to forage as we observed in the St. Lawrence estuary.

The study of habitat occupancy and movement patterns provided evidence of the connectivity among the estuarine habitats, which has a considerable impact on the population dynamics in the St. Lawrence estuary (Morissette *et al.* 2016). Numerous studies have already emphasized the primary role played by habitat connectivity for larval fish survival and recruitment (Houde 2008, Secor 2017). In the St. Lawrence estuary, the study of small spatiotemporal scale movements of striped bass early in life can mainly influence its population dynamics and, therefore, including the connectivity into management plans can increase the efficiency of the re-establishment program.

2.6 Conclusion

The early life stages of striped bass in the St. Lawrence estuary have a similar feeding ecology as other coastal North American populations and presented important contrasts along the salinity-turbidity gradient. In the St. Lawrence estuary, the UP and the O-ETM provided a higher-quality nursery habitat where striped bass had a higher feeding incidence early in the season. After one month, age-0 striped bass, as generalists,

shifted to larger prey items. In upstream habitats, larger striped bass consumed mainly dipteran pupa, while in downstream habitats, smaller striped bass fed on gammarids and mysids. The downstream migration of early life stage striped bass may offer the advantage of new areas of high prey productivity, allowing the growth of small individuals to catch up with that of the already larger individuals, and thereby promote the survival of the young. Thus, results of this study suggest that connectivity pathways between estuarine habitats may be important for the survival of early life stages and the recruitment to the adult population.

2.7 Acknowledgements:

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CHAPITRE III

GROWTH AND MORTALITY OF STRIPED BASS (*MORONE SAXATILIS*) LARVAE AND JUVENILES IN THE ST. LAWRENCE ESTUARY, CANADA

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3.1 Abstract

After being extirpated from the St. Lawrence River in the 1960s, striped bass (*Morone saxatilis*) were reintroduced to the estuary in 2002, and by 2008 they were naturally reproducing. The increase of this recently reintroduced population prompted the need to document its nursery habitats utilisation, which contribute to species recruitment. We analysed mortality and dispersion rates and the growth of larvae and juveniles in relation to their occurrence and migration patterns. From June to September 2014, we collected striped bass distributed in four distinct estuarine habitats: the upstream freshwater section (UP), the oligohaline (O-ETM) and the mesohaline (M-ETM) estuarine turbidity maximum zone, and the downstream polyhaline section (DOWN). Based on striped bass otolith microstructure and microchemistry, 305 back-calculated growth and 36 migration trajectories have been reconstructed. The UP and the O-ETM provided optimal conditions wherein which larvae and juveniles exhibited fastest growth. We propose that migrants adopt an adaptive migration behaviour to avoid suboptimal conditions and strong intraspecific

competition from resident in the upstream habitats. The potential advantage of a downstream migration later in the season might be an ingenious tactic to promote their survival during the early life stages.

Keywords: Early life stages • *Morone saxatilis* • Mortality and dispersion rate • Back-calculated growth • Otolith microchemistry • Migratory contingent

3.2 Introduction

Fluctuations in recruitment induced by variable environmental conditions during the early life history of fishes is a fundamental paradigm of fisheries science (Leggett and Frank 2008, Houde, 2015). Physical and biological properties of a species' habitat affect the survival of early life stages and recruitment through processes such as feeding, growth and dispersion. The timing and extent of prey availability directly influence the risks of starvation, a major cause of mortality during the larval stage (Hjort 1914, Cushing 1990, Rutherford *et al.* 1997). In the search for mechanisms that affect recruitment, previous studies have emphasised the relationship between growth rates and mortality, influenced by environmental conditions (Sirois and Dodson 2000-a, Pepin *et al.* 2015). The link between growth and mortality may influence not only trophic interactions but also the spatio-temporal co-occurrence with predators (Takasuka *et al.* 2016). In addition, hydrodynamics regulate survival and recruitment during early life stages by improving encounter rates with food items (Rothschild and Osborn 1988, Chesney 1989) and controlling dispersal to or retention within nursery habitats (North and Houde 2003, Martino and Houde 2010).

Estuaries provide nursery habitats for several fish species (Sirois and Dodson 2000-a, North and Houde 2003, Winkler *et al.* 2003). Their spatial structure, characterised by strong physical gradients, entails considerable differences in physiological costs that, in turn, influence growth, survival, and recruitment variability (Rutherford and Houde 1996, Clarke and Johnston 1999, Secor *et al.* 2000, Sirois and Dodson, 2000-a, Boeuf

and Payan 2001). In particular, the estuarine turbidity maximum (ETM) offers a large variety of physical and biotic conditions (Sirois and Dodson 2000-a, North and Houde 2003, Winkler *et al.* 2003). Early life stages of fish retained in the ETM region benefit from (1) a visual refuge from predation (Utne-Palm 2002, De Robertis *et al.* 2003), (2) a region of high zooplankton biomass and productivity (North and Houde 2003, Winkler *et al.* 2003, Lapierre and Frenette 2008), and (3) more optimal physical conditions for feeding and growth, that may increase recruitment potential (Rutherford and Houde 1996, North and Houde 2003, Martino and Houde 2010).

Within the St. Lawrence Estuary (SLE), distinct habitats overlap along the salinity-turbidity gradient, each having specific physical attributes that control the distribution of invertebrates and fish at early life stages (Laprise and Dodson 1994, Winkler *et al.* 2003, Vanalderweireldt *et al.* in prep-a). In the fluvial and middle estuary portions of the St. Lawrence River, four estuarine habitats are characterised: (1) the fluvial estuary in the upstream freshwater section (UP), identified by its low turbidity, freshwater, and relatively warm waters; (2) the oligohaline ETM habitat (O-ETM) defined by highly turbid, low salinity waters; (3) the mesohaline-ETM habitat (M-ETM) characterised by turbid, brackish, and colder waters; and (4) the downstream polyhaline section (DOWN) defined by its low turbidity and polyhaline waters having the lowest temperatures of the four estuarine habitats (Vanalderweireldt *et al.* in prep-a). In the SLE, several studies have suggested that the ETM region supports a nursery habitat for estuarine species such as rainbow smelt (*Osmerus mordax*), Atlantic tomcod (*Microgadus tomcod*), white perch (*Morone americana*), and striped bass (*Morone saxatilis*; Laprise and Dodson 1990, Laprise and Dodson 1994, Sirois and Dodson 2000-a, Winkler *et al.* 2003, Morissette *et al.* 2016, Vanalderweireldt *et al.* in prep-a).

Striped bass is an anadromous species, widely distributed in North America from the Gulf of Mexico to the estuary and Gulf of the St. Lawrence (Scott and Crossman 1974). The SLE sustains one of the most northern striped bass populations along the eastern

coast of North America. During the 1960s, the SLE population disappeared due to overfishing, environmental pollution, and habitat destruction (Robitaille *et al.* 2011). Since 2002, a reintroduction program has led to the re-establishment of a striped bass population able to reproduce in the estuary (Robitaille *et al.* 2011). At the onset of striped bass development in the SLE, semi-buoyant eggs and pelagic larvae are distributed near to the salt front in the upper ETM, where two spawning areas have been identified (Robitaille *et al.* 2011, Vanalderweireldt *et al.*, in prep-a). As the first growing season progresses, striped bass juveniles are found in littoral habitats. Several of these striped bass then move toward downstream estuarine habitats (Morissette *et al.* 2016, Vanalderweireldt *et al.* in prep-a).

Along the East Coast of North America, the presence of different migratory contingents within striped bass populations has been frequently observed (Clark 1968, Petitgas *et al.* 2010, Morissette *et al.* 2016). According to Clark, 1968, who first observed discrete striped bass migratory groups in the Hudson River, a contingent is defined as “a group of fish that engage in a common pattern of seasonal migration among feeding, wintering and spawning areas”. In the SLE, Morissette *et al.* 2016 identified three different migratory contingents during the early life stages of striped bass: (1) freshwater residents, (2) oligohaline migrants, and (3) mesohaline migrants. The coexistence of different patterns of migration brings into question the influence of the distribution of early life stages along the salinity gradient on the survival and recruitment success of striped bass. It is believed that resident behaviour ensures the sustainability of the population, while migrants can promote the expansion through colonisation of new habitats (Petitgas *et al.* 2010, Secor 2015). On the contrary, the emergence of new strategies in habitat utilisation may be induced by poor habitat quality, driving residents to search for more suitable conditions, even if these migrations involve additional energetic costs (Dingle and Drake 2007, Brodersen *et al.* 2014, Secor 2015). The newly established striped bass population of the SLE revealed adaptive abilities by their rapid development of a migratory structure in less than 10

years following their initial stocking (Morissette *et al.* 2016). Understanding the establishment, maintenance, and potential expansion of the newly introduced population of striped bass requires investigating the effect of nursery habitats and habitat utilisation on the recruitment of this species (Robitaille *et al.* 2011).

The main objectives of this study are to (1) compare mortality and growth of striped bass larvae and juveniles among the four different habitats in the St. Lawrence estuary and (2) distinguish different migratory contingents of striped bass and to compare their growth as influenced by these migratory patterns. First, we compare mortality estimates, absolute growth rates, and growth trajectories between the four estuarine habitats with striped bass larvae and juveniles collected during pelagic and littoral surveys conducted from June to September 2014. Analyses of the otolith microstructure permit the reconstruction of catch curves and the determination of back-calculated somatic growth. We then use otolith microchemistry on striped bass sampled in September to reconstruct habitat utilisation from hatching to capture, and we then compared growth rate of striped bass within each habitat. Growth trajectories and morphological characteristics of the different migratory patterns were also compared.

3.3 Methods

3.3.1 Study site

The fluvial (freshwater) and middle (brackish water) portions of the SLE stretch from Trois-Rivières (130-km upstream of Quebec City) to Tadoussac (230-km downstream of Quebec City, Fig. 3.1). These two sections of the estuary encompass a wide salinity range of 0 to 25 PSU. Mean annual water discharge is on the order of $12\,600\text{ m}^3\cdot\text{s}^{-1}$ (St. Lawrence Centre 1996). Estuarine circulation is primarily controlled by semi-

diurnal tides with a range 3–5 m in amplitude, and secondarily by neap and spring tide (semi lunar 14 d; Simons *et al.* 2010). The saline front is located at the eastern tip of Ile d'Orléans and marks the upstream limit of the ETM. Shallow bathymetry, estuarine circulation, tides, and the contact of fresh and salt water produce high concentrations of suspended matter in the water column. Depending on river discharges, the ETM can vary from 70–120 km in length (Silverberg and Sundby 1979). Large variations in salinity and turbidity result in a vast range of physicochemical conditions that support various planktonic and nektonic communities (Laprise and Dodson 1994, Winkler *et al.* 2003, Vanalderweireldt *et al.* in prep-a).

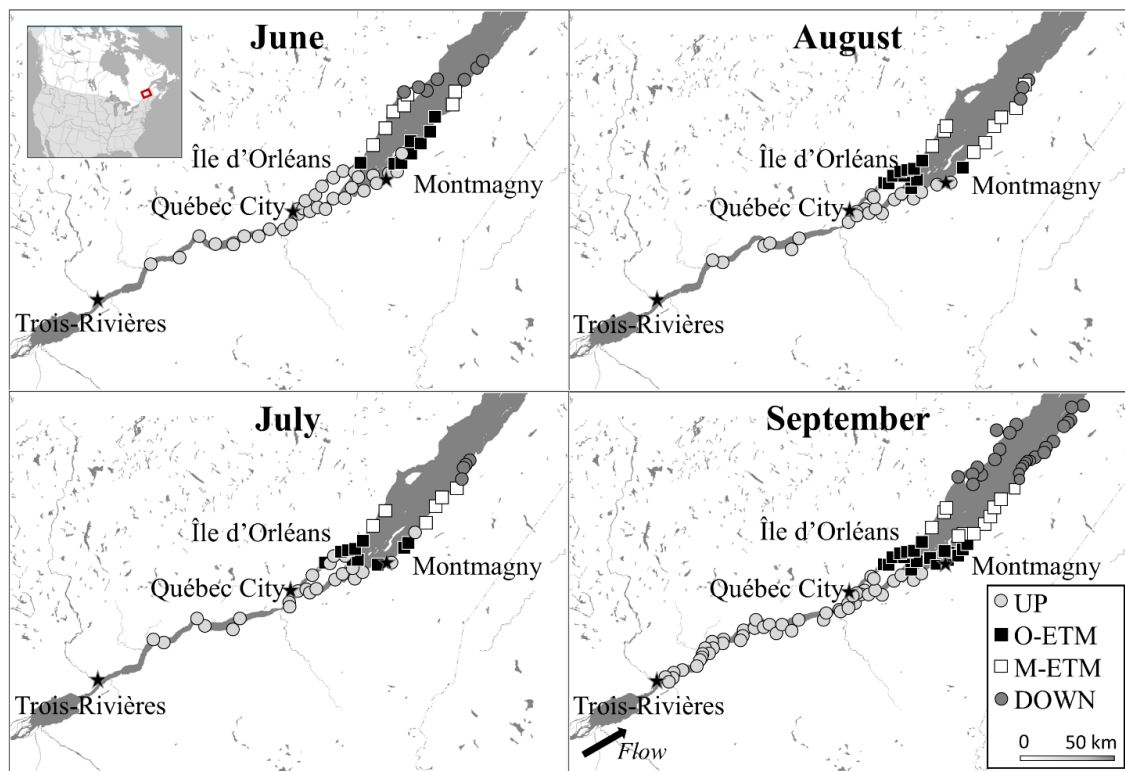


Figure 3.1 Stations location for the pelagic survey (4–8 June) and the littoral surveys (7–16 July, 8–12 August, and 8–22 September 2014). The four estuarine habitats

correspond to light-grey circles in the upstream freshwater section (UP), black squares in the oligohaline estuarine turbidity maximum habitat (O-ETM), white squares in the mesohaline-ETM (M-ETM), and dark-grey circles in the downstream polyhaline section (DOWN).

3.3.2 Field survey

In 2014, early life stages of striped bass were collected across the salinity-turbidity gradient in the fluvial and middle portions of the St. Lawrence estuary during three pelagic surveys (4–8 June, 12–17 June, and 21–28 June 2014) and three littoral surveys (7–16 July, 8–12 August, and 8–22 September 2014). In June, we sampled ichthyoplankton using bongo nets having a 0.5-m-diameter opening and a 333- μm mesh size. We also conducted oblique tows of 10 min in the surface layer (0–5 m). General Oceanics flowmeters registered the filtered water volume, averaging $400.9 \pm 7.1 \text{ m}^3$. During pelagic surveys, 54 stations located on the 5 m isobaths were sampled on three occasions from the upstream freshwater section to the downstream mesohaline section of the estuary (Fig. 3.1). All sampled larvae were anesthetized in a clove solution mixed with 95% ethanol and water collected from the estuary. After collection, samples were immediately fixed in 95% ethanol. From July to September, we carried out three littoral surveys as striped bass are subject to an initial shoreward migration from pelagic to littoral habitats (Robichaud-Leblanc *et al.* 1998). In July, we used a beach seine (12.5-m-long, 3.2-mm mesh, pulled at a depth of 4 m) at 43 stations. In August and September, the surveys used a beach seine (15-m-long, 9.5-mm mesh for the wings, 6.3-mm mesh in the central pocket, pulled at a depth of 1.8 m). In total, 44 and 101 stations were sampled in August and September, respectively (Fig 3.1). In the field, all samples were immediately frozen in dry ice and then transferred into

containers filled with 95% ethanol. For pelagic and littoral surveys, a CTD probe (SBE19, Sea-Bird Electronics, Inc.) measured abiotic variables such as salinity, temperature, and turbidity.

3.3.3 Laboratory analyses

3.3.3.1 Striped bass identification

Early-staged fish were sorted from the pelagic ($n = 13,857$ fish) and littoral ($n = 15,609$ fish) sites. Individual fish were first identified using morphological criteria and were measured under a stereomicroscope (Leica, MZ 12.5; Scott and Crossman 1974, Auer 1982, Waldman *et al.* 1999). To ensure accurate identifications, we performed genetic analyses on striped bass larvae, because they occurred with white perch (*Morone americana*), a congener species which is morphologically very similar during early life stages. Hence, molecular identification can ensure an accurate identification of striped bass. We used mitochondrial DNA sequence data from 216 striped bass larvae and 48 white perch (total of 264 fish). To discriminate the two species, we selected the cytochrome oxidase b gene (CYTb). DNA was extracted from muscle tissues and then stored in 95% ethanol using the DNEasy Tissue kit (Qiagen) protocol. We amplified around 350 bp through polymerase chain reaction (PCR) using the primers Morocytb836r and Morocytb484f (Kearse *et al.* 2012). Amplification success was verified by electrophoresis on a 1.5 % agarose gel with GelRed solution and loading blue dye. PCR products were sent to the Genome Sequencing and Genotyping Platform in Quebec City for sequencing. Sequences were verified and aligned using MEGA5 (Tamura *et al.* 2011) and BIOEDIT v. 7.2.5 (Hall 1999). Sequences were then compared to those of the GenBank database using BLAST

procedures to assign these to either striped bass or white perch (Orrell *et al.* 2002). Of the 264 fishes selected for genotyping, 118 striped bass larvae were confirmed via genetic analysis, from which 100 were correctly identified only using morphological characteristics, while the other 18 corresponded to misidentified white perch larvae. From June to September 2014, 118 larvae and 683 striped bass early life stages were collected in the SLE. Standard length (SL), wet weight, and body depth at the anus were measured on all collected striped bass.

3.3.3.1 Otolith microstructure analysis

For growth and mortality analysis, sagittal otoliths were extracted from a subsample of striped bass larvae and juveniles under a stereomicroscope (Leica, MZ 12.5). Otoliths were mounted on microscope slides with thermoplastic glue (Crystalbond™509; Aremco™ products, NY, USA). To improve readability, large otoliths (> 350 µm) were polished using an abrasive sheet (2000 grit Wetordry™, 3M™) and lapping film (1- and 5-µm lapping film, 3M™). The otoliths were measured using an image-analysis system connected to a light microscope at 50–1000× magnification. Three measurements were taken along the growth axis: core radius (µm), otolith radius (µm), and width of every increment (µm). All otoliths were examined between three and five times by the same reader. All otolith readings were performed without any knowledge of the length or the previous estimated age. If the first three counts differed by less than 10 %, the last count and measurements were kept. Otherwise, a new count was made and kept until three of the previous readings did not differ more than 10%. At the end, 40 otoliths out of 345 were rejected (i.e. 11.59% rejection rate) due to inconsistent readings (Table 3.1). The age of striped bass larvae and juveniles was estimated by

considering that the first growth ring is accreted four days after hatching (Secor and Dean 1989).

Table 3.1 Number of sampled striped bass from June to September 2014, and number of otoliths used for microstructure and microchemistry analyses.

	Habitat	June	July	August	September	Total
Sampled striped bass	UP	16	471	9	4	500
	O-ETM	102	32	36	22	192
	M-ETM		7	32	15	54
	DOWN		2		17	19
	Total	118	512	77	58	765
Otolith microstructure	UP	15	75	8	1	99
	O-ETM	74	27	29	18	148
	M-ETM		7	23	12	42
	DOWN		2		14	16
	Total	89	111	60	45	305
Otolith microchemistry	Freshwater					
	residents				12	12
	M-ETM					
	migrants				12	12
	DOWN					
migrants				25	25	
Total				49	49	

3.3.3.2 Otolith microchemistry analysis

To determine the migratory contingent to which an individual belonged, we used the second sagittal otolith from 49 striped bass captured in September for microchemistry analyses. We followed a precautionary protocol to prevent contamination of the otolith, especially from metals. Otoliths were manipulated in glass Petri dishes using clean plastic forceps, and gloves. In addition, all microchemistry material was washed in 10% nitric acid (trace metal grade 67–70 %, Fisher Scientific, QC, Canada, diluted with ultrapure water) for 24 h and rinsed three times in ultrapure water before drying under a class 100 laminar flow fume hood for 24 h. Otoliths were embedded in epoxy resin (Miapoxy 100, Freeman, OH, USA) and then cut into 1-mm-thick transverse sections using a slow-speed diamond-bladed saw (IsoMet saw; Buehler, IL, USA). The slice exposing the core of the otolith was selected before being polished with an abrasive sheet (2000 grit Wetordry™, 3M™) and lapping film (1- and 5- μm lapping film, 3M™). Sagittal sections were mounted on a petrographic microscope slide using thermoplastic glue (Crystalbond™509; Aremco™ products, NY, USA). All otolith slices were sonicated in ultrapure water for 5 min and dried under a laminar flow fume hood for 24 h.

Otolith trace element concentrations were determined by using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) with an Agilent 7700x ICP-MS coupled to a Resonetics Resolution M-50 Excimer (193 nm) ArF laser at the University of Quebec in Chicoutimi. Laser ablation was performed along a continuous line from the core to the edge of the otolith. Based on a previous study (Morissette *et al.* 2016), the laser beam diameter was set at 19 μm , a frequency of 15 Hz, a fluency

of $5 \text{ J}\cdot\text{cm}^{-2}$, and a speed of $5 \mu\text{m}\cdot\text{s}^{-1}$. To calibrate and control the quality of measurements, we assessed three standard materials (NIST SRM 610, USGS MACS-3 and GP-4) for 60 s after every ten otoliths. Calcium (^{44}Ca) was used as an internal standard and was assumed to be 40.0 % of the otolith mass. The isotopic masses used for each element were set to the most abundant natural isotope and assumed to be representative of the total concentration of that element in the otolith. Element concentrations were calculated from the conversion of isotope counts and were expressed in parts per million (ppm). To provide the relevance to the variations in concentrations, limits of detection (LOD) and quantification (LOQ) were determined for each element. LOD and LOQ were calculated as three times (LOD) and ten times (LOQ) the standard deviation (SD_{blank}) of the gas blank divided by the sensitivity of the instrument signal (Lazartigues *et al.* 2014). As a result, concentrations below the limit of detections were replaced by zero. Following Morissette *et al.* (2016), we kept four elements for identifying migration patterns: ^{24}Mg , ^{55}Mn , ^{88}Sr , and ^{138}Ba .

3.3.4 Data analysis

3.3.4.1 Growth and mortality-dispersion rates calculations

To estimate mortality-dispersion rates, we used a catch-curve analysis (Campana and Jones 1992). Due to different sampling methods, we developed separate catch curves for pelagic and littoral surveys. Abundance-at-age estimates were plotted to describe the exponential rate of decrease. Age-length keys were used to estimate the age of the 460 individuals not aged by otolith analysis (Campana and Jones 1992). Larvae in a given 5-mm length class were randomly attributed an age according to an age probability function for that 5-mm length class (Campana and Jones 1992). The initial

ascending left limb is related to a lower abundance in the youngest age categories compared to the peak of abundance, due to incomplete capture by the sampling gear. This first ascending limb was ignored when fitting the regression, and only data showing a decreasing abundance were used for the analysis (Campana and Jones 1992). The absolute value of the slope of the fitted regression is an estimate of Z , the mortality-dispersion of early life stages in the system. Slopes of the catch curves were compared between habitats using analysis of covariance (ANCOVA) in R (v.3.5.0; R Core Team 2018).

Length back-calculation was based on the daily periodicity of increment formation in striped bass larvae and juveniles (Secor and Dean 1989) and on the proportional relationship between otolith and somatic growth (Fig. 3.2; Campana 1990). To calculate length-at-age, the biological intercept procedure was used (Campana 1990). The biological intercept was set at an age of 4 days to a SL of 4.5 mm and the observed individual core radius (Secor and Dean 1989).

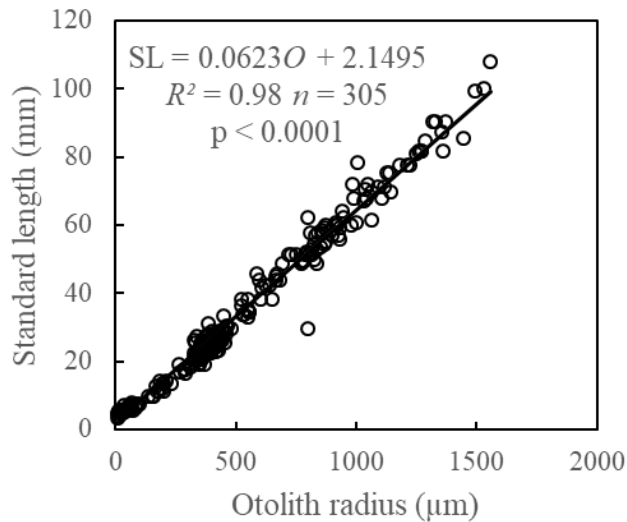


Figure 3.2 Relationship between standard length (SL) and otolith radius (O) of striped bass sampled in the St. Lawrence estuary from July to September 2014.

Absolute growth rate (AGR) was estimated from age day-4 to the date of capture:

$$AGR = \frac{(SL - 4.5 \text{ mm})}{(Age - 4d)}$$

where SL and Age are the standard length and the number of daily increments at capture, respectively. The variables 4.5 mm and 4d are the SL and the age at the biological intercept, respectively (Secor and Dean 1989). Growth trajectories were reconstructed for each individual using back-calculated lengths at five-day intervals. To compare growth trajectories among habitats, we kept individuals that were aged at least 6 days in June, 25 days in July, 60 days in August, and 70 days in September.

3.3.4.1 Determining the migratory contingents

We performed the migratory contingent analysis following the protocol of Morissette *et al.* (2016). Briefly, a split moving window (SMW) analysis was used to identify discontinuities in the patterns of habitat use that represent transitions from one habitat to another (Hedger *et al.* 2008). To this end, the four previously described trace element concentrations were transformed to their standardised principal components (PCA) of the entire otolith profile. To determine the number of principal components to be used for SMW, we followed “eigenvalues equal one” (Kaiser 1960). Before using the SMW method, the window width was determined by autocorrelation analysis for each otolith profile (Webster 1973). We identified the significant habitat boundaries as the window position where the Mahalanobis distance was greater than the sum of the profile mean distance and one standard deviation (SD). If several window positions were adjacent, only the highest calculated Mahalanobis distance was kept and considered as a habitat transition. After identifying discontinuities along otolith profiles, we assigned otolith sections among boundaries within each otolith profile to an estuarine habitat. For this, we assumed that the elemental signal between two transitions was a period of uniform chemical deposition in the otolith. Thus, we calculated the elemental signal as the mean concentration of the four selected elements between two boundaries. SMW-elemental fingerprints were assigned to one of the four previously defined habitats through discriminant function analysis (DFA). To do so, we used margin signals as reference fingerprints to characterise the habitat from which each striped bass was sampled. Mean elemental concentrations of the last 20 μm of the otolith profile were then defined as reference fingerprints for the habitats. The analyses were all performed using R software v.3.5.0 (R Core Team 2018) running the *knitr* (Xie 2015) and *MASS* packages (Venables and Ripley 2002). SMW analysis was performed according to *smw.R* procedures (Rossiter 2013).

We performed growth trajectory and microchemical analyses on 36 striped bass caught in September 2014. For these individuals, we calculated the absolute growth rate (AGR_{habitat}) in each habitat as:

$$AGR_{\text{habitat}} = \frac{(SL_{t1} - SL_{t0})}{D}$$

where SL_{t0} and SL_{t1} are the SL estimated during the last day in the previous habitat and the last day before leaving the new habitat, respectively. D represents the number of days spent in the habitat. The distribution of AGRs among estuarine habitats were analysed using a Kolmogorov–Smirnov test. To compare growth trajectories among migratory contingents, we kept individuals that were aged at least 70 days in September. We compared AGRs using one-way analysis of variance (ANOVA) in R software v.3.5.0 (R Core Team 2018).

3.4 Results

Early in the season, the striped bass larvae were concentrated in the UP and O-ETM pelagic habitats; the fish then migrated toward the littoral habitats. In July, striped bass then dispersed to downstream littoral habitats but were mainly concentrated in the ETM habitats in August and September.

3.4.1 Differences in mortality-dispersion rates between habitats

To estimate the mortality-dispersion rates (Z), we developed cohort-specific catch curves of young-of-the-year striped bass and then compared the resulting Z values of the UP and the O-ETM habitats (Fig. 3.3). For larvae aged 4–21 days (captured during

the pelagic survey), Z was three times higher in the UP ($Z = 0.602$; Fig. 3.3a) than in the O-ETM ($Z = 0.191$; Fig. 3.3b), although this difference was very slightly above the threshold of statistical significance (one-way ANCOVA, $F_{1,18} = 44.305$, $p = 0.053$). For striped bass aged 20–133 days (caught during the littoral survey), Z was significantly higher in the UP ($Z = 0.056$; Fig. 3.3c) than in the O-ETM ($Z = 0.011$; Fig. 3.3d; one-way ANCOVA, $F_{1,36} = 15.508$, $p < 0.001$).

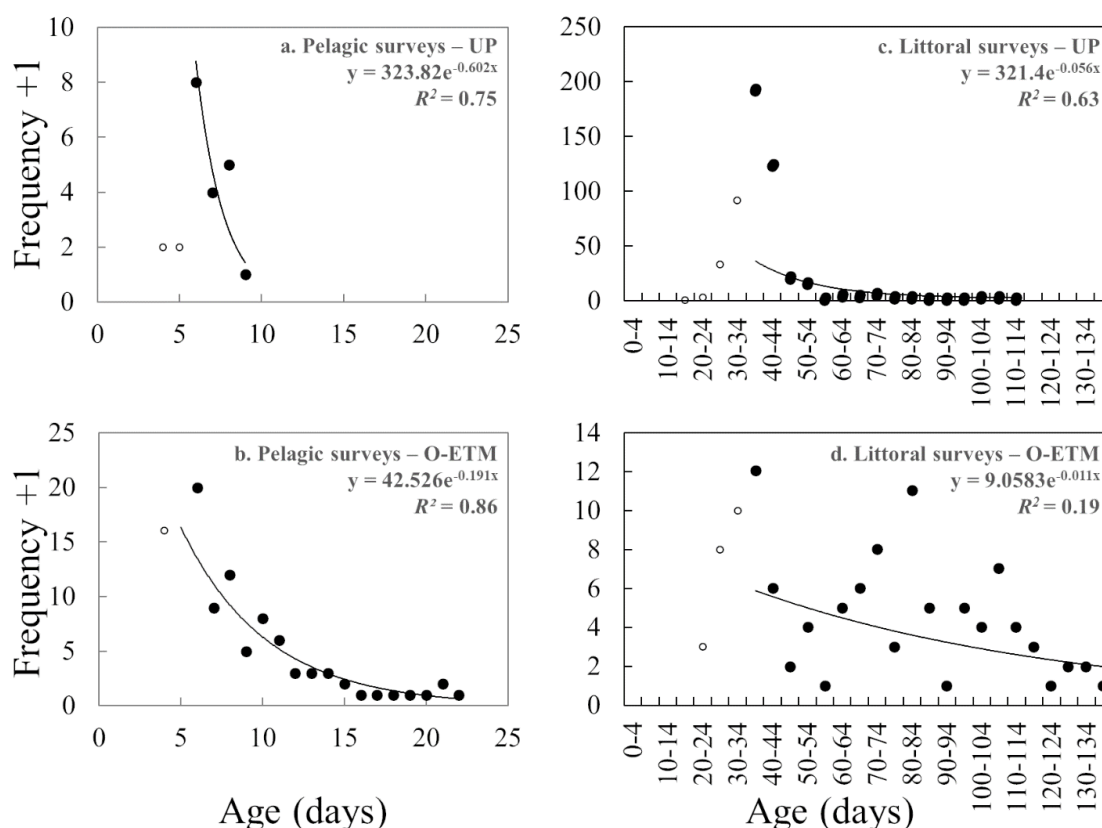


Figure 3.3 Catch curves and exponential coefficients estimating decrease rates (Z) of early life stage striped bass from the pelagic zone in June in (a) the UP habitat and (b) the O-ETM habitat, and from the littoral zone in July–September in (c) the UP habitat

and (d) the O-ETM habitat. This initial ascending limb (empty circles) was ignored when fitting the regression, and only the data having a decreasing abundance were used for analysis (solid circles).

3.4.2 Differences in growth between habitats

The AGR of striped bass larvae and juveniles ranged from 0.12 to 1.16 mm·d⁻¹. In the pelagic zone, larvae distributed in the UP exhibited a significantly higher AGR compared to the O-ETM (one-way ANOVA: $F_{1,64} = 10.36$, $p = 0.002$, Fig. 3.4). In July, the mean AGR in the littoral zone was also higher in the UP than in the M-ETM (one-way ANOVA: $F_{2,109} = 7.382$, $p = 0.001$). However, the AGR of striped bass was similar among all estuarine habitats in August (one-way ANOVA: $F_{2,60} = 2.847$, $p = 0.066$) and September (one-way ANOVA: $F_{2,44} = 2.496$, $p = 0.095$; Fig. 3.4).

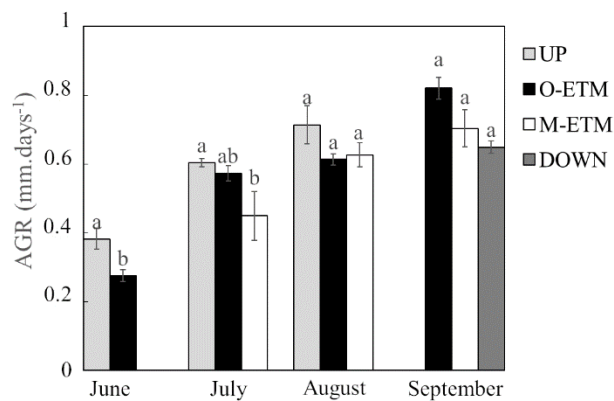


Figure 3.4 Comparison of mean absolute growth rates (AGR) for striped bass early life stages between estuarine habitats for samples collected from June to September 2014. Vertical lines represent standard errors. Bars with different letters indicate groups

having significantly different mean values according to pairwise multiple comparisons tested for significant differences ($p < 0.05$) with the appropriate p -value adjustments.

In the pelagic zone, growth trajectories back-calculated from 4 to 6 days showed that striped bass larvae in the UP grew faster than larvae in the O-ETM (Fig. 3.5; one-way MANOVA: $F_{1,42} = 0.158$, $p = 0.014$). Growth trajectories of striped bass aged 4 to 25 days that were captured in July in the littoral zone varied significantly between habitats (Fig. 3.5; one-way MANOVA: $F_{8,194} = 2.299$, $p = 0.022$). Individuals aged 5–25 days sampled in the UP were significantly larger than individuals of the same age caught downstream in the M-ETM. Striped bass in the O-ETM were intermediate in size (length-at-age); length-at-age was therefore not significantly different from the growth trajectories observed in the UP and the M-ETM (except for striped bass at day 5 and day 25 in the O-ETM being larger than same-aged individuals in the M-ETM). In August, 4–60-day growth trajectories of striped bass were similar among habitats (Fig. 3.5; one-way MANOVA: $F_{22,74} = 1.323$, $p = 0.186$). In September, striped bass growth trajectories, back-calculated for 4–70 days, were also similar among the estuarine habitats, although growth trajectories in the O-ETM were greater than those in the DOWN (Fig. 3.5; one-way MANOVA: $F_{26,42} = 1.557$, $p = 0.099$).

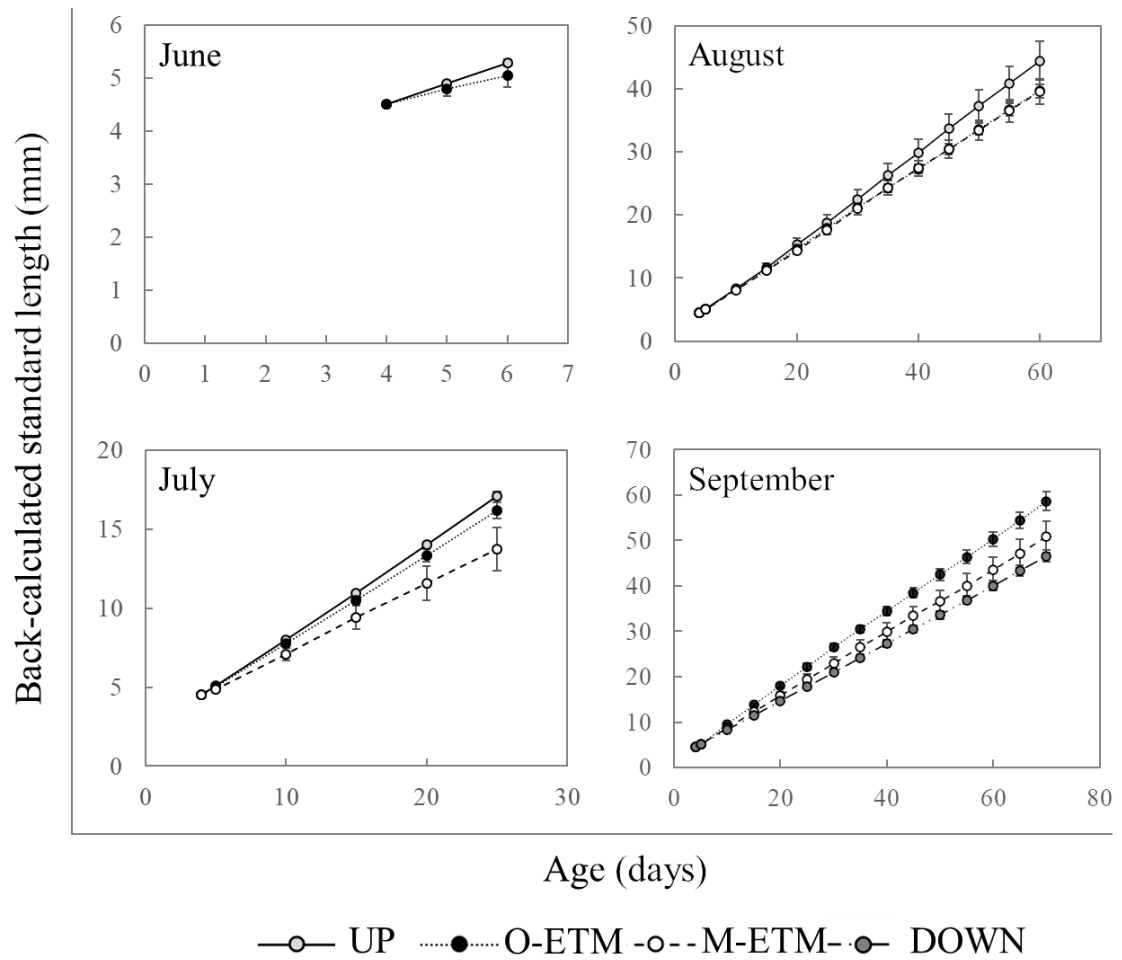


Figure 3.5 Comparison of back-calculated growth trajectories of striped bass sampled from the different estuarine habitats, June–September 2014. Vertical lines represent standard error. Growth trajectories were established at age four days, i.e. the biological origin intercept.

3.4.3 Differences in habitat utilization and growth between migratory contingents

Using the otolith microchemistry of 36 striped bass captured in September 2014, we reconstructed their habitat utilisation from hatching to 90 days of life. Striped bass caught in September hatched slightly more often in the UP (58.3%) than in the O-ETM (41.7%). We observed downstream movements of young-of-the-year striped bass given that at age 90 days, 30.4% were distributed in the DOWN and 17.4% were found in the M-ETM. However, the O-ETM remained the most frequented habitat for striped bass (39.1%) after 90 days, and only a few young-of-the-year striped bass were found in the UP habitat in September at the end of the survey period (13.0%; Fig. 3.6).

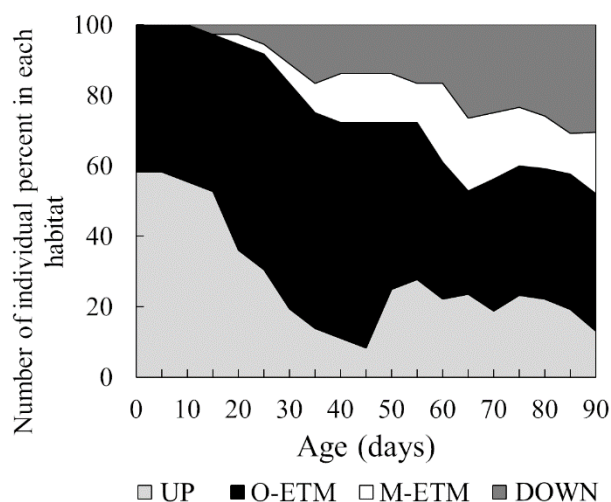


Figure 3.6 Proportions of individuals (%) per habitat over their age. Age estimates are based on otolith microchemistry for 36 striped bass caught in September 2014. Habitats are represented in light grey for UP, black for O-ETM, white for M-ETM, and dark grey for DOWN.

Growth-class frequencies for striped bass showed similar distribution patterns among the habitats (two-sample Kolmogorov–Smirnov tests with Bonferroni corrections, all

$p > 0.05$; Fig. 3.7) However, AGR were slightly higher for striped bass in the UP and the O-ETM (median: 0.70–0.84) compared to the M-ETM and DOWN (median: 0.55–0.69 $\text{mm}\cdot\text{d}^{-1}$).

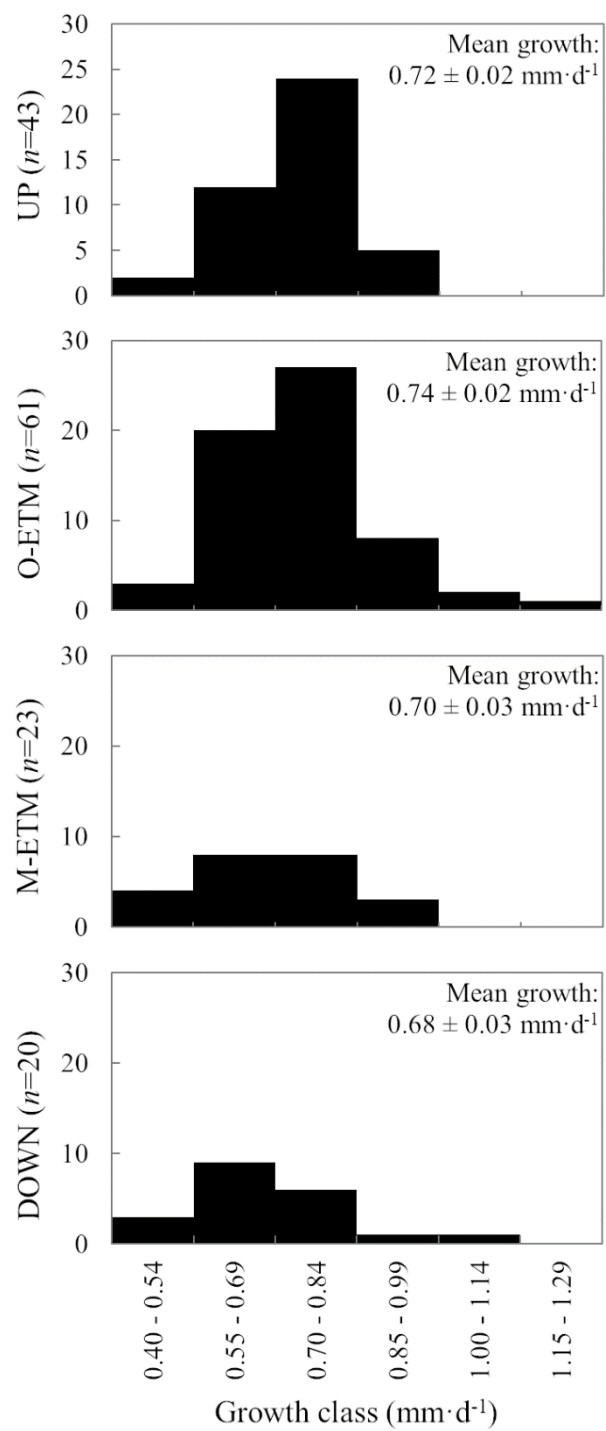


Figure 3.7 Growth frequency distribution of 147 growth segments assigned to the corresponding habitat. Growth reconstruction for each occupied habitat is based on past habitat utilisation and growth reconstructions for 36 striped bass caught in September 2014. Growth segments are described for the growth class of 0.15 mm·d⁻¹.

Patterns of habitat use (Fig. 3.6) reflected the presence of three migratory contingents. We defined freshwater residents as striped bass that remained in and used the two upstream habitats (UP and O-ETM; 24.5%; $n = 12$). Striped bass that transited at least once to the M-ETM and DOWN habitats were characterised as M-ETM migrants (26.5%; $n = 13$) or DOWN migrants (49.0%; $n = 12$), respectively. Back-calculated growth trajectories were compared among migratory contingents from 5 to 70 days. Freshwater residents grew faster than migrants and had significantly higher growth than DOWN migrants (Fig. 3.8; one-way MANOVA: $F_{26,42} = 1.944$, $p = 0.027$). Length-at-age for M-ETM migrants was not different from that observed for DOWN migrants, except at age 30 and at age 35 when M-ETM migrants were significantly longer than DOWN migrants. Thus, at the moment of capture in September, resident striped bass had a higher SL ($F_{2,36} > 7.61$, $p = 0.002$), higher body depth ($F_{2,36} > 8.357$,

$p = 0.001$), and higher wet mass ($F_{2,36} > 7.728$, $p = 0.002$) than DOWN migrants (Fig. 3.9).

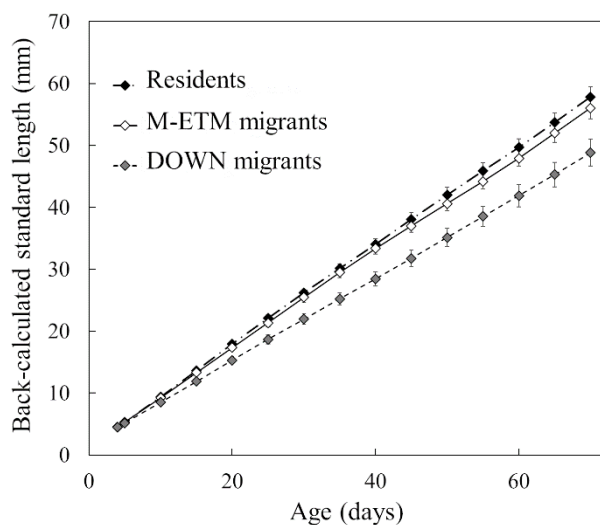


Figure 3.8 Mean back-calculated growth trajectories for freshwater residents, M-ETM migrants, and DOWN migrants of striped bass sampled in September 2014. Error bars represent standard error. Starting point of growth trajectories was set at four days, i.e. the biological origin intercept.

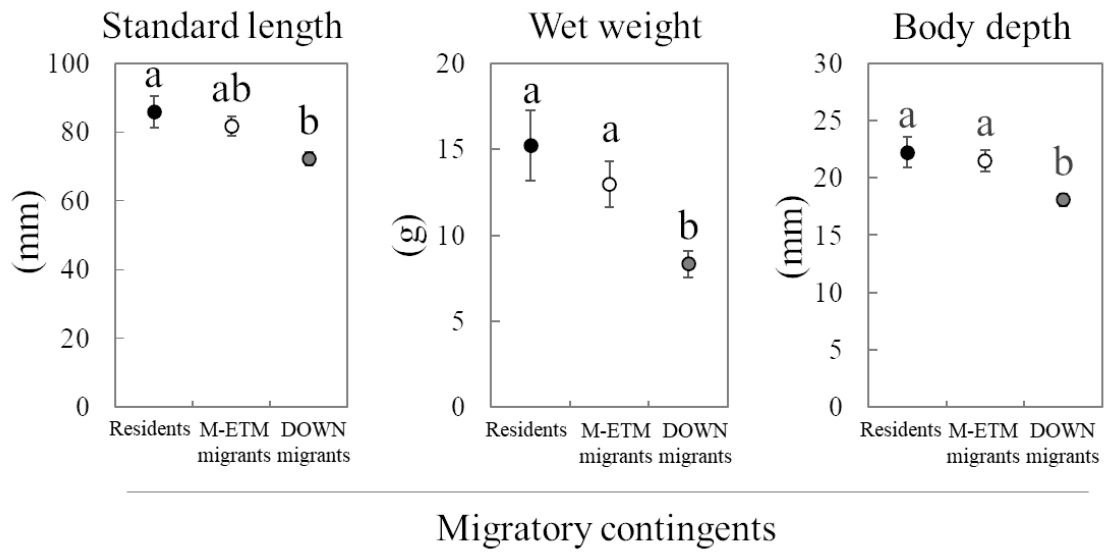


Figure 3.9 Comparison of standard length (mm), wet weight (g), and body depth (mm) (measured from striped bass caught in September 2014) between migratory contingents of residents (black circles), M-ETM (white circles), and DOWN migrants (dark-grey circles). Error bars represent standard error. Values with different letters indicate significant differences of mean values according to pairwise multiple comparisons testing for significant differences ($p < 0.05$) with the appropriate p -value adjustments.

3.5 Discussion

During their first growing season, young-of-the-year striped bass of the re-established SLE population exhibited important contrasts in terms of mortality-dispersion and growth along the estuary.

3.5.1 Mortality and dispersion along the estuary

Mortality-dispersion rates estimated for the SLE population are comparable with previous studies in two nursery areas of Chesapeake Bay, which has similar physical properties to the UP and O-ETM habitats (Secor and Houde 1995, Rutherford *et al.* 1997). For the striped bass population of Chesapeake Bay, mean daily decrease rates (Z) of striped bass larvae were $19 \pm 3\%$ in the Potomac River and $67 \pm 0.5\%$ in the upper Chesapeake Bay estuary. In the SLE, mortality and dispersion rates were three times greater for pelagic larvae inhabiting the UP than larvae in the O-ETM. Starvation, predation, and dispersion are the main causes of mortality that affect the early life stages of fishes (Hjort 1914, Cushing 1990). In the SLE, the study of gut contents revealed that larvae distributed in the UP had more often empty guts compared to striped bass from the O-ETM, suggesting that starvation may be an important cause of mortality in this specific habitat (Vanalderweireldt *et al.* in prep-b). Compared to the UP, the O-ETM habitat was particularly turbid, thereby offering an advantage for larval fish in terms of feeding and reducing risks from predation. As turbid environments accentuate the visual contrast of coloured prey and the background, energy investment into foraging may be decreased (Sirois and Dodson 2000-b), while the risk of predation for the translucent larvae is simultaneously reduced (Utne-Palm 2002, De Robertis *et al.* 2003). In the SLE, there is a possibility that the lower Z values of striped bass in the UP may also be induced by passive or active dispersion of striped bass larvae along the four estuarine habitats. By active vertical movement into water masses of different current speeds and direction, fish larvae with reduced swimming capacity may be able to adjust their position and migrate between habitats in the St. Lawrence estuary (Laprise and Dodson 1990, Gibson *et al.* 2001, Simon *et al.* 2006).

We observed comparable patterns in the littoral zone: daily decrease rates (Z) of striped bass early life stages were six times higher in the UP compared to the O-ETM, at 0.9%

and 5.6%, respectively. Differences in Z between the littoral zones of the UP and the O-ETM stem from both striped bass mortality and dispersion. In the SLE, feeding incidence and success, which were found to be higher in the O-ETM than the UP (Vanalderweireldt *et al* in prep-b), also suggest a higher potential of starvation in the UP than in the O-ETM. Striped bass survival in the O-ETM, may be greater due to a reduced predation pressure from the higher turbidity, similar to that observed in the pelagic O-ETM (Utne-Palm 2002, De Robertis *et al.* 2003).

Furthermore, white perch co-occur in the SLE and may compete for resources and/or provide a size-dependent predation on the early life stages of striped bass. White perch is a congener species of striped bass and they share very similar feeding niches (Limburg *et al.* 1997, St-Hilaire *et al.* 2002). Predation by white perch juveniles on striped bass larvae is suspected to be an important cause of mortality in other systems (McGovern and Olney 1988, Monteleone and Houde 1992).

In the littoral zone, passive dispersal of larvae might have less of an effect on the decrease rate of abundance than for larvae in the pelagic zone, as the retention potential increases for older-staged fish due to their greater swimming capacity (Beamish 1978). The coexistence of several littoral retention zones in the SLE may promote the retention of older early life stages (Laprise and Dodson 1990, Lecomte 2005). The middle estuary of the St. Lawrence is characterised by large bays and shoals along the south shore of the O-ETM, M-ETM, and DOWN; these are believed to contribute to the retention of plankton (Lecomte 2005, Simons *et al.* 2006, St-Onge-Drouin *et al.* 2014). Hence, we hypothesise that from June to September 2014, striped bass in the UP were affected by high starvation and predation, and then dispersed toward the O-ETM. This would explain the strong daily abundance decrease rate in the UP. In contrast, the lower abundance decrease rate observed in the O-ETM was likely due to a reduction in starvation and predation mortality and the arrival of migrating individuals from the UP.

3.5.2 Comparison of growth among estuarine habitats

Observed growth rates of striped bass during the first growing season for the re-established SLE population are consistent with those of the Miramichi River population in the Gulf of St. Lawrence. This latter population is the source population for the SLE restoration program. Both populations experience similar environmental conditions in terms of latitude and length of the growing season. Robichaud-Leblanc *et al.* (1998) observed slow growth rates for larvae sampled in June ($0.32 \text{ mm}\cdot\text{d}^{-1}$) in the Miramichi River. However, juveniles caught from July to September experienced increased growth rates, ranging from $0.75\text{--}1.15 \text{ mm}\cdot\text{d}^{-1}$. Further south, the AGRs of larval striped bass in Chesapeake Bay are similar to those of the SLE population, ranging from 0.06 to $0.48 \text{ mm}\cdot\text{d}^{-1}$ (Shideler 2011). Juvenile striped bass collected from the Hudson River also exhibited comparable mean growth during the summer ($0.8 \text{ mm}\cdot\text{d}^{-1}$; Dey 1981) as that of the SLE population.

For pelagic larvae, AGRs and length-at-age were both higher in the UP compare to the O-ETM. For July, AGRs and length-at-age were both higher for striped bass in the UP than the M-ETM. In contrast, AGRs and growth trajectories were similar for littoral habitats in August and September, although our results suggest that growth decreased further downstream. Growth is a direct consequence of diet quality, the abundance of food resources, the lipid quality of prey, and the energy costs allocated to foraging (Sirois and Dodson 2000-b, Robert *et al.* 2014, Pepin *et al.* 2015). Differential growth rates and length-at-age are further supported by the significant differences prey distribution and availability as well as in feeding characteristics between estuarine habitats (Vanalderweireldt *et al.* in prep-a, in prep-b). In the SLE, contrasts in striped bass growth also reflect differences in the physical characteristics of the habitats (Vanalderweireldt *et al.* in prep-a). The growth of fish in their early life stages can be affected by water temperature (Rutherford and Houde 1996, Secor *et al.* 2000) and

salinity (Secor *et al.* 2000, Boeuf and Payan 2001). In the SLE, the higher water temperatures (18.1–24.2 °C) in the UP and the O-ETM, compared to habitats further downstream (Vanalderweireldt *et al.* in prep-a), are better for growth (Secor *et al.* 2000, Duston *et al.* 2004) while the higher salinity of the M-ETM and DOWN, (Vanalderweireldt *et al.* in prep-a) and osmoregulation may also impose important physiological costs that negatively affect the growth of striped bass (Secor *et al.* 2000, Duston *et al.* 2004). In the coming decades, it is likely that climate changes will induce important changes in estuarine habitat features. For the new population of striped bass, the climate change may probably promote the advantage of downstream habitats.

3.5.3 Migratory contingents as an adaptive strategy

Individual reconstruction of habitat use confirmed the findings of Morissette *et al.* (2016). Only 12 years after the first stocking, we observed differential migratory behaviour within the re-established striped bass population. We found three migration contingents, which suggests that an adaptive migration strategy exists within this population, potentially to increase recruitment. We also showed that the re-established SLE population can meet its needs by searching for and exploiting other habitats than their natal habitats, and this migration can begin as soon as they become juveniles. Migration strategies are adaptive processes to a given environment. Several studies have emphasised the influence of habitat quality and suitability as key factors for initiating this migration behaviour (Chapman *et al.* 2011, Secor 2015). In some cases, migration processes are distress signals due to a suboptimal habitat, forcing individuals to migrate and search for more suitable conditions that meet their needs (Dingle and Drake 2007, Secor, 2015). Size-dependent emigration may also represent a trade-off between increased predation risk and increased forage opportunities within a new habitat.

What drove young striped bass to migrate in the St. Lawrence estuary? The growth trajectories, SL, mass, and body depth traced by contingency affiliation show how resident striped bass in the UP and O-ETM benefited from existing conditions when compared to migrants. At the onset of growth, we suspect that migrants did not encounter the necessary resources to perform as well as the residents, possibly because of high intraspecific competition. Our findings lend support to suboptimal environmental conditions being responsible for migration downstream of the O-ETM habitat, even if the lower turbidity and clearer waters in the DOWN (Vanalderweireldt *et al.* in prep-a) increases the risk of predation. The benefit of a migration to more saline habitats, which are generally highly productive environments, may be moderated by the energetic cost of this migration (Secor 2015). Migrants into the DOWN had different feeding niches and a higher feeding success than striped bass distributed in the upstream habitats (Vanalderweireldt *et al.* in prep-b). Striped bass migrants to the M-ETM and DOWN may find new feeding opportunities, represented by mysids especially abundant in the M-ETM. In contrast, highly competitive, fast-growing striped bass remained in the UP and O-ETM and exploited the upstream habitats where conditions seemed to be optimal. Overall, downstream migration are likely an advantageous tactic to increase the potential of survival of less competitive and smaller individuals.

3.6 Conclusions

Our results in the SLE highlight the contribution of the UP and O-ETM habitats in the SLE as the main nurseries during the early life history of striped bass. These nursery habitats are essential for the recruitment of the new population, as compared to more downstream habitats. Given that mortality or dispersal was highest in the UP, striped

bass may experience important levels of intraspecific competition, high predation pressure, and/or resource limitation in this habitat, thereby selecting individuals for fast growth. Thus, a few very successful striped bass may stay in the UP, whereas less successful striped bass die or disperse further downstream. The O-ETM habitat provides likely optimal conditions where striped bass were usually more abundant, had lower mortality-dispersal rates, and experienced faster growth. This study confirmed the coexistence of three migratory contingents in the SLE. Freshwater residents are distinguished from migrants by their higher growth rates and other morphological attributes. Our findings lend support to the idea that suboptimal conditions are responsible for migrant behaviour to sites downstream of the O-ETM habitat, even if the energetic costs of migration are significant and predation risk is increased. These results emphasise the potential advantage of downstream migration as an ingenious tactic for increasing the potential survival of poor competitors.

3.7 Acknowledgements

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CHAPITRE IV

CONCLUSION GÉNÉRALE

Cette étude doctorale contribue à l'approfondissement de nos connaissances sur l'écologie des jeunes stades de vie des poissons dans les milieux estuariens. De juin à septembre, les habitats estuariens du Saint-Laurent ont été caractérisés dans la zone pélagique, et pour la première fois, dans la zone littorale. Tout au long de la saison de croissance, cette étude identifie les facteurs environnementaux abiotiques et biotiques qui vont avoir une incidence sur l'alimentation, la croissance et la mortalité des jeunes stades de vie du bar rayé. L'étude de l'utilisation des habitats estuariens a permis de confirmer une seconde fois la coexistence de plusieurs patrons de migration divergents au sein de la nouvelle population. La nouvelle population de bar rayé du Saint-Laurent est actuellement engagée dans un processus de ré-établissement, et revêt un grand intérêt écologique par les stratégies qu'elle exhibe. L'identification des habitats essentiels au recrutement de la nouvelle population est un apport crucial qui sera utile à l'élaboration d'une gestion favorisant le ré-établissement du bar rayé.

4.1 Caractérisation des habitats estuariens du Saint-Laurent dans la zone pélagique et littorale

4.1.1 Caractérisation physique des habitats estuariens

De juin à septembre, quatre habitats estuariens ont été caractérisés dans la zone pélagique et littorale :

(1) le premier habitat estuarien, appelé **UP** correspond à la portion d'eau douce et se distingue par sa faible turbidité, ses plus chaudes températures et sa teneur en oxygène dissous modérée;

(2) Le second habitat, l'**O-ETM**, correspond à la section oligohaline de l'ETM et est caractérisé par une salinité très faible, une très forte turbidité, une température élevée et une oxygénation de son eau modérée.

(3) Le troisième habitat estuarien, appelé ici **M-ETM**, correspond à la section mésohaline de l'ETM. Il est caractérisé par un accroissement très important de la salinité, une très forte turbidité, de plus fraîches températures et une augmentation de la teneur en oxygène dissous.

(4) Le quatrième habitat estuarien, appelé **DOWN** est caractérisé par une salinité polyhaline, des eaux claires beaucoup plus froides et une oxygénation accrue.

4.1.2 Caractérisation biologique des habitats estuariens

De juin à septembre, les habitats estuariens ont montré des contrastes biologiques importants le long des gradients de salinité-turbidité, décrits dans cette étude en termes de concentration de chlorophylle-*a*, d'abondance de proies et d'assemblages ichtyologiques.

En juin, les habitats pélagiques UP et O-ETM ont montré des concentrations plus élevées de chl-*a* et des densités plus importantes de cladocères *Bosmina* sp., de cyclopoïdes et de copépodes *Eurytemora affinis*. Plus en aval, une forte densité de cyclopoïdes et de calanoïdes fut observée dans l'habitat M-ETM, et une très forte densité de calanoïdes dans l'habitat DOWN. Dans la zone pélagique, l'abondance de l'ichtyoplancton augmentait le long du gradient de salinité. Les assemblages de larves de poisson étaient dominés par le baret (*Morone americana*) dans l'UP; le baret, le bar rayé et l'éperlan arc-en-ciel (*Osmerus mordax*) dans l'O-ETM et par l'éperlan-arc-ciel dans les habitats amont.

De juillet à septembre, les concentrations de chl-*a* estimées le long du littoral étaient supérieures dans l'habitat O-ETM. L'habitat UP présentait peu de proies, principalement représenté par les gammaridés, et plus faiblement par les pupes de diptères. Au contraire, une plus forte abondance de proies a été estimée dans l'ETM, représentée essentiellement par les gammaridés dans l'O-ETM et les mysidacés dans le M-ETM. Tout au long de la saison de croissance, peu de proies ont été identifiées dans l'habitat DOWN comparé aux autres habitats estuariens. Le long du littoral, l'abondance de poissons était très homogène entre les habitats. Cependant, les assemblages ichtyologiques différaient de par leurs compositions. En juillet, l'habitat UP était dominé par des taxons d'eau douce tels que l'alse savoureuse (*Alosa sapidissima*), les catostomidés, et la perchaude (*Perca flavescence*) tandis que les habitats en aval étaient dominés par le baret et l'éperlan arc-en-ciel. En août, l'alse savoureuse et les catostomidés étaient dominants dans l'UP, tandis que le baret était très abondant dans l'O-ETM et M-ETM. En septembre, le fondule barré (*Fondulus diaphanus*) et la perchaude étaient les principaux contributeurs de l'UP. Dans les habitats O-ETM et M-ETM, le baret était de nouveau le taxon le plus abondant tandis que l'habitat DOWN était dominé par l'éperlan arc-en-ciel et l'épinoche tachetée (*Gasterosteus wheatlandi*).

4.2 Écologie des jeunes stades de vie du bar rayé

4.2.1 Utilisation des habitats estuariens des larves et juvéniles du bar rayé

Au cours de la première saison de croissance, les larves et les juvéniles du bar rayé ont montré une utilisation dynamique de l'ensemble des habitats estuariens.

En juin, les larves pélagiques du bar rayé étaient concentrées principalement dans l'habitat O-ETM. Dans une moindre mesure, une densité beaucoup plus faible de larves a été observée dans l'habitat UP. De récentes études suggèrent l'utilisation de deux frayères par la nouvelle population de bar rayé (1) à l'embouchure de la rivière du Sud, dans l'O-ETM et (2) à proximité du port de Québec dans l'UP (Fisheries and Ocean Canada 2017, Valiquette *et al.* 2017). En juin, la distribution des larves de bar rayé concorde fidèlement avec la localisation de ses deux frayères.

Dans les habitats UP et O-ETM, les larves de bar rayé vont évoluer dans un environnement d'eau douce à légèrement saumâtre et dans des conditions idéales de température, propice au développement des jeunes stades du bar rayé (Secor *et al.* 2000, Duston *et al.* 2004). En effet, les processus d'osmorégulation mis en place lors de l'accroissement de la salinité entraînent un coût physiologique important chez les poissons. De plus, la diminution importante de la température le long du gradient de salinité pourrait ralentir la croissance et le développement des jeunes stades. De surcroît, les conditions d'alimentation et de survie des larves de bar rayé pourraient être favorisées dans l'habitat O-ETM. Dans un habitat turbide tel que l'O-ETM, la plus forte turbidité pourrait favoriser la détection visuelle des proies pigmentées tandis que les larves translucides seraient quant à elles plus difficilement détectables par les prédateurs (Miner et Stein 1996, Abrahams et Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003).

Dans l'UP et l'O-ETM, les larves de bar rayé vont trouver des densités importantes de ses proies préférentielles, le cladocère *Bosmina* sp., et le copépode *E. affinis* (Robichaud-LeBlanc *et al.* 1997, Shideler et Houde 2014). Dans ces deux habitats, les larves se maintiennent dans des habitats de plus faibles densités ichtyoplanctoniques, dominés principalement par le baret et l'éperlan arc-en-ciel. Ces résultats suggèrent que les larves de bar rayé sont sujettes à une faible compétition interspécifique dans les habitats UP et O-ETM.

Dès juillet, nos résultats confirment l'utilisation de la zone littorale et de l'ensemble des habitats estuariens par le bar rayé. En juillet, le bar rayé était distribué principalement dans l'UP, à proximité de la frayère de la rivière du Sud. En août et septembre, les bars rayés occupaient essentiellement les habitats O-ETM et M-ETM. Plusieurs études suggèrent que les conditions de salinité et de température des habitats UP, O-ETM et M-ETM seraient plus propices au développement des juvéniles du bar rayé que dans l'habitat DOWN (Cox et Coutant 1981, Cech *et al.* 1984, Secor *et al.* 2000, Duston *et al.* 2004, Cook *et al.* 2010). De plus, les fortes valeurs de turbidité mesurées dans l'O-ETM et le M-ETM pourraient favoriser l'alimentation des bars rayés tout en réduisant les risques de prédation (Miner et Stein 1996, Abrahams et Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003).

De juillet à septembre, les habitats O-ETM et M-ETM étaient caractérisés par de fortes abondances de proies contrairement aux habitats UP et DOWN. L'abondance des poissons du littoral était homogène le long du gradient de salinité, suggérant une compétition interspécifique similaire entre les habitats estuariens. Cependant, les jeunes bars rayés ont rencontré des assemblages ichtyologiques très distincts le long du gradient de salinité. En juillet, les bars rayés étaient concentrés dans l'habitat UP où l'assemblage ichtyologique était dominé par l'alose savoureuse, les catostomidés, et la perchaude. En août et septembre, le bar rayé était distribué principalement dans les habitats O-ETM et M-ETM où le baret était le taxon dominant.

Dans la zone pélagique, l'UP et l'O-ETM offrent un environnement propice au développement des larves de bar rayé de par les propriétés biophysiques de ces habitats et où la compétition interspécifique semble réduite. Cependant, la très forte turbidité mesurée dans l'O-ETM pourrait favoriser les conditions d'alimentation et réduire le risque de prédation comparé à l'habitat UP. Dans la zone littorale, l'habitat O-ETM offre de nouveau les meilleures conditions pour l'alimentation et le développement des jeunes stades de vie du bar rayé. Dès août, l'habitat M-ETM offre un compromis écologique intéressant entre l'accès à de nouvelles proies, représentées par les mysidacés, et l'accroissement du coût physiologique induit par la salinité mésohaline et les plus faibles températures. Au contraire, DOWN semble être l'habitat le moins propice au développement des jeunes bars, où l'environnement physique semble très coûteux physiologiquement et les ressources peu abondantes comparées à l'ETM. Tout au long de la saison de croissance, la distribution des jeunes stades de vie du bar rayé était très semblable à celle du baret. Le baret est une espèce congénère qui se caractérise par une niche écologique très similaire au bar rayé, et ainsi, qui pourrait constituer un important compétiteur (Limburg *et al.* 1997, St-Hilaire *et al.* 2002, Shoji *et al.* 2005).

4.2.1 Alimentation des jeunes stades de vie du bar rayé

De juin à septembre, le bar rayé a montré une alimentation généraliste et diversifiée, influencé aussi bien par son ontogénie que par sa distribution dans l'estuaire du Saint-Laurent.

Au début de l'alimentation exogène, les larves de bar rayé se sont nourries principalement de copépodes et de diatomées dans l'UP, de copépodes et de cladocères *Bosmina* sp. dans l'O-ETM. Les larves distribuées dans l'O-ETM présentaient une incidence et un succès d'alimentation plus importants que pour l'habitat UP, bien que

ces différences n'étaient pas significatives. L'amélioration des conditions d'alimentation suggérée dans l'O-ETM pourrait résulter de la contribution plus importante du cladocère *Bosmina* sp. dans l'alimentation des larves issues de l'O-ETM comparé à l'UP. De plus, les eaux turbides de l'O-ETM pourraient favoriser la détection des proies pigmentées, ce qui pourrait être un avantage important pour l'alimentation des larves (Boehlert et Morgan 1985, De Robertis *et al.* 2003).

À partir de juillet, les bars rayés de plus grandes tailles ont montré un changement drastique d'alimentation, composée de proies plus énergétiques. En juillet et août, nos résultats suggèrent que les bars rayés étaient de plus grande taille et avaient de meilleures conditions d'alimentation dans l'UP comparé à l'O-ETM et le M-ETM. En juillet, l'alimentation était principalement composée de pupes de diptères dans l'habitat UP et de gammaridés *Gammarus* sp. dans l'O-ETM et le M-ETM. En août, les jeunes bars ont consommé principalement des pupes de diptères, des gammaridés et des copépodes dans l'UP et l'O-ETM et des mysidacés dans le M-ETM. En septembre, l'alimentation des bars rayés était dominée par les gammaridés dans l'O-ETM et le M-ETM et par les mysidacés dans le DOWN. En septembre, nos résultats suggèrent que de plus petits bars rayés ont migré vers l'habitat DOWN où nous avons observé une augmentation significative du succès d'alimentation.

Le long du littoral, cette étude souligne l'alimentation opportuniste du bar rayé, dont la composition de l'alimentation est à l'image de la distribution de ses proies.

Les résultats de cette étude soulignent l'importance des pupes de diptère dans l'alimentation des bars de l'habitat UP. Toutefois, l'habitat UP présentait une faible abondance de proies, principalement représenté par les gammaridés, et moindrement par les pupes. Nous suggérons qu'une très forte consommation de pupes de diptère par les poissons du littoral pourrait s'opérer dans l'habitat UP, réduisant significativement son abondance. Cet écart important pourrait aussi s'expliquer par une sélection chez le

bar rayé en faveur des pupes de diptère qui constituent des proies de plus haute valeur calorifique comparativement aux gammaridés (Cummins and Wuycheck 1971, Wissing et Hasler 1971). Dans les habitats O-ETM et M-ETM, la composition de l'alimentation du bar rayé concorde fidèlement avec les fortes abondances de gammaridés et de mysidacés observés dans ces habitats. En septembre, les bars rayés distribués dans l'habitat DOWN se sont nourris principalement de mysidacés qui constituent aussi des proies de haute valeur nutritive (Tyler 1973). Ces résultats contrastent avec la faible abondance de mysidacés estimée dans l'habitat DOWN. Nous suggérons que cet écart important pourrait résulter d'une exploitation importante des mysidacés par les poissons du littoral et/ou d'une sous-évaluation de leurs abondances. Les mysidacés sont des organismes rapides, difficiles à échantillonner et qui pourraient se regrouper en amas d'individus.

Lors des premiers stades du développement du bar rayé, cette étude suggère de meilleures conditions pour l'alimentation des larves distribuées dans l'O-ETM puis chez les juvéniles des habitats UP et O-ETM. À partir de juillet, le bar rayé présente un changement drastique dans son alimentation, influencé par son ontogénie et lui permettant probablement d'optimiser son développement. L'élasticité des comportements d'alimentation de l'espèce lui permet de se disperser dans tous les habitats estuariens et d'occuper différentes niches écologiques. En exploitant l'ensemble des habitats estuariens, le bar rayé réduit probablement la compétition inter- et intraspécifique et améliore son potentiel de survie.

4.2.3 Mortalité et dispersions des larves et des juvéniles de bar rayé

De juin à septembre, les valeurs de mortalité – dispersion estimées à partir de courbes de captures étaient entre trois à six fois plus importantes dans l’habitat UP que dans l’O-ETM. Chez les jeunes stades de vie, ces estimés de mortalité– dispersion peuvent s’expliquer soit par la mortalité associée au jeûne et à la prédation, soit par la dispersion des jeunes stades entre les habitats (Hjort 1914, Anderson 1988, Cushing 1990). En juin, les larves de bar rayé présentaient une incidence d’alimentation trois fois plus importante dans l’O-ETM comparée à l’UP, suggérant une mortalité associée au jeûne réduite dans l’O-ETM. De plus, la très forte turbidité de l’habitat O-ETM offre un refuge visuel chez les larves et les juvéniles peu colorés, ce qui pourrait réduire la mortalité associée à la prédation (Miner et Stein 1996, Abrahams et Kattenfeld 1997, Utne-Palm 2002, De Robertis *et al.* 2003). Dans l’estuaire du Saint-Laurent, il est aussi vraisemblable que les processus de dispersion jouent un rôle majeur dans les estimations de décroissance des habitats UP et O-ETM. Dans le Saint-Laurent, les larves de bar rayé pourraient avoir la capacité de se disperser dans les habitats estuariens, comme cela a déjà observé chez les larves d’éperlan-arc-ciel et de poulamon Atlantique (Dodson *et al.* 1989, Laprise et Dodson 1989, 1990). En ajustant leurs positions verticales dans la colonne d’eau, les larves utilisent différentes masses d’eau leur permettant de se mouvoir (Norcross et Shaw 1984, Gibson *et al.* 2001). Dès juillet, nous suggérons que les jeunes bars rayés aient été moins affectés par le courant qu’en milieu pélagique, étant donné que le potentiel de rétention s’accroît avec la taille et les capacités natatoires des individus (Beamish 1978). De plus, la présence de nombreuses zones de rétention le long du littoral suggère que les jeunes bars ont pu se maintenir plus facilement dans les habitats estuariens (D’Anglejan *et al.* 1981, St-Onge-Drouin

et al. 2014), comme cela a été confirmé pour l'éperlan arc-en-ciel (Laprise et Dodson 1989, Lecomte 2005).

4.2.4 Croissance des larves et des juvéniles de bar rayé

Cette étude de doctorat souligne des différences importantes des taux de croissance du bar rayé le long du gradient de salinité. En juin, les larves pélagiques distribuées dans l'UP présentaient des croissances plus rapides que dans l'O-ETM. De juillet à septembre, cette étude suggère des taux de croissance plus importants chez les bars rayés distribués dans l'UP et l'O-ETM, comparés aux habitats plus en aval. En utilisant la chimie des otolithes, nous avons été capables de relier la croissance passée en fonction de l'occupation des habitats estuariens. Ces dernières analyses supportaient de nouveau que les bars rayés présentaient de plus forts taux de croissance dans les habitats UP et O-ETM comparativement aux habitats M-ETM et DOWN.

La croissance est principalement affectée par les propriétés biophysiques de l'habitat (Secor *et al.* 2000, Duston *et al.* 2004), la qualité de l'alimentation (Wainright *et al.* 1996, Castonguay *et al.* 2008, Robert *et al.* 2009, 2014, Pepin *et al.* 2015) et les pressions de sélection (Miller *et al.* 1988, Takasuka *et al.* 2003, 2007). Les propriétés de l'habitat physique dans lequel les jeunes bars rayés évoluent peuvent entraîner des coûts physiologiques différents et ainsi, influencer l'énergie allouée pour la croissance. De précédentes études ont montré que les eaux plus turbides pourraient positivement influencer la croissance en favorisant la détection de proies et ainsi, en réduisant les dépenses énergétiques allouées à la recherche de nourriture (Sirois et Dodson 2000-b, Utne-Palm 2002, Shoji *et al.* 2005). De surcroît, les plus fortes salinités et les plus faibles températures mesurées dans les habitats M-ETM et DOWN pourraient engendrer un coût physiologique important chez les jeunes stades de vie et influencer

négalement la croissance (Rutherford et Houde 1996, Secor *et al.* 2000, Boeuf et Payan 2001, Duston *et al.* 2004).

En juin, nos résultats suggèrent de meilleures conditions d'alimentation dans l'O-ETM comparé à l'UP pour le développement des larves. En juillet, les habitats UP et O-ETM semblent supporter les conditions les plus propices à l'alimentation du bar rayé. En septembre cependant, les bars rayés distribués dans le DOWN présentaient un meilleur succès d'alimentation comparé aux habitats amont. Ces résultats nous suggèrent que la croissance du bar rayé ne peut pas s'expliquer uniquement par son alimentation.

Enfin, les différences de croissance observées entre les habitats pourraient s'expliquer en partie par une plus forte pression de sélection dans l'habitat UP, comme le suggèrent les valeurs importantes de mortalité et dispersion. Dans l'habitat UP, les bars rayés aux croissances rapides seraient enclins à un meilleur potentiel de survie de par la réduction de la période de forte mortalité des premiers stades (Chambers et Leggett 1987, Houde 1987) et par la diminution des pressions de prédatons comparées à leurs conspécifiques (Miller *et al.* 1988, Takasuka *et al.* 2003, 2007). Lors des premiers stades de développement, la survie n'étant pas aléatoire parmi les individus d'une cohorte donnée; elle serait donc sélective dans l'habitat UP pour les croissances rapides.

À la lumière de ces résultats, la croissance du bar rayé ne peut s'expliquer par un unique facteur, mais plutôt par un ensemble de facteurs résultants de l'habitat biophysique, de l'alimentation et des pressions de sélection. On peut ainsi penser que les bars rayés distribués dans l'habitat O-ETM bénéficient des meilleures conditions biophysiques pour la croissance. À l'opposé, l'habitat DOWN semble être l'habitat le plus coûteux énergétiquement, peu propice au développement des jeunes stades de vie du bar rayé.

4.2.5 Mouvements migratoires au sein de la nouvelle population de bar rayé

La reconstitution des mouvements migratoires passés confirme pour la seconde fois la coexistence de trois contingents migratoires au sein de la nouvelle population de bar rayé du Saint-Laurent (Morissette *et al.* 2016). L'étude de l'occupation passée des habitats estuariens suggère (1) un contingent résident des habitats UP et O-ETM, deux contingents migrants (2) vers l'habitat M-ETM et (3) vers l'habitat DOWN. Le maintien de trois patrons de migration divergents deux ans après la précédente étude (Morissette *et al.* 2016) suggère une structure migratoire qui est stable dans le temps.

Dans l'estuaire du Saint-Laurent, quel mécanisme est à l'origine des comportements de migration du bar rayé ? Les bars rayés résidents sont caractérisés par des croissances plus rapides et des caractéristiques morphologiques supérieures comparées aux migrants. Nous émettons l'hypothèse que les comportements de migration ont été induits par des conditions défavorables à l'alimentation et à la croissance des jeunes stades de vie. Par conséquent, les migrations sont des processus adaptatifs et conditionnels qui permettent aux individus moins compétitifs de partir à la recherche d'habitats plus propices à leur développement et à leur survie. Les migrations sont des compromis écologiques entre le coût physiologique associé au déplacement, l'augmentation des risques de prédation et l'opportunité d'accroître son potentiel de survie par la découverte d'un habitat plus favorable (Secor 2015).

Enfin, la diversité des comportements migratoires et l'utilisation extensive de l'estuaire démontrent la diversité des habitats essentiels à la nouvelle population du bar rayé du Saint-Laurent. Dès juillet, une portion importante des bars rayés entreprend des migrations en aval vers les habitats M-ETM et DOWN. Pour autant, les comportements de résidence dans les habitats UP et O-ETM sont fréquents chez la nouvelle population. La reconstitution de l'utilisation passée des habitats montre que près de 78% des migrants occupaient toujours l'UP et l'O-ETM après 30 jours, et que 46 % occupaient

toujours l'UP et l'O-ETM après 60 jours. Ainsi, loin de diminuer l'importance des habitats estuariens M-ETM et DOWN, ces résultats soulignent la contribution de l'ensemble des habitats estuariens pour le développement des jeunes stades de vie de la nouvelle population de bar rayé. La coexistence de mouvements de migration divergents démontre les capacités adaptatives de cette nouvelle population, capable de rechercher et d'exploiter tous les habitats estuariens donc elle a besoin pour se ré-établir, et ce, dès le stade juvénile. Afin de favoriser la pérennité et le rétablissement du bar rayé, les mesures de gestion ne doivent pas se focaliser uniquement sur l'habitat le plus productif, mais protéger l'ensemble des habitats estuariens utilisé par la nouvelle population. La diversité et le maintien de mouvements migratoires divergents de résidence et d'exploration contribuent aux mécanismes de régulation de la nouvelle population du bar rayé, et assurent sa stabilité, sa résilience et sa productivité.

Depuis 2013, les travaux issus du réseau de suivi annuel du recrutement du bar rayé suggèrent une abondance stable des juvéniles dans les habitats UP et O-ETM (Valiquette *et al.* 2017). Il est vraisemblable que la capacité de support des habitats UP et O-ETM soit déjà atteinte et ainsi, que la compétition intraspécifique soit à l'origine des migrations vers les habitats M-ETM et DOWN. Auquel cas, les habitats UP et O-ETM ne seraient donc plus en mesure de supporter de nouveaux individus et la taille maximale de la population dans ces deux habitats serait déjà atteinte. De cette façon, on pourrait s'attendre à ce que l'accroissement démographique de la nouvelle population de bar rayé favorise l'expression des contingents migrants. La saturation des habitats UP et O-ETM serait à l'origine des comportements de migration vers des habitats alternatifs. Sur ce dernier point, les observations issues du réseau de suivi confirment l'augmentation constante des juvéniles migrants depuis 2013 (Valiquette *et al.* 2017).

4.3 Recrutement de la nouvelle population de bar rayé : qui sont les survivants ?

Les résultats obtenus lors de cette étude sont en accord avec les hypothèses de croissance mortalité qui orientent la recherche sur l'écologie des jeunes stades de vie (Pepin 1991, Meekan et Fortier 1996, Sirois et Dodson 2000-a, Shima et Findlay 2002, Shoji et Tanaka 2006, Pepin *et al.* 2015). De juin à septembre, nos résultats montrent une augmentation importante de la croissance moyenne chez le bar rayé, suggérant que les survivants sont des individus aux croissances rapides. Lorsque l'on compare la croissance journalière au cinquième jour de développement des larves de bars rayés échantillonnés en juin ($0,36 \pm 0,02 \text{ mm}\cdot\text{jr}^{-1}$) et des survivants échantillonnés en juillet ($0,54 \pm 0,01 \text{ mm}\cdot\text{jr}^{-1}$), août ($0,60 \pm 0,02 \text{ mm}\cdot\text{jr}^{-1}$) et septembre ($0,66 \pm 0,03 \text{ mm}\cdot\text{jr}^{-1}$), nos résultats suggèrent une forte sélection à la faveur des croissances rapides.

Plusieurs facteurs peuvent expliquer la sélection pour les croissances rapides, de par justement la réduction de la période de très forte mortalité lors des premiers stades de vie (hypothèse du *stage-duration* Chambers et Leggett 1987, Houde 1987). Les résultats de cette étude suggèrent un accroissement très important de la croissance journalière au cinquième jour de développement entre juin et juillet. En outre, les valeurs de mortalité-dispersion sont 11 à 17 fois plus importantes en juin qu'en juillet et septembre pour les habitats UP et O-ETM respectivement. Ces résultats supportent l'existence d'une première période critique de très forte mortalité chez les larves de bar rayé.

La sélection pour les croissances rapides peut aussi s'expliquer par le fait que les individus aux plus fortes croissances seraient moins vulnérables à la prédation que leurs conspécifiques (hypothèse du *bigger-is-better*, Miller *et al.* 1988) et plus aptes à l'évitement des prédateurs (hypothèse de *growth-selective predation*, Takasuka *et al.* 2003, 2007). Sur ce dernier point, nous ne savons pas pour le moment dans quelle mesure les jeunes stades de vie du bar rayé seraient exposés à une forte pression de

prédation. Bien que non documentée dans l'estuaire du Saint-Laurent, la prédation par le baret sur les jeunes stades de vie du bar rayé est une cause importante de mortalité dans d'autres systèmes (McGovern et Olney 1988, Monteleone et Houde 1992).

Dans les habitats estuariens, les processus spatiaux dont les mécanismes d'écoulement, de rétention et la connectivité entre les habitats sont susceptibles d'influencer la survie des jeunes stades et le recrutement des populations de poisson (Sinclair 1988, North et Houde 2003, Houde 2008). Dans la baie de Chesapeake, plusieurs études ont souligné l'impact des régimes hydrologiques sur le recrutement du bar rayé (North et Houde 2003, 2006). Dans l'estuaire du Saint-Laurent, les régimes d'écoulement subissent d'importantes fluctuations spatio-temporelles, influencées principalement par les marées et les crues printanières (Simons *et al.* 2010). Les variations des régimes d'écoulement sont susceptibles d'affecter le recrutement de la nouvelle population par la modification des propriétés biophysiques des habitats estuariens, par l'altération des zones de rétention larvaire et par la diminution de la connectivité entre les habitats. Pour autant, nous ne connaissons pas l'influence du régime hydrologique du fleuve Saint-Laurent sur le succès de recrutement de la nouvelle population.

Enfin, bien que nous ayons observé des valeurs de mortalité-dispersion plus fortes dans l'UP que dans l'O-ETM, nos résultats montrent que ces deux habitats ont contribué à parts égales au recrutement de la nouvelle population. En effet, les résultats issus de la chimie des otolithes ont montré qu'en septembre, les bars rayés survivants provenaient aussi bien de l'habitat UP (58%) que de l'O-ETM (42%).

Dans l'estuaire du Saint-Laurent, il est vraisemblable que la nouvelle population de bar rayé soit sujette à une seconde période de forte mortalité, lors de la période hivernale. Les populations les plus septentrionales de bar rayé sont caractérisées par une remontée automnale en eau douce à légèrement saumâtre pour se soustraire des basses températures de l'eau de mer. En hiver, les conditions climatiques très rudes pourraient

engendrer chez les jeunes de l'année une mortalité sélective pour la taille (Hurst et Conover 1998, 2003, Martino *et al.* 2012). À l'automne, les individus en dessous d'une certaine taille n'auraient pas les réserves nécessaires pour survivre à un jeûne prolongé et seraient en outre plus sujets à la prédation. Nous ne savons pas pour le moment dans quelle mesure la période hivernale affecte le recrutement de la nouvelle population de bar rayé. Sur ce dernier point, un projet de recherche en collaboration avec le MFFP et le CREAE est actuellement en cours et permettra de documenter cette deuxième période de forte mortalité.

4.4 Désignation de l'habitat essentiel des larves et des juvéniles de bar rayé dans l'estuaire du Saint-Laurent

Lors du stade larvaire, l'UP et l'O-ETM forment des habitats d'alevinage essentiels à l'alimentation, la croissance et la survie des larves de bar rayé et contribuent à parts égales au recrutement de la nouvelle population. Cependant, une plus forte pression sélective pourrait s'exercer dans l'habitat UP, et favoriserait la sélection de larves performantes aux croissances rapides. À l'inverse, l'habitat O-ETM a montré de meilleures conditions pour l'alimentation où les larves de bar rayé, plus abondantes, présentaient une mortalité réduite. Tout au long de la saison de croissance, les conditions les plus favorables à l'alimentation, à la croissance et à la survie du bar rayé ont été identifiées dans l'habitat O-ETM de par ses propriétés physiques, et l'abondance de ses proies. Dès juillet, les bars rayés du littoral se sont dispersés dans tous les habitats estuariens. En élargissant leurs répartitions, ils ont très probablement réduit la compétition intraspécifique des habitats amont en exploitant de nouvelles ressources. Plus tard dans la saison, l'habitat M-ETM semble fournir un compromis écologique intéressant pour le développement de l'espèce avec un environnement

certes plus coûteux physiologiquement, mais permettant l'exploitation d'une nouvelle niche écologique. L'étude de la croissance suggère que les individus résidents de l'UP et l'O-ETM étaient caractérisés par des croissances plus rapides comparées aux migrants. L'étude de l'alimentation souligne néanmoins l'avantage des migrations tardives vers l'habitat DOWN, permettant à l'espèce d'améliorer ses conditions d'alimentation et d'exploiter de nouvelles ressources. La dispersion du bar rayé dans l'ensemble des habitats estuariens démontre les capacités adaptatives de cette nouvelle population, capable de coloniser de nouveaux habitats estuariens pour augmenter son potentiel de survie et se ré-établir.

4.5 Contribution et originalité de l'étude

Cette thèse de doctorat est une étude pionnière sur l'écologie de la nouvelle population du bar rayé dans l'estuaire du Saint-Laurent. Cette étude s'inscrit directement dans les objectifs fixés par le *Programme de rétablissement du bar rayé* qui vise le maintien d'une population autonome (Robitaille *et al.* 2011). Elle répond à un besoin d'approfondir les connaissances sur l'utilisation des habitats estuariens et la capacité de support du Saint-Laurent. Par ailleurs, les résultats présentés soulignent la nécessité de considérer l'ensemble de l'écosystème comme unité de gestion pour favoriser le rétablissement de l'espèce. Au cours des prochaines années, elle permettra la mise en place de mesures d'une gestion éclairée et de prises de décisions réglementaires basées sur une meilleure information. Dans l'estuaire du Saint-Laurent, la nouvelle population de bar rayé est toujours sujette à d'importantes pressions anthropiques, à l'origine de la disparition de la population ancestrale. Au cours des prochaines années, il est vraisemblable que la demande pour l'ouverture de la pêche augmentera exigeant, entre autres, une meilleure compréhension du recrutement de l'espèce. En outre, la

croissance du trafic maritime pourrait accentuer les travaux de dragage et menacer l'habitat du bar rayé (ex. : entretien de la voie navigable, agrandissement des zones portuaires, etc.). Toutefois, la diversité des comportements migratoires de la nouvelle population suggère une tolérance importante de l'espèce aux perturbations induites par les activités humaines.

Cette thèse de doctorat apporte une contribution originale au domaine de l'écologie des jeunes stades de par son sujet d'étude. Le bar rayé, engagé dans un processus de rétablissement est un exemple probant de colonisation d'un milieu par une nouvelle espèce. Le processus en cours dans l'estuaire du Saint-Laurent pourrait ainsi s'apparenter à une expérience à grande échelle. Les informations acquises soulignent la complexité des comportements migratoires du bar rayé, qui utilisent et s'adaptent à l'ensemble des habitats estuariens du Saint-Laurent. De plus, cette étude se distingue de par le fait qu'elle documente l'écologie des jeunes stades, et ce, tout au long d'une saison de croissance. Elle enrichit nos connaissances sur l'utilisation de l'estuaire comme pouponnière à poisson. Dans l'estuaire du Saint-Laurent, de nombreuses études ont permis la caractérisation du milieu pélagique (Winkler *et al.* 2003, Martineau *et al.* 2004, Favier et Winkler, 2014, Cabrol *et al.* 2015). Par contre, la zone littorale n'avait jamais été documentée, alors qu'elle est très largement utilisée par les jeunes stades de vie des poissons.

Enfin, l'originalité de cette thèse tient aussi du fait nous avons été capables de combiner les résultats issus de la microstructure des otolithes et de la chimie des otolithes. Par ces analyses, nous avons déterminé une croissance instantanée en fonction de l'occupation de l'habitat. Peu d'études ont à ce jour relié la croissance journalière avec l'occupation de l'habitat chez les jeunes stades, et portaient principalement sur l'anguille *Anguilla* sp. (Arai *et al.* 1997, Marui *et al.* 2001, Chen *et al.* 2008, Kuroki *et al.* 2008).

4.6 Limitation de l'étude

Lors de cette étude doctorale, il existe une discontinuité importante dans la méthodologie effectuée pour capturer les larves et les juvéniles du bar rayé. En juin, les larves de bar rayé ont été échantillonnées en milieu pélagique en utilisant un filet bongo. De juillet à septembre, les jeunes de l'année ont été échantillonnés le long du littoral à la seine de rivage. Cette différence de méthodologie est fondée sur l'hypothèse que les larves de bar rayé sont pélagiques, tandis que les juvéniles effectuent une première migration vers la zone littorale où ils recherchent des eaux peu profondes et abritées (Robichaud-Leblanc *et al.* 1998, Robitaille 2004). Cette différence de procédés se traduit dans nos données par une catégorie de taille que l'on n'a pas réussi à échantillonner, de longueur standard entre 9 et 15 mm. Il aurait été judicieux de vérifier cette hypothèse en échantillonnant simultanément les zones pélagiques et littorales. De plus, nous ne pouvons écarter l'hypothèse que les larves de bar rayé habitent elles aussi la zone littorale. Ce dernier point aurait pu être documenté par un échantillonnage de l'ichtyoplancton le long du littoral.

Une limite importante de cette étude de doctorat provient aussi de la désignation des habitats. Lors de l'identification des habitats estuariens, des analyses de regroupement ont été utilisées à partir des propriétés physiques de l'environnement, sans prendre en compte la connectivité entre les stations. Dans l'estuaire du Saint-Laurent, le chenal séparant les deux rives est une barrière physique importante qui pourrait influencer l'organisation spatiale des communautés de poissons (Lecomte, 2005). Il serait ainsi très intéressant de documenter les aptitudes de dispersion et de migration des jeunes stades de vie du bar rayé le long du gradient de salinité. De plus, le microhabitat dans lequel les jeunes bars vont réellement évoluer n'a pas été pris en compte dans la définition des habitats estuariens. Dans l'estuaire du Saint-Laurent, les larves d'éperlan arc-en-ciel et le poulamon atlantique utilisent les migrations verticales couplées au

courant des marées pour se maintenir et s'alimenter (Laprise et Dodson, 1989). Il serait donc pertinent de décrire à une plus fine échelle le microhabitat dans lequel le bar rayé évolue.

Enfin, l'étude de l'alimentation des jeunes stades de vie du bar rayé est aussi limitée par le fait qu'elle est uniquement basée sur la dissection des contenus stomacaux. L'analyse des contenus stomacaux offre une image instantanée de l'alimentation. Cependant, certaines proies plus longues à digérer pourraient être surestimées dans les contenus stomacaux au détriment de proies plus rapides. Contrairement à l'étude des contenus stomacaux, les analyses isotopiques permettent de comprendre l'histoire, l'ontogénie de l'alimentation (Post 2002, Fry 2006). L'utilisation des analyses isotopiques du carbone et de l'azote permettent d'identifier la provenance du carbone et le niveau trophique de l'individu. Il aurait été pertinent aussi de documenter la sélectivité des proies par le bar rayé (ex. : indice de sélectivité, Schoener 1968). Bien que l'alimentation du bar rayé semble opportuniste, les résultats de cette étude suggèrent que le bar rayé pourrait avoir des proies préférentielles.

4.7 Perspectives de recherche

Cette thèse doctorale répond à un besoin de documenter l'établissement de la nouvelle population de bar rayé. Il n'en demeure pas moins que l'approfondissement de nos connaissances suscite de nouvelles questions quant à la gestion de l'espèce et ouvre la voie vers de nouvelles perspectives de recherche.

4.7.1 La nouvelle population de bar rayé, au cœur d'un processus de rétablissement

La nouvelle population de bar rayé de l'estuaire du Saint-Laurent est actuellement engagée dans un processus de rétablissement, et revêt un grand intérêt écologique de par le modèle théorique qu'elle prodigue. Lors de l'établissement d'une espèce, la nouvelle population va façonner son écosystème et influencer son réseau trophique (altération des flux d'énergie, compétition, mortalité sélective, etc.; Mittelbach *et al.* 1995, Sarrazin et Barbault 1996, Ripple et Beschta 2012). Dans l'estuaire du Saint-Laurent, le bar rayé est un super prédateur en haut de la chaîne trophique. Son rétablissement est susceptible d'avoir de profondes répercussions sur son habitat. Il est ainsi probable que les habitats biologiques décrits dans cette thèse ne soient plus à l'image de la situation actuelle ou future. Dans ce contexte, un nouvel échantillonnage des habitats biologiques dans les zones pélagiques et littorales permettrait d'éclaircir ce point. Un nombre réduit de stations clefs représentatives des habitats estuariens pourraient être revisités. Ces nouvelles connaissances nous permettraient de documenter l'influence du rétablissement du bar rayé sur son écosystème.

D'autre part, les suivis standardisés effectués par le MFFP suggèrent un accroissement démographique important de la nouvelle population du bar rayé depuis 2013 (Fisheries and Oceans Canada 2017). Auquel cas, on pourrait s'attendre à ce que l'augmentation du bar rayé dans l'estuaire du Saint-Laurent engendrerait des répercussions importantes sur l'écologie de la population et sur ses comportements de migration. Ce dernier point pourrait être documenté par l'utilisation des échantillons des jeunes de l'année issus du réseau de suivi standardisé du recrutement du bar rayé (Fisheries and Oceans Canada 2017). Pour cela, les bars rayés juvéniles pourraient être disséqués pour l'étude des contenus stomacaux, la microstructure et la microchimie des otolithes en utilisant la même méthodologie que lors de cette étude de doctorat. Cette nouvelle étude nous permettrait de dresser un portrait global des mécanismes sous-jacents au recrutement de l'espèce, et de vérifier la pérennité future de nos résultats.

4.7.2 Modèle d'utilisation des habitats estuariens par le bar rayé

Les estuaires sont de véritables pouponnières à poisson, et sont très utilisés par le bar rayé (Robichaud-Leblanc *et al.* 1996, Able *et al.* 2012). Dans cette étude de doctorat, nous avons été capables de décrire différents habitats estuariens et de documenter leurs utilisations par l'espèce. Il serait intéressant de comparer la distribution et l'utilisation des habitats estuariens le long du gradient de salinité entre les populations américaines de bar rayé. Auquel cas, cette étude pourrait fournir un outil technique pour caractériser les habitats estuariens, et un modèle conceptuel pour la gestion du bar rayé. Plusieurs études ont souligné la forte association des larves de bar rayé avec le copépode *E. affinis* et le cladocère *Bosmina* sp. dans la région du front salin et de la ZTM (North et Houde 2006, Martino et Houde 2010, Campfield et Houde 2011). Peu d'études se sont intéressées aux migrations tardives des juvéniles dans les habitats estuariens (Robichaud-Leblanc *et al.* 1998, Mohan *et al.* 2015). Similairement à notre étude, des mesures de salinité et de turbidité pourraient être utilisées dans d'autres systèmes afin de caractériser les habitats estuariens. En Amérique du Nord, le bar rayé fait l'objet de nombreux suivis standardisés, comme dans la baie de Chesapeake (Durell et Weedon 2011, Northeast Fisheries Science Center 2013, Fisheries and Oceans Canada 2017). Une comparaison de l'utilisation de l'habitat entre différentes populations de bar rayé permettrait d'améliorer nos connaissances sur le fonctionnement des systèmes estuariens, sur l'écologie du bar rayé et sur son habitat essentiel. Selon les différents modèles d'utilisation des habitats, ces nouvelles connaissances pourraient nous permettre d'affiner nos prédictions quant au rétablissement du bar rayé dans l'estuaire du Saint-Laurent.

4.7.3 Relation interspécifique du bar rayé

Très bien adapté aux estuaires, le bar rayé constitue l'un des piscivores les plus importants de ce milieu et ainsi, représente un élément important de la biodiversité. Dans l'estuaire du Saint-Laurent, la réintroduction d'un prédateur comme le bar rayé a vraisemblablement influencé les assemblages ichtyologiques. Suite au rétablissement de l'espèce, il semble aujourd'hui important de décrire les relations du bar rayé avec les autres espèces de poisson qui pourraient constituer ses proies, ses prédateurs ou ses compétiteurs. Dans l'estuaire du Saint-Laurent, la population ancestrale de bar rayé avait fait l'objet de peu d'études décrivant ses interactions avec les autres espèces (Robitaille 2001, 2005, 2010), ce qui ne nous permet pas aujourd'hui de statuer de son impact (Robitaille *et al.* 2011). Lorsqu'une nouvelle population se reconstitue, on s'attend à ce qu'il y ait une redistribution des ressources au sein de l'écosystème. Ainsi, les ressources exploitées par le bar rayé pour être néfaste à la productivité d'autres espèces de poisson. Bien que non documentées, plusieurs espèces piscivores pourraient rentrer en compétition avec le bar rayé comme le doré (*Sander* sp.) et le baret, espèce congénère du bar rayé (Robitaille et Girard 2002). Les connaissances recueillies dans cette thèse mettent en lumière la forte association du bar rayé avec le baret. Cette association entre les deux espèces a aussi été observée dans la baie de Chesapeake (North et Houde 2003, 2006, Campfield et Houde 2011), et les rivières du Nouveau-Brunswick (Mansueti 1964, Thistle 2011), suggérant que le bar rayé et le baret recherchent les mêmes types de proies et d'habitat. Dans l'estuaire du Saint-Laurent, les travaux réalisés par le réseau de suivi du recrutement annuel soulignent l'augmentation de la présence des barets juvéniles (Fisheries and Oceans Canada 2017). L'accroissement démographique des populations de bar rayé et de baret pourrait suggérer l'existence d'un prédateur commun et ainsi, d'une division des pressions de prédation entre les deux espèces. En outre, la prédation du baret sur les jeunes stades de vie du bar rayé est une importante cause de mortalité dans d'autres systèmes (McGovern et Olney 1988, Monteleone et Houde 1992). Enfin, il est aussi probable que le rétablissement du bar rayé ait modifié la distribution d'autres espèces de poisson

dans l'estuaire du Saint-Laurent. Une meilleure connaissance de ce réseau d'interactions permettrait le développement d'indicateurs sur l'état de santé de la nouvelle population et des espèces avec lesquelles le bar interagit tout en veillant à ce que son rétablissement ne se fasse pas au détriment des espèces indigènes.

Sur ce dernier point, l'étude des contenus stomacaux des poissons du littoral permettrait d'éclaircir les relations de compétition et de prédation dans l'estuaire du Saint-Laurent. Il s'agirait ici d'analyser un sous-échantillon des poissons échantillonnés lors de cette étude de doctorat. Cette étude permettrait de documenter :

- (1) les espèces qui utilisent les mêmes niches écologiques et qui risquent de rentrer en compétition avec les jeunes stades de vie du bar rayé pour les ressources
- (2) les prédateurs des jeunes stades de vie du bar rayé.

Sur ce deuxième point, il serait aussi judicieux de compléter cette étude par un nouvel échantillonnage des espèces piscivores. Les poissons s'alimentent préférentiellement de proies plus petites, comme chez le bar rayé qui s'alimentent de proies de moins de 40 % de sa longueur totale (Hartman, 2000, Scharf *et al.* 2009). Il serait pertinent d'échantillonner des espèces piscivores de plus grande taille et susceptibles de consommer du bar rayé.

4.7.4 Indice d'habitat du bar rayé

Lors de cette étude doctorale, nous avons caractérisé quatre habitats estuariens de juin à septembre dans lequel le bar rayé évolue. Il serait cependant très intéressant de caractériser la niche spécifique des larves et des juvéniles du bar rayé. Pour cela, nous pourrions utiliser les données d'habitat à l'échelle de la station afin d'estimer un indice d'habitat : que préfère le bar rayé ? Quelles stations sont évitées par l'espèce ? Cet

indice d'habitat pourrait nous permettre de prédire la distribution future de l'espèce : seules les stations répondant au besoin du bar rayé seraient susceptibles d'être occupées. De plus, la création d'un indice d'habitat fondé sur la niche spécifique du bar rayé permettrait de prédire l'impact écologique de nouvelles perturbations, dont les changements globaux, sur la nouvelle population de bar rayé.

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