Émergences, aires de concentration et croissance des larves de hareng atlantique (*Clupea harengus*) dans l'estuaire moyen du Saint-Laurent

Mémoire présenté

dans le cadre du programme de maîtrise en Océanographie

en vue de l'obtention du grade de maître en sciences

PAR

© LAURENCE LÉVESQUE

Avril 2017

Composition du jury :

Jean-Claude Brêthes, président du jury, Université du Québec à Rimouski

Gesche Winkler, directrice de recherche, Université du Québec à Rimouski

Patrick Ouellet, codirecteur de recherche, Pêches et Océans Canada

Catherine Couillard, codirectrice de recherche, Pêches et Océans Canada

Pascal Sirois, examinateur externe, Université du Québec à Chicoutimi

Dépôt initial le 13-09-2016 Dépôt final le 24-04-2017

REMERCIEMENTS

Ce gros projet a pu être réalisé grâce à l'apport de nombreuses personnes et leur aide m'a été essentielle à la réalisation de ce mémoire. J'adresse mes remerciements à ma directrice, Gesche Winkler, qui savait me motiver et toujours m'aligner vers le bon chemin à prendre pour bon nombre de décisions. Ses talents en recherche en font une chercheure et professeure remarquable et ses conseils m'ont été forts utiles tout le long de ma maîtrise.

Je tiens à remercier aussi mes codirecteurs Catherine Couillard et Patrick Ouellet, sans qui ce projet n'aurait pas vu le jour. Leur expertise provenant de différents domaines m'a beaucoup apporté, a bien animé nos discussions et fait progresser mon travail de manière remarquable ! J'ai énormément appris avec eux, à développer ma curiosité intellectuelle et à parfaire mon parcours éducatif.

Ce projet a été mis sur la table avec Catherine, Patrick mais aussi Nadia Ménard, que je ne pourrai jamais assez remercier pour ce geste. Elle m'a offert sa confiance en m'offrant cette maîtrise et je lui en serai toujours très reconnaissante. J'ai vécu trois années merveilleuses à en apprendre sur ce petit poisson que je trouve maintenant fascinant ! Nadia a toujours été là pour m'appuyer dans les moments les plus durs (et les meilleurs aussi !) et savait comment me motiver au maximum, elle restera une figure importante au cours de ma vie, je n'en doute pas.

Je remercie également tous les gens qui m'ont aidé sur le terrain au cours de la saison. Je pense entre autre à Jean-Pierre Allard, Domynick Maltais, Peter Galbraith, Laure Devine, Gérard Therrien, Francis Lapointe, Manuela Conversano, Sarah Duquette, Samuel Turgeon, Pierre Beaufils, Félix Ledoux et Shona-Gabrielle Bélanger. Un merci spécial aussi à Guy Verreault qui m'a permis d'analyser quelques larves de ses échantillons, cela a apporté beaucoup à mes résultats.

Finalement, je remercie Québec Océan pour m'avoir apporté l'opportunité de parfaire mes connaissances dans le milieu de l'océanographie au Québec en participant à plusieurs colloques. Je remercie également l'UQAR pour m'avoir offert une bourse de mobilité pour un congrès international. Parcs Canada, la Direction des Sciences, la Gestion des Océans de Pêches et Océans, le MFFP et l'UQAR-ISMER ont aussi offert beaucoup pour le financement et la logistique pour que ce projet se réalise.

J'offre une pensée toute spéciale aussi à mes ami(e)s et collègues de l'ISMER, de Parcs Canada, mes proches et ma famille pour m'avoir supporté tout au long de ce projet. Merci !

RÉSUMÉ

L'unité reproductive de printemps de hareng atlantique (*Clupea harengus*) a subi un déclin important depuis le début des années 2000 dans le sud du golfe du Saint-Laurent. Une unité reproductive du printemps ainsi qu'une d'automne de la même métapopulation migreraient jusque dans l'estuaire moyen du Saint-Laurent pour se reproduire. Il n'y a pas eu d'étude sur le sujet depuis deux décennies. Pour mieux situer le statut du hareng dans l'estuaire, le premier objectif de l'étude consistait à vérifier si la distribution spatio-temporelle des aires de frai et de rétention est restée comparable à celle décrite il y a 20 ans, d'évaluer le nombre de cohortes produites, leurs abondances relatives et la persistance des larves de hareng dans l'aire d'étude. Le second objectif était d'explorer les différences de taux de croissance et de condition entre les cohortes en lien avec les variations de température. L'échantillonnage a été fait l'été 2014 à partir de petits bateaux de recherche en utilisant des filets bongo et conique ainsi qu'une sonde CTD. Les résultats ont révélé que la distribution spatio-temporelle des aires de frai n'avait pas changé. La densité relative de la cohorte de printemps reste plus élevée que celle d'automne dans l'estuaire moyen. De la rétention larvaire a aussi été détectée dans l'aire d'étude. Par contre, les stratégies de reproduction semblaient changées, car plus de cohortes sont apparues durant l'été, un résultat non démontré dans les études précédentes. La longueur des larves à l'émergence était plus grande pour celles qui ont émergé au printemps. Des différences de température ou de stratégies de reproduction pourraient être à l'origine de cette différence significative de longueur. Les taux de croissance différaient significativement entre cohortes, celles ayant émergé dans des températures plus chaudes grandissant plus vite. Cependant, en corrigeant pour les différences de températures en utilisant la somme des degrés-jours, la température n'était pas le seul facteur expliquant les différences observées entre les taux de croissance. La condition des larves ayant émergé au printemps était meilleure que pour celles émergées à l'été. Une combinaison entre la nourriture et la température peut influencer la croissance et la condition. Ces résultats appuient une recommandation de protection de l'estuaire moyen du Saint-Laurent entre mai et octobre, la période pendant laquelle le hareng y fraie, les larves y grandissent et y sont retenues. Les stades embryonnaires et larvaires sont vulnérables et différentes activités humaines pourraient avoir un impact sur le recrutement du hareng dans l'estuaire du Saint-Laurent.

Mots clés : Hareng atlantique, larves, taux de croissance, condition larvaire, température, cohorte, aire de rétention

ABSTRACT

The Atlantic herring (*Clupea harengus*) spring spawning unit has experienced a strong decline in the South of the Gulf of St. Lawrence since the beginning of the 2000s. Components of the same metapopulation would migrate in spring and fall into the St. Lawrence Middle Estuary to spawn. However, no studies have focused on the presence of herrings in this region for the last two decades. To better understand the status of the herring population, the first objective was to verify if the spatiotemporal distribution of herring spawning grounds remained the same as twenty years ago, to evaluate the number of larval cohorts produced, their relative abundance and the persistence of larvae in the study area. The second objective was to explore the differences in larval growth and condition among cohorts in relation to temperature variations. Sampling was conducted from small research vessels during the summer 2014, using bongo and conical nets and a CTD probe. My results revealed that spawning grounds and times were similar to those described 20 years ago. There was also no change in relative densities, with higher densities recorded in spring compared to those found in fall. Larval retention occurred as well in the study area. However, reproductive patterns have changed, as more larval cohorts appeared over the summer period. Length-at-hatch was larger for larvae hatched during springtime. Temperature and/or differences in strategies of reproduction could explain this significant difference. Growth rates of cohorts varied significantly according to hatching dates, with faster growth for cohorts hatched in the warmest months. Nevertheless, correcting for differences in temperatures by using the sum of degree-days of each cohort revealed that temperature was not the only environmental factor responsible for inter-cohort growth variation. Condition of larvae hatched in springtime was significantly better than that of larvae hatched in the summertime. Combination of food availability and temperature could influence the growth and the condition. These results support a recommendation to protect the St. Lawrence Middle Estuary from May to October, the time period when herring spawning, larval retention and growth occurred in this area. Embryonic and larval stages are vulnerable and human activities could impact herring recruitment in the St. Lawrence Estuary.

Keywords: Atlantic herring, larvae, growth rate, larval condition, temperature, cohort, retention area

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

MFFP	Ministère des Forêts, de la Faune et des Parcs
EMSL / SLME	Estuaire moyen du Saint-Laurent / St. Lawrence Middle Estuary
GSL	Golfe du Saint-Laurent / Gulf of St. Lawrence
OPANO / NAFO	Organisation des pêches de l'Atlantique Nord-Ouest / Northwest Atlantic Fisheries Organization
COSEPAC / COSEWIC	Comité sur la situation des espèces en péril au Canada / Committee on the Status of Endangered Wildlife in Canada
MPO / DFO	Pêches et Océans Canada / Fisheries and Oceans Canada
PMSSL / SSLMP	Parc marin du Saguenay–Satin-Laurent / Saguenay–St. Lawrence Marine Park
ZPM	Zone de protection marine
PC	Parcs Canada / Parks Canada
BRL	Banc de Rivière-du-Loup
ASA	Anse Sainte-Anne
MTZ	Maximum turbidity zone
LEP	Loi sur les espèces en péril

INTRODUCTION GÉNÉRALE

BIOLOGIE DU HARENG ATLANTIQUE

Le hareng atlantique (*Clupea harengus*) est un poisson pélagique et une espèce fourragère d'importance dans les écosystèmes marins et estuariens. C'est une espèce de clupéidé très étudiée et d'une importance capitale pour l'économie car il est pêché depuis longtemps (Kirkley *et al.*, 2011). Dans l'Atlantique Est, le hareng est retrouvé de la pointe sud du Groenland et de l'Islande jusqu'à la baie de Biscay au Sud et la mer de Barents au Nord (en incluant la mer du Nord et la mer Baltique), tandis que dans l'Atlantique Ouest, on le retrouve du Labrador (Terre-Neuve, Canada) à Cape Hatteras (Caroline du Nord, É-U) (Whitehead, 1985). L'estuaire moyen du Saint-Laurent (EMSL), situé au Québec, est une aire importante pour la reproduction de plusieurs espèces fourragères qui font partie du réseau trophique de la région, comme le hareng atlantique (*Clupea harengus*), le capelan (*Mallotus villosus*), l'éperlan arc-en-ciel (*Osmerus mordax*) et possiblement le lançon d'Amérique (*Ammodytes americanus*) (Laprise et Dodson, 1989; Fortier et Gagné, 1990; Fortier *et al.*, 1992).

Dynamique de reproduction du hareng Atlantique

Le hareng atlantique a probablement la structure de stock la plus complexe de tous les poissons (Iles et Sinclair, 1982). Il migre pour frayer dans les estuaires et les baies de l'Atlantique Nord plusieurs fois par an, surtout au printemps et à l'automne. Par exemple,

les unités reproductives de la mer Baltique, de la mer du Nord, de l'Islande et de la Norvège frayent à différents moments de l'année. Quant à elles, les unités reproductives du nord-est de l'Atlantique frayent en hiver-printemps et en été-automne, dépendamment de la température de l'eau (Cushing, 1967; Haegele et Schweigert, 1985). On observe également plusieurs évènements de frai au sein d'une même saison produisant différentes cohortes de larves. Dans la baie de Greifswald (mer Baltique), il y a deux évènements distincts d'émergence de hareng atlantique au printemps, une en mars/avril et une en avril/mai (Polte *et al.,* 2013). Plusieurs espèces de poissons démersaux et pélagiques utilisent une stratégie de succession de cohortes de larves. Ainsi, les cohortes de larves sont produites en vue d'être en synchronie avec la production de leurs proies (Lambert, 1984). Deux cohortes qui se suivent se nourrissent alors de copépodes ayant une taille différente, ce qui a pour effet de réduire la compétition entre cohortes, ou entre espèces. Par exemple, le hareng a une gueule plus grande que celle du capelan (*Mallotus villosus*) et peut se nourrir de copépodes plus gros que le capelan peut avaler (Lambert, 1984). De plus, des évènements de frai successifs contribuent à la survie des espèces itéropares puisque cette stratégie multiplie les chances de retrouver des conditions environnementales favorables à la croissance dans un habitat très variable comme l'EMSL (McQuinn, 1997a). Chez le hareng, ce sont les individus plus gros et plus âgés qui fraient en premier, les individus plus jeunes frayant plus tard dans la saison (McQuinn, 1997a).

Origine des migrateurs de l'EMSL et leur dynamique de reproduction

La population du nord-ouest de l'Atlantique est divisée en plusieurs unités de reproduction (« spawning populations » de McQuinn, 1997a) qui fréquentent diverses régions pour se reproduire. La pêche au hareng de la baie des Chaleurs (incluant l'estuaire maritime), de la Côte-Nord du golfe du Saint-Laurent (GSL) et de l'ouest de Terre-Neuve est gérée en trois zones de pêche, les sous-divisions 4R, 4S et 4T de l'Organisation des

Pêches de l'Atlantique Nord-Ouest (OPANO) (Figure 1), chacune ayant leurs propres unités de reproduction (McQuinn, 1997a). Le hareng qui migre dans l'estuaire moyen du Saint-Laurent (EMSL) proviendrait du sud du golfe (McQuinn, 1997a), utilisé comme aire d'alimentation et de croissance, et il a donc été inclus dans la sous-division 4T. L'unité reproductive frayant dans l'EMSL ferait donc partie d'une métapopulation. On décrit une métapopulation comme étant une gamme d'unités reproductives locales reliées ensemble par différents degrés de flux génétiques (McQuinn, 1997a). Cependant, les unités reproductives frayant au printemps et à l'automne dans St. Georges Bay en Nouvelle-Écosse, dans d'autres endroits du GSL et dans le golfe du Maine sont génétiquement distinctes (Kornfield *et al.,* 1982; Lambert, 1984; Lambert et Ware, 1984). Dans les années 1980, on décrivait une unité reproductive de hareng présente dans l'EMSL différente des autres harengs du GSL et caractérisée par des tailles plus petites et des otolithes de forme différente (Côté *et al.,* 1980; McQuinn, 1997a) et on le qualifiait de «pygmé». Par contre, une caractérisation génétique concluante n'a jamais été faite (Munro *et al.,* 1998). Une étude plus récente basée sur des analyses morphométriques (Lambert, 1990) démontra que ce phénotype dans l'unité reproductive du printemps, et plus précisément dans le site de frai de l'île Verte, existe encore. Ainsi, près de la moitié des harengs de l'EMSL émergerait et grandirait dans la population de l'île Verte, mais l'étude démontra aussi l'hypothèse qu'une certaine proportion (23%) des harengs se reproduisant dans l'EMSL aurait grandi ailleurs que dans l'estuaire, notamment dans le sud du GSL ou plus précisément dans le sud-ouest du golfe (Figure 1).

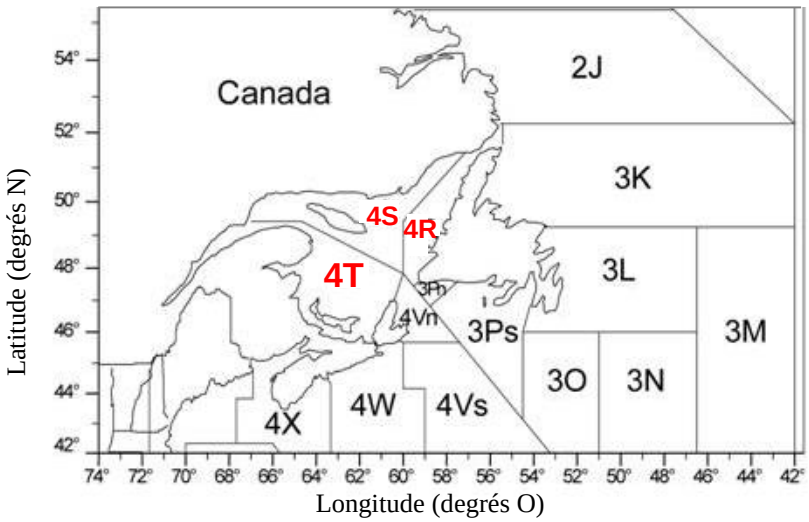


Figure 1. Carte des zones de pêche 4R, 4S et 4T de l'Organisation des Pêches de l'Atlantique Nord-Ouest (OPANO). Les zones en rouge sont situées dans le golfe du Saint-Laurent (COSEPAC, 2009).

Dans l'EMSL, le frai du hareng se produit en deux temps; au printemps et à l'automne (Fortier et Leggett, 1982; Fortier et Gagné, 1990; Munro *et al.*, 1998). Les deux unités reproductives sont morphologiquement différentes. Celle du printemps détient à 50% les caractéristiques des petits harengs «pygmés» de l'EMSL alors que celle d'automne, où les individus proviendraient en majorité du GSL, sont plus gros (McQuinn, 1997a). Les dates de frai ne semblent pas très variables d'une année à l'autre, mais les dates d'émergences semblent varier en fonction de la température de l'eau car elle influence le développement des œufs (Henri *et al.*, 1985; Bérubé et Lambert, 1997; Munro *et al.*, 1998). La berge ouest de l'île Verte a été la première frayère documentée dans l'EMSL (Côté *et al.*, 1980; Iles et Sinclair, 1982; McQuinn *et al.*, 1983; Fortier et Gagné, 1990; Lacoste *et al.*, 2001) (Figure 2). Par la suite, la pointe sud-ouest de l'île aux Lièvres a aussi été répertoriée comme une frayère importante (Munro *et al.*, 1998; Lacoste *et al.*, 2001)

(Figure 2). Des étalements substantiels d'œufs ont été retrouvés en zone côtière ainsi que sur les berges de la rive sud et des îles de l'EMSL (Munro *et al.*, 1998), notamment: l'archipel des îles de Kamouraska et des îles Pèlerins, l'île Rouge, l'île aux Pommes, la baie de Rivière-du-Loup, l'île aux Basques, l'archipel des îles Razades et l'île Saint-Barnabé (Figure 2). Par contre, lorsqu'utilisées, les frayères de l'île Verte et de l'île aux Lièvres restent les plus grosses frayères de cette unité de reproduction (Munro *et al.,* 1998).

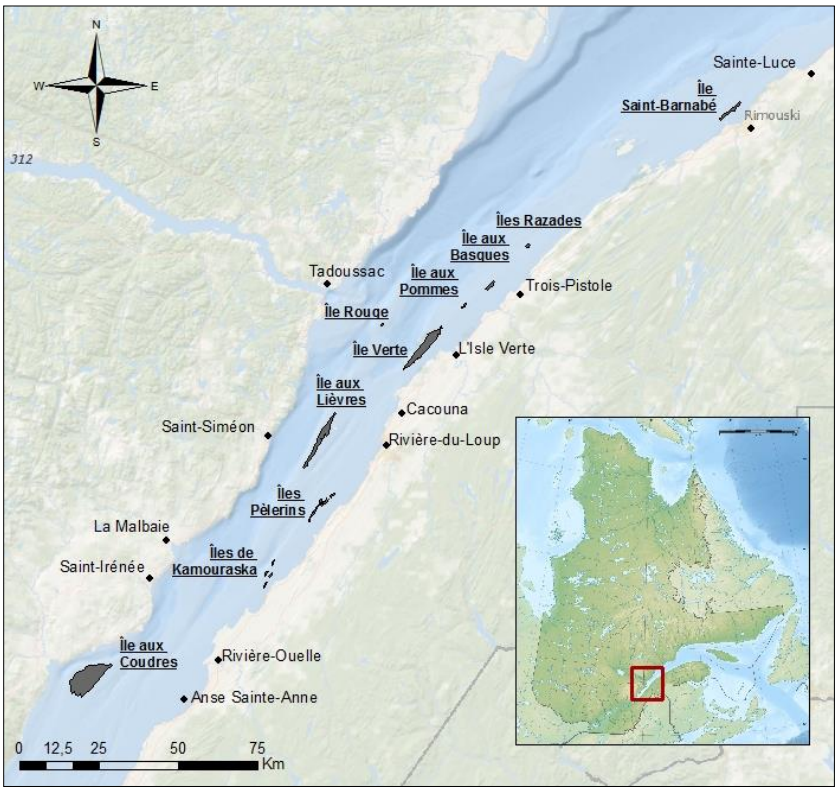


Figure 2. Carte illustrant les îles autour desquelles des œufs de hareng (Munro *et al.*, 1998) ont été retrouvés dans l'estuaire moyen et l'estuaire maritime du Saint-Laurent.

Historiquement, les larves de hareng émergent au printemps entre la mi-mai et le début de juin, généralement dans la première semaine de juin (Able, 1978; Fortier et

Leggett, 1982; McQuinn *et al.,* 1983; Munro *et al.,* 1998). Un second évènement d'émergence a été observée durant les premières semaines de juillet (Henri *et al.,* 1985). Quant aux reproducteurs d'automne, ils se regroupent vers la fin d'août dans les environs du chenal sud (Lacoste *et al.,* 2001). Le frai d'automne ne donnerais qu'une émergence, autour de la troisième semaine de septembre (Fortier et Gagné, 1990; Munro *et al.,* 1998). Finalement, le hareng est pêché à l'automne à Sainte-Luce et durant le printemps et l'été à Sainte-Luce et à Saint-Irénée (Figure 2), démontrant la présence de harengs adultes dans l'estuaire durant l'été (Bérubé et Lambert, 1997). Des harengs de printemps prédominaient dans la pêche à la fascine et l'examen des stades de maturité des harengs capturés en 1997 a montré que la plupart de ceux-ci auraient frayé en mai et juin (Bérubé et Lambert, 1997).

Abondance du hareng de printemps et d'automne dans l'EMSL

Peu d'études ont porté sur l'abondance du hareng de printemps et d'automne dans l'EMSL. Un suivi ichtyologique réalisé dans des pêches à fascine qui a eu lieu de 1986 à 1995 a démontré une abondance stable de hareng de printemps dans l'EMSL (Saint-Irénée, Cacouna; Figure 2), mais une augmentation des prises totales de hareng au début des années 1990 (Bérubé et Lambert, 1997). De plus, la densité larvaire moyenne observée dans les baies de l'anse Sainte-Anne et de Rivière-du-Loup (Figure 2) au cours des années 2002-2013 démontrait une grande variabilité (Bourget et Bélanger, 2015; Couillard *et al.*, 2017). Aucun suivi des pêches de harengs juvéniles et adultes dans l'ESML n'a été effectué après celui de Bérubé et Lambert (1997). Selon ces auteurs, d'après les variations des taux de capture dans les pêches à la fascine, le hareng adulte qui venait frayer à l'automne n'était plus présent de 1986 à 1995. Les résultats de la pêche à la senne dans la division 4T de l'OPANO indiquaient que la biomasse des géniteurs d'automne avait décliné dans les années 1970 (Cleary, 1983; MPO, 2005; LeBlanc *et al.,* 2012). Cependant, depuis le début des années 2000, les résultats des suivis de stock des géniteurs d'automne du ministère des

Pêches et des Océans du Canada (MPO) démontrent une augmentation et une certaine stabilité des taux de captures pour l'unité reproductive d'automne de la baie des Chaleurs, contrairement à la population des géniteurs de printemps, pour lesquels les relevés acoustiques et le suivi des débarquements démontrent une forte diminution depuis le début des années 2000 (MPO, 2005; LeBlanc *et al.*, 2012).

L'ESTUAIRE MOYEN DU SAINT-LAURENT : UN HABITAT DYNAMIQUE CONCENTRANT LES LARVES DE HARENG

Circulation estuarienne dans l'EMSL

En général, la circulation dans un estuaire se fait en deux couches distinctes dont les directions sont opposées. La masse d'eau de surface, plus légère car plus douce, provient de l'amont et coule en surface en direction de l'océan. La masse d'eau profonde, plus salée et dense, provient de l'océan et coule sous la couche de surface vers l'amont. Cette double circulation existe pour garder en équilibre la concentration de sel à travers l'estuaire (Ketchum, 1952). Dans l'EMSL, le flux résiduel de la masse d'eau profonde, couplé avec les marées, est presque zéro ou légèrement vers l'amont durant le jusant, et vers l'amont avec une vitesse plus rapide durant le flot (D'Anglejean et Ingram, 1976; Fortier et Leggett, 1983; El-Sabh et Murty, 1990). D'Anglejean (1981) a démontré qu'un front de turbidité-salinité-température important se développait au milieu de l'EMSL, à la hauteur de Rivière-Ouelle et de l'île aux Coudres. Ce front migre vers l'aval durant le printemps, car poussé par la crue printanière. De cette décharge, couplée avec des vitesses plus grandes des masses d'eau passant dans des passages restreints entre les îles (ex. Île aux Lièvres), résulte une plus grande advection et des marées descendantes plus longues au printemps (mai-juin) (D'Anglejean, 1981). Le flux résiduel vers l'amont dans le fond de l'EMSL est donc plus

fort lorsque la crue printanière crée une forte descente vers l'aval de la masse d'eau supérieure (Couillard *et al.*, 2017). Finalement, le stress latéral (situé en face de Cap-à-l'Aigle surtout), engendré par la vitesse différente d'entrée de la marée entre les chenaux nord et sud amène des échanges de particules en amont de l'île aux Lièvres et proche de l'île Verte (D'Anglejean, 1981). Les larves de poissons doivent donc contrer ou tirer avantage de ces effets pour éviter d'être transportées hors de l'EMSL.

Déplacement des larves dans la colonne d'eau et aires de concentration

Lorsque les larves de hareng éclosent, elles ont une flottabilité négative leur permettant de rester proche du fond (Courtois *et al.*, 1982; Fortier et Leggett 1982; Henri *et al.*, 1985). Les petites larves planctoniques avec sac vitellin agissent comme des particules en suspension et diffusent passivement d'une masse d'eau à l'autre (Fortier et Leggett, 1982). Ainsi, les larves avec sac vitellin sont transportées vers l'amont par la masse d'eau du fond (Fortier et Leggett, 1983). Le transport en amont plus important dans la couche de fond ramène effectivement les larves de hareng plus en amont et le front de stratification limiterait aussi leur advection vers l'aval (Fortier et Gagné, 1990). Les travaux de Bauer *et al.* (2013) ont démontré l'effet du vent sur la rétention de jeunes larves dans le lagon de Greifswalder, dans la mer Baltique. De la même manière, les épisodes de vents du nord-ouest ont aussi une influence sur ce transport en amont sur les larves venant se nourrir dans la couche de surface et se feraient pousser dans la baie de Rivière-du-Loup (Couillard *et al.*, 2017), où elles seraient retenues car la vitesse des courants résiduels des eaux profondes est moindre et la baie agirait comme un puits pour les larves de poissons (de Lafontaine, 1990). Ultimement, le cycle tidal observé durant la période d'émergence larvaire et le stade planctonique des larves déterminent le nombre de larves retenues dans l'EMSL et qui pourront migrer dans les aires de rétention par la suite (Henri *et al.*, 1985). Les larves gardent leur sac vitellin peu de temps suivant leur éclosion; des larves se nourrissant de

source exogène ont été répertoriées au début de juin (Powles *et al.*, 1984; Fortier et Gagné, 1990).

Lorsque les larves grandissent, elles se concentrent dans des aires de rétention. Ces aires ont la propriété de limiter l'advection et la dispersion larvaire, par exemple à travers des zones de fronts, et sont identifiables par une concentration de larves localisées et qui persiste une certaine période de temps (Iles et Sinclair, 1982; Fortier et Leggett, 1983; Fortier et Gagné, 1990). Dans l'estuaire moyen du Saint-Laurent, les larves d'éperlan arc-en-ciel (*Osmerus mordax*) (Dauvin et Dodson, 1990) et de poulamon atlantique (*Microgadus tomcod*) (Laprise et Dodson, 1990) se regroupent dans des aires de rétention. Les facteurs contribuant à l'efficacité de ces aires dans l'EMSL sont les gradients de température, les apports d'eau douce (Iles et Sinclair, 1982), la turbidité (Dauvin et Dodson, 1990), l'occurrence de proies favorites (Fortier et Leggett, 1983) et la minimisation des interactions interspécifiques (Laprise et Dodson, 1989).

Les plus grosses larves de hareng acquièrent la capacité de suivre leurs proies principales, les copépodes, qui effectuent des migrations nycthémérales (Fortier et Leggett, 1983; Fortier et Gagné, 1990). Elles deviennent alors vulnérables et moins protégées par le front de stratification décrit précédemment et il peut en résulter un transport hors de l'EMSL par advection lors de leur présence en surface. Pour éviter l'exportation, elles ont acquis la capacité d'utiliser le transport sélectif en fonction des marées présent dans l'estuaire. Les larves se déplacent dans la masse d'eau de surface lors du flot de marée et redescendent dans les masses d'eau profondes durant le courant de jusant (Fortier et Leggett 1983; Fortier et Gagné 1990; Lacoste *et al.*, 2001). Ainsi, les larves se déplacent toujours graduellement vers l'amont. Elles auraient la capacité de rejoindre plus facilement des aires de rétention connues comme celle de l'île aux Coudres (Able, 1978; Fortier et Gagné, 1990; Lacoste *et al.*, 2001).

FACTEURS ABIOTIQUES ET BIOTIQUES AFFECTANT LA CROISSANCE ET LA CONDITION LARVAIRES

Durant les premiers jours suivant l'émergence, la croissance larvaire est influencée principalement par la température de l'eau, car cela contrôle l'activité métabolique et le taux de résorption du sac vitellin (Fey, 2001; Oeberst *et al.,* 2009; Hufnagl et Peck, 2011). En règle générale, les larves de hareng émergeant en eau froide (< 6°C) sont plus petites (Fey, 2001) et la croissance larvaire augmente avec la température (Fey, 2001). Il est possible que les températures élevées (18-20°C) agissent négativement sur la croissance (Fey, 2001), ce qui a été démontré en laboratoire. Par contre, cela peut varier dans la nature, comme le démontre une autre étude (Oeberst *et al.,* 2009) dans la mer Baltique. À mesure que les larves grandissent, d'autres facteurs peuvent influencer la croissance. Pour les plus vieilles larves, le taux de croissance en milieu naturel peut être surestimé en raison de la sélection vers de plus grandes larves qui subissent moins de prédation que les petites larves moins bien nourries (Hauss et Peck 2009; Oeberst *et al.,* 2009). D'autres facteurs peuvent aussi entrer en jeu, comme l'abondance et la qualité des proies zooplanctoniques retrouvées dans le milieu (Arula *et al.,* 2012). Dans l'EMSL, les harengs se reproduisant à l'île Verte ont démontrés des taux de développement, d'absorption de sac vitellins, de croissance et de mortalité adaptés à leurs conditions environnementales, qui sont typiques des eaux froides aussi retrouvées dans les populations de l'Atlantique Est (McQuinn *et al.,* 1983). La température a aussi un effet sur les différences morphologiques notées sur les otolithes des harengs de l'île Verte (Côté *et al.,* 1980).

La condition larvaire est un facteur important à considérer pour déterminer le statut des cohortes. La condition somatique des larves est tout spécialement importante car les stades embryonnaires et larvaires sont vulnérables chez les poissons. La condition peut être influencée par différents paramètres environnementaux. Par exemple, la turbidité affecte la condition des larves d'éperlans arc-en-ciel (Sirois et Dodson, 2000) ainsi que les fronts de

stratification, où il est possible que les larves se retrouvent proche de leur limite de tolérance en température et salinité (Casini *et al.*, 2006; Diaz *et al.*, 2009). À l'opposé, la condition des larves d'anchois (*Engraulis anchoita*) était améliorée dans des eaux bien mélangées et caractérisées par un front, favorisant l'enrichissement en éléments nutritifs et la rétention (Diaz *et al.*, 2011). Dans l'EMSL, où les conditions de courants, température, salinité et turbidité varient grandement en fonction des régions et de la saison (D'Anglejean, 1981), il est probable que les concentrations de proies varient en fonction de la turbidité, du vent et de la production primaire (Runge et Simard, 1990).

Dans d'autres régions, comme dans le nord-ouest de l'Atlantique et dans le Pacifique, la saison et la densité intraspécifique affectent aussi la condition des harengs adultes (Winters et Wheeler, 1993). Les larves sont soumises à des facteurs similaires dans les endroits où elles se concentrent et il est possible que la densité, produisant de la compétition, soit responsable d'une certaine perte de condition et de croissance (McGurk *et al.*, 1993; Diaz *et al.*, 2009). Aussi, les aires de rétention des larves peuvent être favorables à la formation d'agrégations de zooplancton, facteur important pour la croissance des larves (Fortier et Leggett, 1983). La valeur nutritive du plancton ingéré peut aussi varier selon les proies disponibles et affecter la condition des larves (Fox *et al.*, 1999; Arula *et al.*, 2012). Par exemple, une augmentation de la croissance et de la condition sont perceptibles chez les jeunes larves de hareng s'alimentant de gros zooplanctontes au moment de leur première injestion (Arula *et al.*, 2012). Finalement, un équilibre est nécessaire entre la quantité et la qualité de la nourriture disponible (Paulsen *et al.*, 2014) et la taille des larves et cet équilibre, au moment de l'absorption du sac vitellin, détermine le succès de l'alimentation assez tôt dans le développement (Hufnagl et Peck, 2011).

PROBLEMATIQUE

Le hareng est une espèce de poisson fourrage à la base du réseau alimentaire desservant bon nombre d'espèces dans l'EMSL. Les harengs adultes, les larves et/ou les œufs alimentent l'eider à duvet (*Somateria mollissima*), les goélands marin (*Larus marinus*) et argenté (*Larus argentatus*), la plie canadienne (*Hippoglossoides platessoides*) (Munro *et al.*, 1998), la morue franche (*Gadus morhua*) (Dawe *et al.*, 2012), le phoque gris (*Halichoerus grypus*) (Harvey *et al.*, 2012) et le phoque du Groenland (*Pagophilus groenlandicus*) (Beck *et al.*, 1993).

Jusqu'au début des années 2000, la taille de la population de bélugas du Saint-Laurent (*Delphinapterus leucas*) était considérée stable (MPO, 2014). C'est à partir du début des années 2000 que la population de béluga aurait connu un déclin (Mosnier *et al.*, 2014). Le faible effectif de la population et la tendance au déclin ont fait en sorte que la population a récemment été décrétée en voie de disparition (COSEWIC, 2014). Plusieurs hypothèses ont été avancées pour tenter d'expliquer les causes de la situation du béluga du Saint-Laurent (MPO, 2013). Le hareng de l'EMSL se retrouve dans l'aire de distribution estivale du béluga du Saint-Laurent et a été rapporté comme une source énergétique importante précédant tout juste le moment où les femelles gestantes bélugas mettent bas (Lesage et Kingsley, 1995). Depuis la fin des années 1990, plusieurs variables environnementales ont connu des changements importants pouvant avoir un effet négatif sur le béluga du Saint-Laurent, dont une baisse de biomasse de hareng de l'unité reproductive de printemps du stock 4T du sud du golfe (Plourde *et al.*, 2013). La baisse d'effectifs a seulement été documentée dans le GSL et puisqu'une partie des harengs de printemps remonte l'estuaire pour frayer, il est possible que le déclin ait affecté l'unité reproductive de printemps de l'EMSL. L'absence de données sur l'état du stock de hareng de printemps de l'EMSL a été identifiée comme étant une lacune de connaissance (MPO, 2013).

Il est important de comprendre si un changement dans l'importance relative entre les géniteurs de printemps et d'automne s'est opéré dans l'EMSL en coïncidence avec la baisse du nombre de géniteurs de printemps dans le stock 4T du GSL. Le manque d'information sur le hareng larvaire de l'EMSL depuis 1998 rend d'autant plus important d'effectuer une étude sur le sujet car le stade larvaire est le plus sensible lors du développement de cette espèce fourragère. Le hareng devient donc une espèce clé à l'intérieur des limites d'une aire marine protégée nationale, le Parc marin du Saguenay–Saint-Laurent (PMSSL). La protection de l'écosystème et des espèces qui s'y trouvent est un mandat important au sein du PMSSL. Le hareng est une espèce pêchée commercialement tant pour la consommation que pour l'utilisation comme appât, et la conservation des stocks de hareng et de la diversité de leurs unités reproductives est une priorité pour le ministère des Pêches et des Océans du Canada. La protection de l'habitat et des proies des espèces en péril comme le béluga est aussi un mandat de protection que le gouvernement doit respecter (MPO, 2012a) selon la Loi sur les espèces en péril (LEP) et cette étude contribuera à fournir des informations pouvant servir à accroître les mesures de protection.

OBJECTIFS

Le premier objectif consistait à explorer la distribution actuelle spatio-temporelle des moments d'émergence de larves de hareng atlantique dans l'ESML, leurs importances relatives et la distribution des plus grandes larves dans l'aire d'étude. Des comparaisons avec les événements d'émergence passées ont été faites pour voir si des changements de distribution ont eu lieu depuis les 20 dernières années.

Le second objectif visait à déterminer et comparer les taux de croissance et la condition des différentes cohortes de larves de hareng dans l'EMSL. Pour tenter de comprendre ces différences, l'évaluation de l'influence des conditions environnementales

(température, degrés jours) sur ces deux paramètres a été étudiée. L'importance d'autres facteurs environnementaux a été discutée.

Ce mémoire est présenté sous forme d'article scientifique en anglais, comprenant une introduction et une conclusion générale en français.

CHAPITRE 1
EMERGENCES, CONCENTRATION AREAS AND GROWTH OF LARVAL ATLANTIC HERRING (*CLUPEA HARENGUS*) IN THE SAINT-LAWRENCE RIVER MIDDLE ESTUARY

1.1 INTRODUCTION

Estuaries are widely recognized as important spawning and nursing grounds for many marine fish species (Haedrich, 1983). The St. Lawrence Middle Estuary (SLME), Quebec (Canada), is an important area for the reproduction of schooling fish populations which play an important role in the food web, namely the Atlantic herring (*Clupea harengus*), the capelin (*Mallotus villosus*), the rainbow smelt (*Osmerus mordax*) and possibly the sand lance (*Ammodytes americanus*) (Laprise and Dodson, 1989; Fortier and Gagné, 1990; Fortier et al., 1992). According to existing information, Atlantic herring coming to spawn in the SLME is part of a metapopulation that is exploited within the Gulf of St. Lawrence (GSL) and west coast of Newfoundland (McQuinn, 1997a). Morphometric studies suggested that part of the herrings spawning in spring in the SLME have not spent their early life stages in the SLME (Lambert, 1990; McQuinn, 1997a). An unknown proportion of these adult herring could grow in the southern GSL (McQuinn, 1997a). The SLME herring are currently part of the southern GSL herring stock, in which a decline in the spring component has been reported since 1997 (LeBlanc *et al.*, 2012). However, in the absence of a monitoring program of the SLME spawning unit(s), it is not known if the spring spawners, spawning activity and abundance of larvae in the SLME were also affected by this decline in herring stock.

Atlantic herring spawns at different times of the year in the northeast and northwest Atlantic (Cushing, 1967). Spawning sites and larval stages of herring in the Estuary have been widely studied in the 1980s and 1990s, but there has been no studies on this

component since Munro *et al.* (1998). A study conducted 20 years ago in the SLME showed that different groups of herrings entered the SLME to spawn in spring and autumn (Munro *et al.,* 1998). This two-year study demonstrated that spawning dates did not change significantly among years whereas dates of hatching events varied in time (Munro *et al.,* 1998). Spawning began around mid-May (Munro *et al.,* 1998) while spring hatching occurred around the end of May and the first half of June, predominantly on the first week of June (Able, 1978; Fortier and Leggett, 1982; McQuinn *et al.,* 1983; Munro *et al.,* 1998). A second hatching event occurred during the first two weeks of July (Henri *et al.,* 1985). Adult herrings have also been observed during the summer in two localities of the St. Lawrence Estuary (Bérubé and Lambert, 1997). Herrings also spawned during autumn in the SLME, where migrating spawners arrived around late summer (Lacoste, 2001) and newly hatched larvae were captured around mid-September (Fortier and Gagné, 1990). Spawning sites located in the SLME might have changed as well since the studies done 20 years ago. Yolk-sac larvae have a negative buoyancy and can therefore stay near the bottom, avoiding advection out of the Estuary by strong downstream currents (Courtois *et al.,* 1982; Fortier et Leggett, 1982; Henri *et al.,* 1985). As herring larvae grow, they concentrate in so-called retention areas further upstream. The locations of these areas might have also changed since the last 20 years.

Temperature plays an important role in the embryo-larval development and growth (Fey, 2001). Larvae hatching in colder water (< 6°C) are generally smaller and larval growth increases with warmer temperatures (Fey, 2001). Depending of other environmental and biological conditions in field studies, high temperatures have been reported to affect positively (Oeberst *et al.,* 2009) or negatively (Fey, 2001) larval condition. Other factors include the presence of fronts, which can bring larvae close to their salinity or temperature tolerance limit (Casini *et al.,* 2006; Diaz *et al.,* 2009). Turbidity as well is an important factor. A mixed water column can inject nutrients important for herring prey (Costalago *et al.,* 2015; Diaz *et al.,* 2011). Larval condition is intricately linked to availability of suitable

preys at critical time of development. Therefore, factors affecting zooplankton abundance, size and distribution like salinity, turbidity and temperature also indirectly impact herring larval condition by affecting their prey (Casini *et al.*, 2006; Diaz *et al.*, 2011; Arula *et al.*, 2012).

Atlantic herring that spawn in the SLME are considered an oily fish and represent a rich source of nutrients for many predatory species, especially for female gestating belugas (*Delphinapterus leucas*) and their calves (Lesage and Kingsley, 1995; MPO, 2010; Lefebvre *et al.*, 2012). Exploitation of herring spawning schools by belugas was suggested by Lesage and Kinsley (1995). Observations of important schools of herring, where pods of belugas congregated, were recorded with a scientific echosounder in known spawning areas of the SLME in 2014 (Parks Canada, unpubl. data). The SLME is part of a conservation area, the Saguenay–St. Lawrence Marine Park (SSLMP) enclosing the essential habitat of the beluga whale under the Species at Risk Act (MPO, 2012a). St. Lawrence beluga whales are considered an endangered species (COSEWIC, 2014) as their abundance has been decreasing since the beginning of the millennium. Since the 1990s, changes in environmental factors could have negatively affected the beluga, and one of the possible causes of the population decline could be low availability of important food resources like the Atlantic herring over their summer grounds (Plourde *et al.*, 2013). Herring recruitment in the SLME might be an important component of the spring spawning stock. It is thus important to evaluate current herring spawning grounds in the SLME, the moment of larval hatching, larval growth and condition. There exists a relation between condition of larval herring and recruitment (Westerhagen and Rodenthal, 1981). Recruitment and survival of adult fishes is highly dependent on larval survival (Cushing, 1990). Larval mortality through predation and lack of food can be high, especially through the Hjort's critical period, where they first feed (Hjort, 1914; Leggett and Deblois, 1994). Larval fishes are quite vulnerable to environmental stressors, coming from natural causes (e.g.: abnormally high water temperatures) or anthropogenic causes (e.g.: addition of nutrients from sewage

spills and agriculture) (Costalago *et al.*, 2015). This would influence the year-class strength and therefore recruitment and survival of adults.

Spring herring spawning in the SLME might have declined along with the 4T stock in the GSL since the late 1990s. In order to better understand the dynamics of early life stages of herring in the SLME and to ensure protection of this key species, larval growth and condition must be studied. The first objective of this study was to explore the current spatiotemporal distribution of herring larval hatching events in the SLME, their relative importances and the distribution of older larvae in the area. Comparisons with past hatching events were conducted in order to see if any changes in distribution occurred since the last studies 20 years ago. The second objective was to determine and compare larval growth and condition among successive larval cohorts. In order to understand these differences, the link between larval condition and environmental factors like surface temperature and degree-days were explored.

1.2 MATERIAL AND METHODS

1.2.1 Study area

The SLME comprises the area between the eastern tip of Île d'Orléans and Tadoussac, for a total length of 180 km (Sirois and Dodson, 2000) (Figure 3). In spring, herring spawning sites in the SLME included coastal areas around Rivière-du-Loup (Henri *et al.*, 1985; Bérubé and Lambert, 1997; Lacoste, 2001), the western coast of Île Verte (Côté *et al.*, 1980; Iles and Sinclair, 1982; McQuinn *et al.*, 1983; Fortier and Gagné, 1990; Lacoste *et al.*, 2001) and the southwestern tip of Île aux Lièvres (Munro *et al.*, 1998). Most of the studies mentioned above were focused on the spring component of the herring population in the SLME. Only a small number of studies included observations on autumn spawners, reporting abundances of autumn spawners and larvae in the southern channel,

between Îles aux Lièvres and Rivière-du-Loup (Figure 3) (Able, 1978; Fortier and Gagné, 1990). Following hatching, larvae stay near that area and/or were advected upstream. Herring larvae concentrate mostly in coastal regions (Powles *et al.,* 1984), including islands, and along the southern shore. Areas of retention include Île aux Coudres (upstream of Île aux Lièvres) (Able, 1978; Fortier et Gagné, 1990; Lacoste *et al.,* 2001) and the bay of Rivière-du-Loup (Figure 3) (Couillard *et al.,* 2017). Larval herring presence was also recorded in the northern channel in the past (Fortier and Leggett, 1982; Courtois and Dodson, 1986), but there was no reported occurrence of spawning there (Munro *et al.*, 1998). Deposition of demersal eggs at the southwestern tip of Île aux Lièvres and on the western coast of Île Verte was observed repeatedly in the past (Munro *et al.,* 1998).

1.2.2 Sampling

The main sampling effort was focused in the area where important spawning activity and retention were previously documented; around the islands and in the southern channel (Figure 3). A total of 25 sampling stations were distributed at fixed locations in coastal areas between La Malbaie and Baie Sainte-Catherine, extending to the southern shore from Île Verte to Kamouraska, mostly along the northern and southern shore, Île Verte and Île aux Lièvres near the coastline (0.5 to 2 km, Figure 3). From June to October 2014, herring larvae were captured in the SLME aboard the MV Alliance (Eagle Craft), a 11 m vessel from Parks Canada (PC) or the MV Krill (Lifetimer, 8.22 m), a vessel from the Department of Fisheries and Oceans Canada (DFO). Sampling took place at a two or three weeks interval from 2/6/2014 to 3/10/2014 (Table 1). Stations 1 to 3 (Île Verte area, Figure 3) were less frequently visited after the period of spring spawning (Table 1). Stations 13-16-17-18-19-27 and 28 (Figure 3) along the northern coast were visited only from July 11 onwards (Table 1). From July 11, stations 20 to 25 were more frequently visited to increase our effort in the area of interest, the southern channel. Due to daytime operation, only 5 to 8

stations were visited each sampling day. Due to weather constraints, sampling could be omitted two or three weeks in a row.

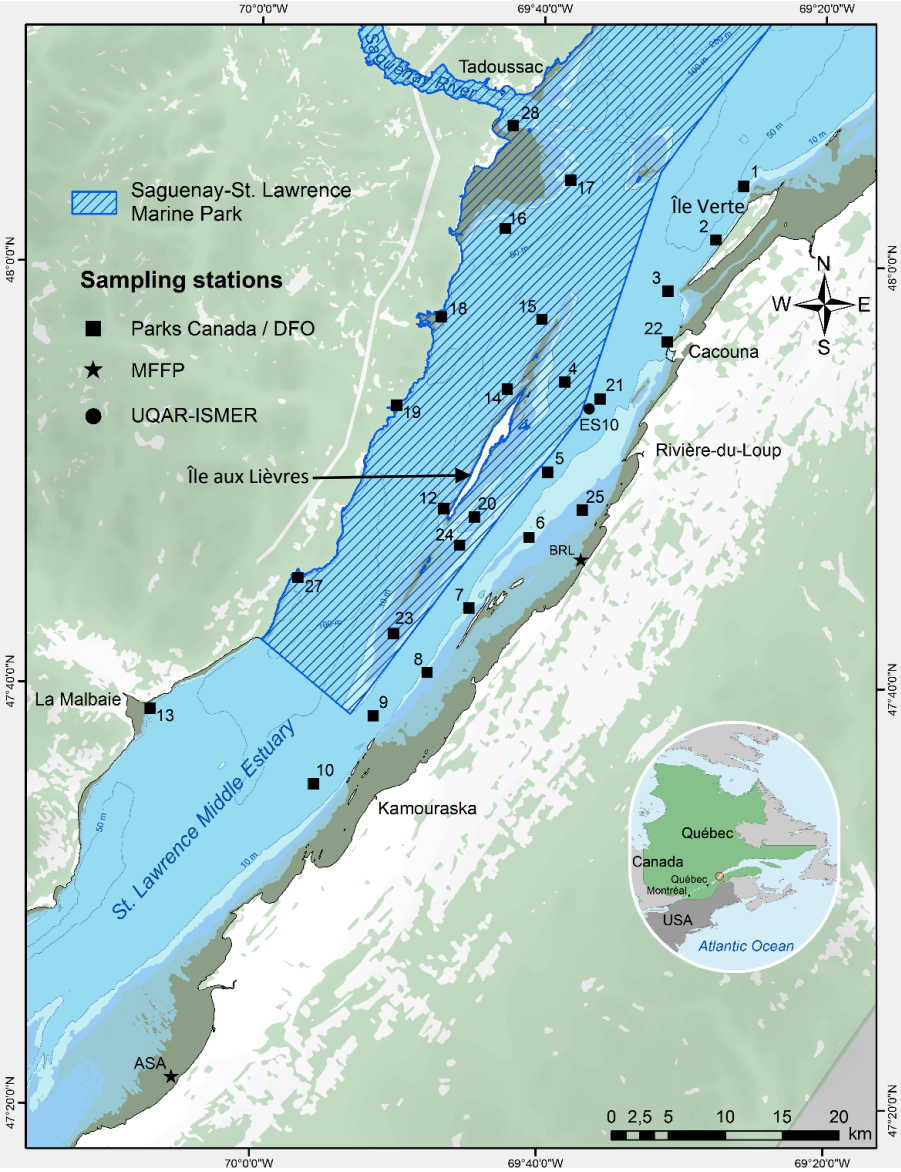


Figure 3. Study area and position of sampling stations visited from June to October 2014 in the St. Lawrence Middle Estuary. Different symbols represent different vessels operated by organisms shown in the legend.

Table 1. Sampling stations coordinates and sampling dates for every station in the study area. Sampling dates in bold represent sampling with the vessel MV Krill

Stations	**Coordinates**		**Sampling dates in 2014**				
	N	**W**	**June**	**July**	**August**	**September**	**October**
1	48°03'51.3"	69°25'49.9"	5;10;18	**24**			
2	48°01'18.4"	69°27'47.1"	5;10;18	**24**			
3	47°58'51.8"	69°31'08.8"	5;10;18	**24**	15	3;22	
4	47°54'30.8"	69°38'23.0"	11;18	**24**	15	3;**17**;22	3
5	47°50'13.3"	69°39'32.8"	2;11;18	**30**	**21**	**17;24**	3
6	47°47'07.2"	69°40'49.0"	2;11	**30**	**21**	**17;24**	
7	47°43'44.8"	69°45'00.0"	11;17	**30**		**17**	
8	47°40'40.0"	69°47'53.7"		**30**			
9	47°38'35.0"	69°51'38.7"	17				
10	47°35'19.1"	69°55'46.9"		**30**			
12	47°48'27.2"	69°46'50.8"	2;11;17	**11;31**	**20**	**24**	
13	47°38'48.8"	70°07'18.4"			**20**		
14	47°54'09.4"	69°42'26.1"	2;11;17	**31**	**20**	**24**	
15	47°57'28.8"	69°40'02.0"	11;17	**10;31**	**20**		3
16	48°01'47.0"	69°42'41.0"		**11**			
17	48°04'05.5"	69°38'04.4"		**11**	**20**		
18	47°57'33.1"	69°47'09.0"		**11**	**20**		
19	47°53'19.9"	69°50'14.0"		**11**	**20**		
20	47°48'04.1"	69°44'40.3"		**11;30**	**21**	**17;24**	
21	47°53'43.6"	69°35'53.4"		**24**	15	3;**17**	3
22	47°56'27.2"	69°31'09.8"		**24**	15	3;**24**	
23	47°42'29.3"	69°50'16.4"		**30**	**20**		
24	47°46'43.5"	69°45'42.1"		**30**	**21**	**17**	
25	47°48'26.3"	69°37'04.9"		**30**	**21**	**17;24**	
27	47°45'06.0"	69°57'03.1"			**20**		
28	48°06'39.2"	69°42'11.2"			**20**		
ES10	47°53'14.7"	69°36'38.6"				25	
BRL	47°46'05.6"	69°37'09.8"		7-17			
ASA	47°21'21.6"	70°05'29.3"		4-16			

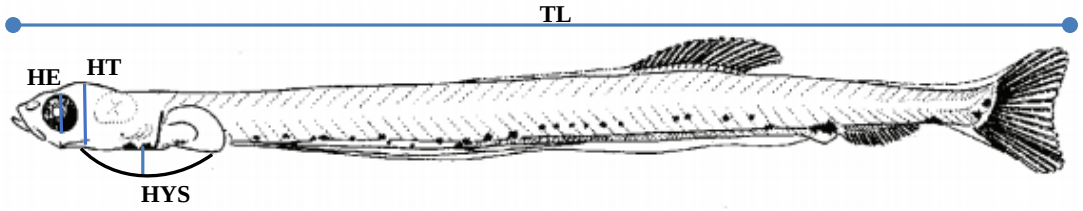
At each sampling station, a conductivity/salinity (PSU), temperature (°C) and depth (m) probe (CTD) was first deployed from the surface to 2 m off the bottom of the water column. Mean surface (≈ 0 to 5-10 m) and deep layer temperatures were calculated from CTD data above and below the thermocline, respectively. Herring larvae were collected by Bongo nets (diameter: 60 cm; mesh size: 333 µm) in June with saw-tooth tows of 10 minutes at a speed of 1-3 knots throughout the whole water column (5 m off the bottom). From July to October, sampling was done alternating between a conical plankton net of 0.75 m diameter and mesh size of 500 µm when using the smaller vessel, the MV Krill, and a 1 m diameter net (same mesh size) on the vessel MV Alliance. The MV Alliance could withstand a much bigger tow weight than the MV Krill, allowing the usage of a larger net to increase the capacity to sample larger larvae (total length ≈ 20 mm) and a higher volume of water. Nets were equipped with standard mechanical flowmeters (General Oceanics model 2030R). In general, the whole water column was sampled since studies showed that yolk-sac herring larvae were found deeper, near the bottom (Henri *et al.*, 1985) while older larvae migrated due to the daily tidal movement (Fortier and Leggett, 1983; Fortier and Gagné, 1990). However, at the deep north shore stations (80-90 m), only the potential zone of larger (>10.9 mm) herring larvae occurrence was sampled at a maximum depth of 20 to 30 m (Fortier and Leggett, 1982). When maximal sampling depth was below 10 m, horizontal tows were used. Herring larvae were first anesthetized with a solution of 0.05% clove oil in sampling site surface water and then preserved in ethanol (95%). Ethanol was changed after 24 h for long-term preservation.

Herring larvae from Banc de Rivière-du-Loup (BRL) and Anse Sainte-Anne (ASA) were made available by the Ministère des Forêts, de la Faune et des Parcs (MFFP). The sampling was part of a monitoring program in those two areas, described in Bourget and Marquis (2014). Lastly, ES10 station was sampled once by G. Winkler, Université du Québec à Rimouski – Institut des Sciences de la Mer (UQAR-ISMER) on the CORIOLIS II, a 50 m research vessel operated by REFORMAR. Herring larvae were captured with a

conical plankton net (diameter: 100 m; mesh size: 335 µm) through an oblique tow that lasted 10 minutes.

1.2.3 Herring larvae enumeration, classification and morphometric measurements

Herring larvae were identified in the laboratory using information in Fahay (2007). Pictures of individual larvae were taken by a binocular Leica MZ7.5 equipped with a camera Moticam 5 5.0 MP, with the software Motic Image Plus 2.0. Measurements were made using the software Image-Pro Insight (Figure 4). When available, a maximum of 50 larvae were measured per sample. When present, we randomly selected 25 yolk-sac larvae and 25 post yolk-sac larvae and only unbroken larvae were selected. Larvae were classified on the basis of their total length (TL) and height of yolk sac (HYS). The height of the eye (HE) and head thickness (HT) were used to determine larval condition.



TL – Total length
HYS – Height of yolk sac
HE – Height of the eye
HT – Head thickness

Figure 4. Total length (TL), height of yolk sac (HYS), height of the eye (HE) and head thickness (HT) of an Atlantic herring larvae (Doyle, 1977).

Yolk fullness was determined with the height of the yolk sac where a HYS of 0-0.3 mm gave a fullness from 0.1 to 49.9%, HYS of 0.3-0.45 mm a fullness of 50-69.9% and HYS of 0.45-0.6 mm a fullness of 70-100% (Figure 5). Therefore, newly hatched larvae (category 1a) have a TL ≈ 5-9 mm and a yolk-sac fullness of 70-100%, slightly older larvae (category 1b) had also a TL ≈ 5-9 mm and a yolk-sac fullness of 50-70% and larvae with yolk-sac fullness of 0-50% (TL ≈ 9-11.5 mm) were still classified as yolk-sac larvae (category 1c). Large larvae (category 2) had a TL ≈ 11.5-30 mm, no yolk sac and were classified as post yolk-sac larvae.

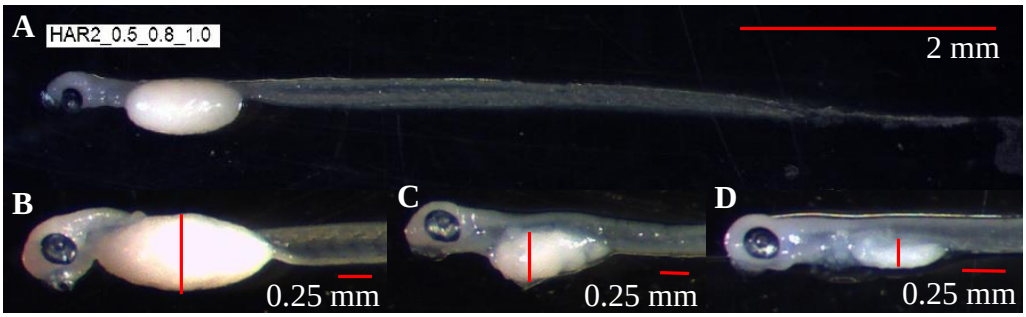


Figure 5. (A) An example of an Atlantic herring larva with a full yolk sac (TL = 7.36 mm, category 1a). Yolk-sac larvae at different developmental stages, with different height of yolk sac (HYS) where B: HYS = 0.52 mm, 1a; C: HYS = 0.39 mm, 1b and D: HYS = 0.16 mm, 1c.

Occurrence and abundance of the smallest yolk-sac larvae (category 1a, Figure 5B) served to identify timing of hatching events throughout the sampling season. Small larvae that were of the same length of category 1a yolk-sac larvae sampled on the same date and station and showed signs of lost yolk sac (or torn apart) were also counted as small yolk-sac larvae. An exception stood for small larvae (TL ≈ 6.86 – 9.39 mm) without yolk sac captured on August 15. These small larvae were still labeled as newly hatched since their short lengths stood out of the generally large larvae captured at that time. Possibly, the

hatching was missed by a few days and they already had absorbed their yolk sac. From bongo nets, larval densities (number per 100 m^3 of water filtrated calculated with flowmeters) were estimated as the mean number of herring larvae taken by both nets. For estimating the abundance of yolk-sac larvae hatched around emergence dates, categories 1a-c were considered. Yolk-sac larvae grew fast and the yolk decreased quickly, therefore all yolk-sac larvae captured around the emergence date have a high probability of being part of the same cohort. For those stations that were visited twice in the same period of time (e.g.: station 25 visited on Sept. 17 and 24), the mean of both dates was calculated for mapping. The densities were mapped with the program PBSmapping (Schnute *et al.*, 2015) in the R environment (version 3.2.1, R Core Team, 2015).

To test the differences of TL between larvae among hatching events, a Kruskal-Wallis test on ranks was performed since not all assumptions were respected (variance was not homogeneous), along with a Tukey's multiple comparison test.

1.2.4 Length frequency distribution and identification of larval cohorts

The software FiSAT II (Fisheries and aquaculture software, 2006) was used to assign larvae to their respective cohort. The software used the method of NORMSEP which applies the maximum likelihood concept to separate the normally distributed components of size-frequency samples (Gayanilo *et al.*, 2005). It required a number of cohort that we observed and their estimated modal total length. To do so, the mean length of yolk-sac larvae of categories 1a-c was calculated for each larval hatching event. Then, the expected length of these larvae over time was estimated using mean monthly growth rates reported previously for Atlantic herring larvae sampled in the same region for the spring cohort (Fortier and Gagné, 1990) (Table 2). This is the usual way to differentiate cohorts, not only the FiSAT program uses expected growth rate to calculate new cohorts but the R package

mixdist also need these parameters (Du, 2002). The estimated length was entered in the software FiSAT II at each sampling date for the cohorts that were most likely to appear during those dates (e.g.: on sampling date June 10-11, only the predicted lengths of cohorts 1 and 2 were entered while on sampling date September 3, means of cohorts 1, 2, 3, 4 and 5 were entered). Therefore, estimated growth was compared to observed length data in order to identify cohorts. Histograms of total length frequencies were built from all measured larvae sampled at all stations. Finally, the output resulted in histograms by sampling dates that were used to define successive cohorts. A detailed table of the assignment of each larva to their respective cohort based on their total lengths is presented in the annex (Annex; Table A1). When the software could not identify a mean of length, expected growth rates from literature were used, with the equation relating temperature to growth for the spring cohort in the study from Fortier and Gagné (1990): $G = 0.011^{e}(0.599*T)$.

Table 2. Growth rates reported for Atlantic herring in the St. Lawrence Middle Estuary (Fortier and Gagné, 1990).

Month	**June**	**July**	**August**	**September**	**October**
Growth rate (mm/day)	0.16	0.28	0.46	0.19	0.15

If a sampling event lasted two consecutive days, the mean of the total length predicted was calculated (e.g.: June 10-11 where predicted length for cohort 1 on June 10 is 8.91 mm and on June 11 is 9.07 mm so the mean would be 8.99 mm). A range of ±2 mm around the mean was used to assign larvae to cohorts in the length frequency histograms. A more restrictive range of ±1 mm around the mean was used when cohorts followed closely one another (cohorts 1 and 2 most of the time). Standard deviations and separation indexes

were calculated. Separation index is the ratio of the unbiased estimate of the sample standard deviation to its root mean square measurement error (Wright and Stone, 1999). When cohorts were too close to be distinguished using the software alone (e.g.: cohorts 1 and 2 most of the time, when the number of larvae was too small and/or when multiple cohorts were present and difficult to be distinguished), the expected body length using past observed growth rates was used to follow larvae in time and assigned them to their respective cohort. When assignment to a cohort was impossible (undetermined), larvae were not included in the following analyses.

1.2.5 Growth rate and calculation of degree-days

Observed growth rates were represented by the slope of the linear regression of mean total length (TL) and the day of the year. For each cohort, sum of degree-days (SDD) at each sampling dates were calculated using the mean of daily surface water temperatures (above thermocline, so taking into consideration temperatures of the first 5 to 10 m below the surface) measured by CTD over the whole sampling area in 2014 sampling season. Surface temperatures of all sampled stations were taken into consideration for the analysis except sampling stations where less than 5 herring larvae were captured, since we used these data for growth analyses. Therefore, this process has eliminated stations in the northern channel (13, 16, 17, 18, 19, 27 and 28) and others near Kamouraska Islands (9 and 10) (Figure 3). Surface temperatures between sampling dates were estimated with the help of a polynomial fit with three orders describing the relationship between the observed surface temperature and the date of the sampling summer season of 2014 (Figure 6).

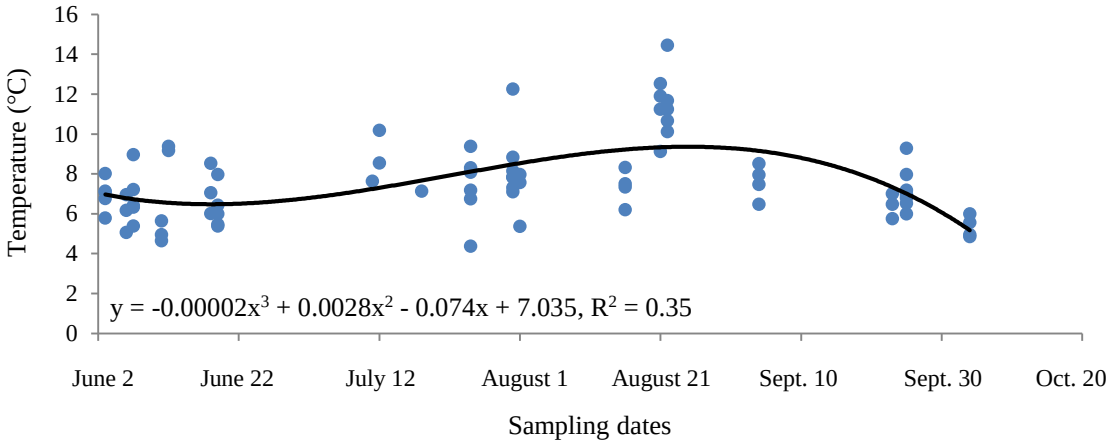


Figure 6. Polynomial fit (order 3) of the surface temperatures against sampling dates in 2014, in the sampling area in the St. Lawrence Middle Estuary. Different dots represent different stations sampled on the same date.

1.2.6 Larval herring condition

Larval herring condition was calculated using regressions of a condition-sensitive morphometric variable, the head thickness (HT), on a condition-insensitive morphometric variable, the height of the eye (HE) (Ehrlich *et al.*, 1976; McGurk, 1989; Bollens and Sanders 2004). Here, categories 1a-b-c were all considered as category 1 (yolk-sac larvae) and category 2 still represented post yolk-sac larvae. The reason for this classification laid in the differences in feeding habits of larvae. Yolk-sac larvae depend on endogenous reserves from their yolk, while post yolk-sac larvae fed on exogenous food. Therefore, environmental factors affecting yolk-sac larvae condition were expected to be different than those affecting post yolk-sac larvae, the latter mostly impacted by prey availability and quality.

Condition of larvae was compared among cohorts, during different months through the relationship between HT and HE, assessed by least-squares regressions. For the purpose of this study, we arbitrarily assessed that the number of data points must exceed 10 for proper regression (not the case for yolk-sac larvae of cohorts 3 and 4 in July, post yolk-sac larvae of cohorts 1 and 2 in June and 4 and 5 in September). Prior verification of the homoscedasticity and normal distribution of residuals was performed using the White and the Shapiro-Wilk tests, respectively. In some cases, the Shapiro-Wilk test for normality was not respected. In these cases, screening for outliers with the distance of Cook pinpointed problematic data points that were not true outliers (distance of Cook < 1) (Annex; Table A2). The removal of these data points brought back the normality of the relationship without changing the results of the following analysis of variance/covariance (ANOVA/ANCOVA). Therefore, the problematic data points were kept in the analysis. After confirmation of the homogeneity of slopes, ANCOVA was conducted to determine if there was a statistically significant effect of cohorts on HT after controlling for HE. Y-intercepts represented larval herring condition (Bollens and Sanders, 2004). Therefore, only differences between HT were presented graphically. The graphic representation of homogenised slope was not presented, but the results were put in a table. ANCOVA was followed by a Tukey's multiple comparisons test when significant.

1.3 RESULTS

1.3.1 Distribution and relative importance of yolk-sac herring larvae densities

Locations and relative importance of successive herring larvae hatching events varied in time. The first spring cohort sampled hatched around June 2-5 at Île Verte (st. 1, 2 and 3), where a maximal density of 268 yolk-sac larvae 100 m^{-3} was recorded on June 5 at

station 3 (Figure 7). A second hatching event of smaller intensity occurred shortly after. Newly hatched herring larvae were sampled on June 10-11 and were found at Île Verte but also near Île aux Lièvres (st. 12 and 14) and in the southern channel (st. 5 and 6) (Figure 7). On June 10-11, maximal densities of yolk-sac larvae of 47 ind. 100 m^{-3} and 46 ind. 100 m^{-3} occurred in the southern channel (st. 6) and at station 15, respectively. In summer, three hatching events appeared, two in July (July 10-11 and July 31) and one on August 15. Densities of these three groups of yolk-sac larvae were relatively low compared to the June cohorts, with a maximum of 12 yolk-sac larvae 100 m^{-3}. During the summer, hatching events were mainly located in the southern channel and off the northeast tip of Île aux Lièvres (Figure 7). The autumn hatching event was the second most important, showing a peak density of 233 yolk-sac larvae 100 m^{-3}, recorded on September 24 at station 6. This hatching was mainly located in the southern channel and no herring larvae were observed neither around Île Verte nor Île aux Lièvres (Figure 7). Overall, there were six main hatching events, hence six cohorts from June to September 2014.

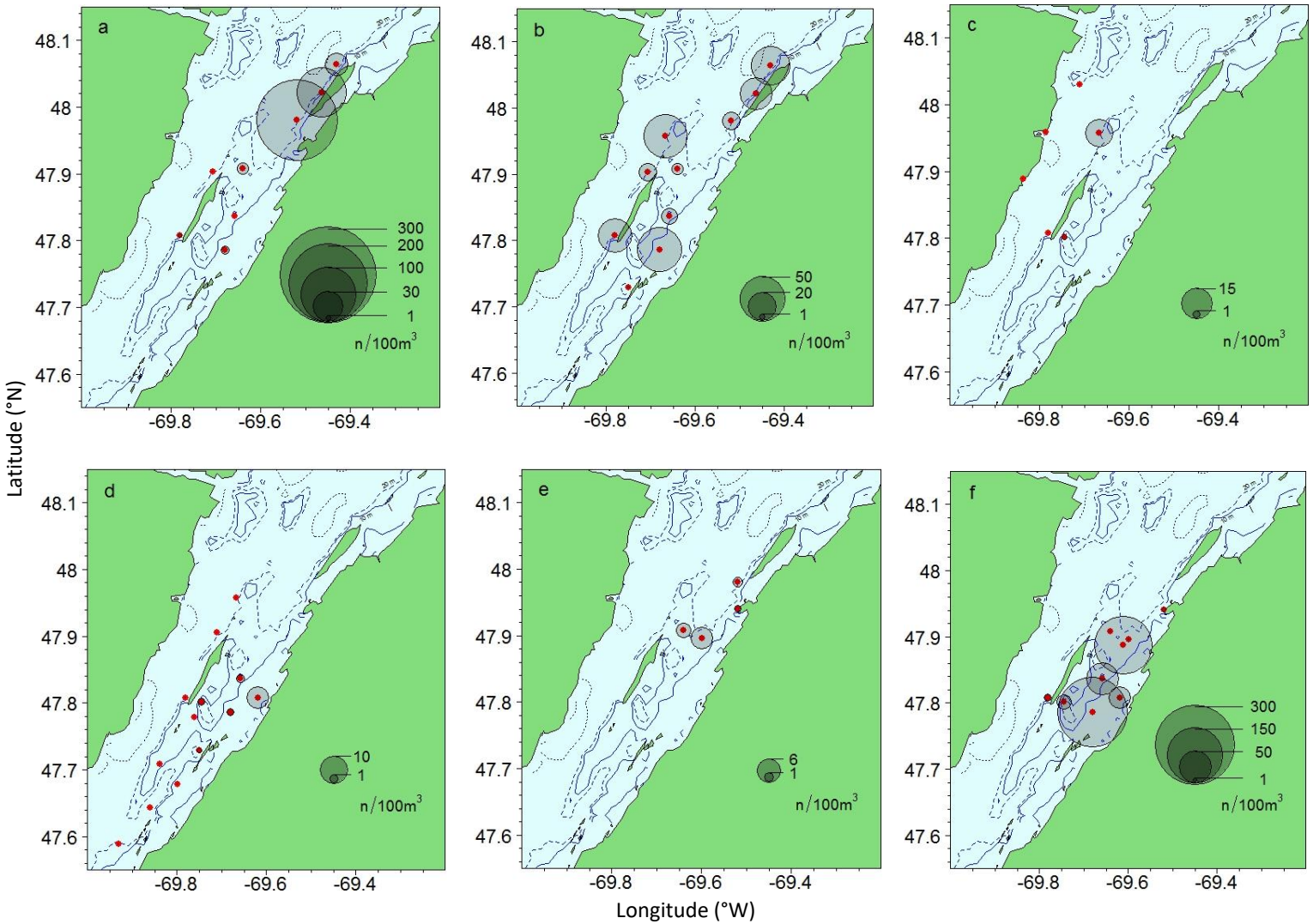


Figure 7. Distribution and densities of yolk-sac herring larvae (categories 1 a-c; Total length ≈ 5-11.5 mm), between June and September 2014 in the St. Lawrence Middle Estuary. (a) June 2, 5; (b) June 10,11; (c) July 10, 11; (d) July 30, 31; (e) August 15; (f) September 24, 25.

Altogether, spring hatching events represented 71% of the total yolk-sac larvae density sampled in the St. Lawrence Middle Estuary in 2014 (Figure 8). The autumn hatching event represented 27%, while summer hatchings showed the smallest percentages, overall making a total of 2% of yolk-sac larvae density.

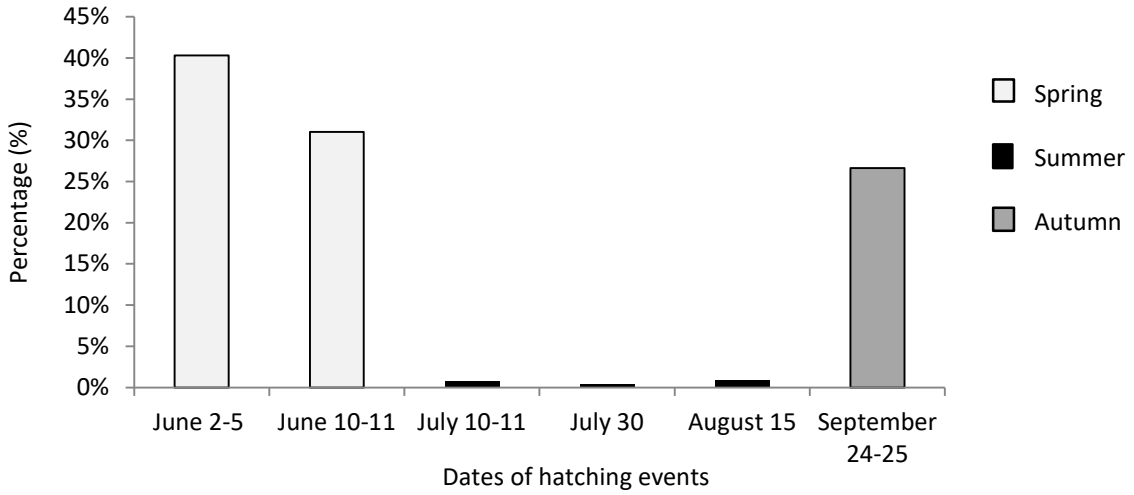


Figure 8. Proportions of total yolk-sac herring larvae (categories 1 a-c; Total length ≈ 5-11.5 mm) sampled in spring, summer and autumn 2014 in the St. Lawrence Middle Estuary.

1.3.2 Distribution and relative importance of post yolk-sac herring larvae densities

As the season progressed, post yolk-sac larvae (TL ≈ 11.5-30 mm) were found at much smaller densities, ranging from 0.3 to 30 larvae 100 m^{-3}. Post yolk-sac larvae were found in the southern channel most of the season (Figure 9). However, in August and September, no occurrence of post yolk-sac larvae was noted around the northeast tip of Île aux Lièvres.

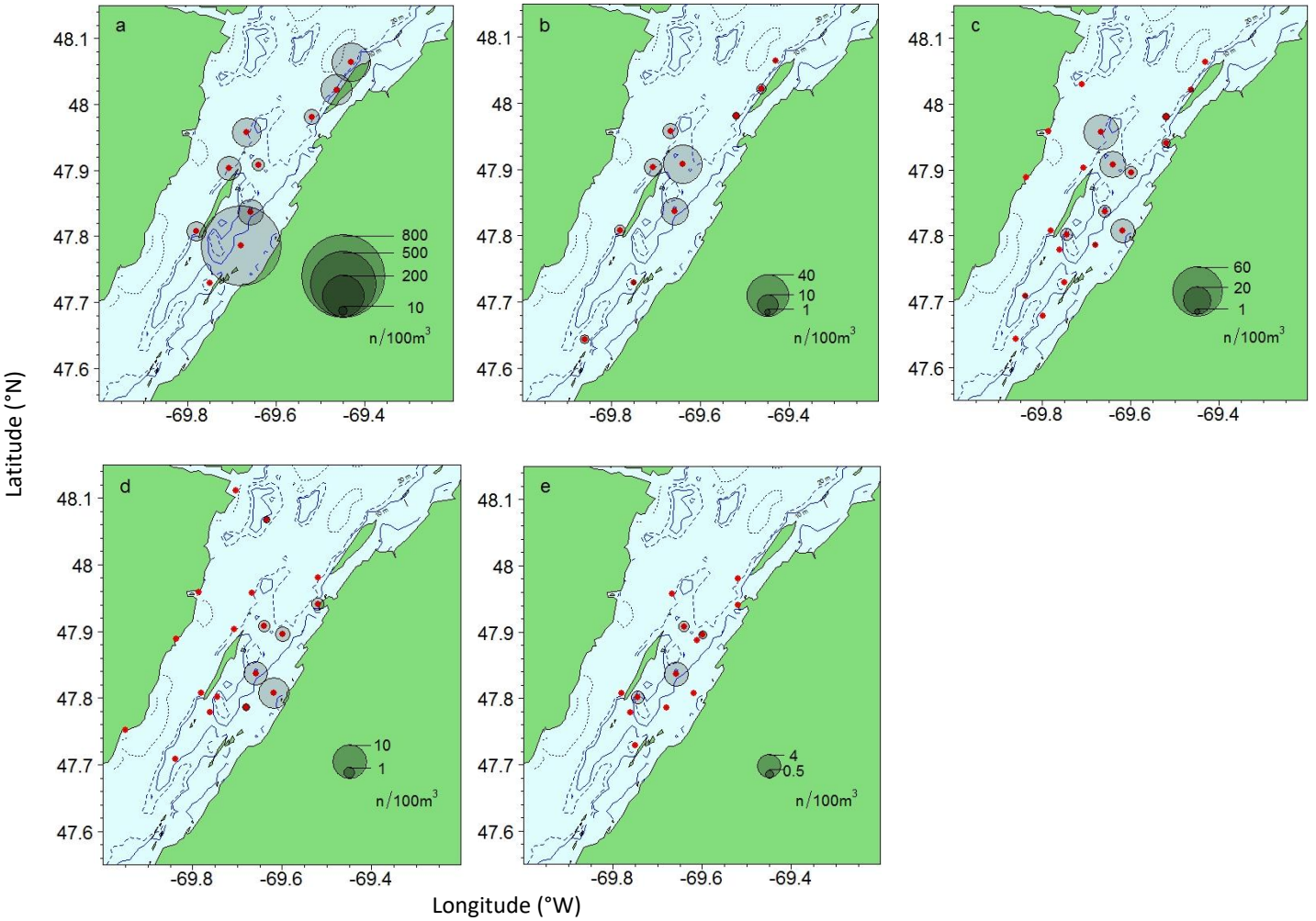


Figure 9. Distribution and densities of post yolk-sac herring larvae (category 2; Total length ≈ 11.5-30 mm), between June and October 2014 in the St. Lawrence Middle Estuary. (a) June 2, 5, 10 and 11; (b) June 17 and 18; (c) July 10, 11, 24, 30 and 31; (d) August 15, 20, 21 and September 3; (e) September 17, 22, 24, 25 and October 3.

1.3.3 Differences in TL of newly hatched larvae (yolk-sac larvae, category 1b)

To determine if there were differences in TL of small size yolk-sac larvae at different periods in the season, presumably collected after different hatching events, only samples with a sufficient number ($n > 30$) of yolk-sac larvae of comparable yolk volume, hence of the category 1b, generally more numerous than the category 1a larvae, were considered in the analysis (ANOVA not significant; $p = 0.094$). Therefore, three hatching events were retained for comparison of TL: two in the spring (June 5 and June 10-11) and one in the autumn (Sept. 24). Total body length of newly hatched herring larvae varied significantly among cohorts (Figure 10). Interquartile ranges of length (Q1-Q3) for cohort 1, 2 and 6 were respectively 7.47-8.35 mm, 7.89-8.66 mm and 7.33-7.96 mm. A test for homogeneity of variance showed unequal variances among groups (Levene: $p = 0.0006$) and therefore the Kruskal-Wallis test was used for comparisons among cohorts. A posteriori Tukey test revealed that the median TL of cohort 6 (7.53 mm) was significantly lower than cohorts 1 (8.05 mm; $p = 0.0057$) and 2 (8.35 mm; $p < 0.0001$) and TL of cohorts 1 and 2 were barely significantly different ($p = 0.0205$). During those three hatching events (cohorts 1, 2 and 6), the mean water temperature (°C) above and below the thermocline was higher in September compared to June (Table 3).

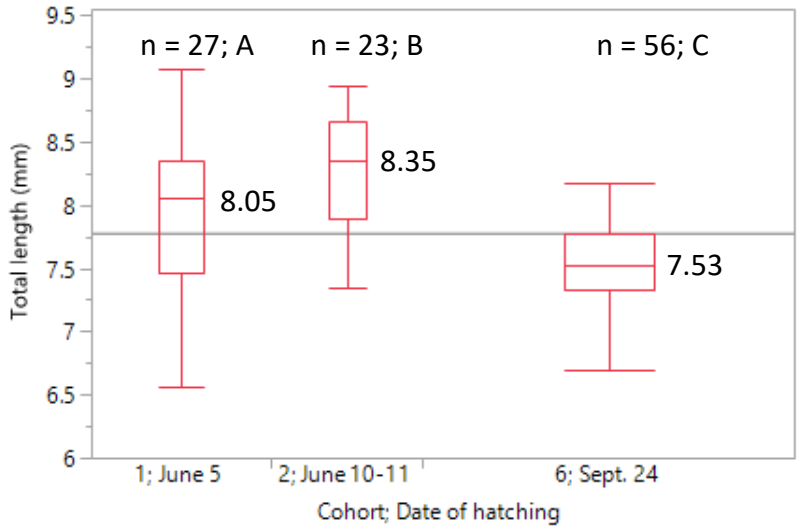


Figure 10. Effect of hatching time on total body lengths (TL) of yolk-sac herring larvae (category 1b) sampled in 2014 in the St. Lawrence Middle Estuary. Medians are reported next to their corresponding red lines. Total numbers of measured larvae (n) for each cohort are indicated. Different letters indicate statistically significant differences (KW; $p \leq 0.005$).

Table 3. Mean water temperatures at dates of herring larvae hatching events for all sampled stations combined in the St. Lawrence Middle Estuary.

Sampling date	Mean surface temperature (°C)	Mean bottom temperature (°C)
June 2 – Cohort 1	6.96	3.81
June 10 – Cohort 2	5.08	3.27
September 24 – Cohort 6	7.25	5.94

1.3.4 Length frequency histograms and cohorts' growth

The first larval cohort that could be followed through most of the sampling period hatched on June 2-5 with a great abundance of yolk-sac larvae of TL ≈ 7.52 mm (cohort 1 in red; Figure 11, Table 4). This cohort could be followed until the beginning of August. A

second cohort of smaller abundance (17% of all larvae captured) appeared on June 10 and 11 (cohort 2, blue; Figure 11, Table 4) and followed closely cohort 1, again until the beginning of August. Software FiSAT II identified two modes on June 17-18, one at 10.06 mm and another one at 14.31 mm (Figure 11). According to previously reported growth rates and water temperatures, cohorts 1 and 2 should have larvae with total length spanning from 8 to 12 mm approximately. Therefore, the 14.31 mm mean proposed by FiSAT II represent larvae that were either part of cohort 1 (and grew faster) or hatched before initiation of our sampling campaign. Expected length calculated according to previous data was used to identify cohorts 1 and 2 at later dates (Table 4). Length frequency distribution was multimodal on July 10, 11, 16 and 17 where small larvae of a newly hatched cohort appeared (cohort 3, green). Older larvae were also found, but in lower frequency (20% on July 16-17) (TL ≈ 15-20 mm; Table 4). Cohort 3 was followed until September 3 (Figure 12). Cohort 4 (purple) hatched near July 30, while cohort 5 hatched near August 15, when the distribution was again multimodal. A total of 28% of all larvae captured on this date represented larger and older larvae (TL ≈ 20.9-27.6 mm) (Figure 12, Table 4). Cohorts 4 and 5 were followed until the end of September and the beginning of October (Figure 12). Cohort 6 (grey) appeared on September 22, 24 and 25 in great abundance (Figure 12). Few older, larger larvae were also found at the end of September and beginning of October (TL ≈ 22.3-32.8 mm, Table 4). A more detailed table can be found in the annex for exact cohort association and length limits (Table A1).

As the season progressed, it was more difficult to differentiate cohorts. This was the case for July 24 and July 30, where all cohorts were mixed. A small number of larvae that could not be followed afterwards hatched around July 24 (cohort *, dark green, Figure 11) but they were not included in the following analyses on larval condition since they appeared only three times (Figures 11, 12). It is possible that this cohort was not well identified on July 30 as well. Larger larvae presumably of cohorts 3 and/or * were captured on September 3, but this represented only a total of 5 larvae (Figure 12).

Table 4. Distribution of length classes for each cohort of herring larvae sampled in 2014 in the St. Lawrence Middle Estuary.

Length categories	Cohort 1 TL (mm)	Cohort 2 TL (mm)	Cohort 3 TL (mm)	Cohort 4 TL (mm)	Cohort 5 TL (mm)	Cohort 6 TL (mm)
1a, 1b, 1c	5.32 - 11.41	6.66 - 9.96	6.98 - 8.92	6.54 - 8.64	6.86 - 9.39	5.42 - 9.46
2	11.42 - 26.58	9.97 - 24.97	8.93 - 30.42	8.65 - 26.88	9.40 - 23.46	na

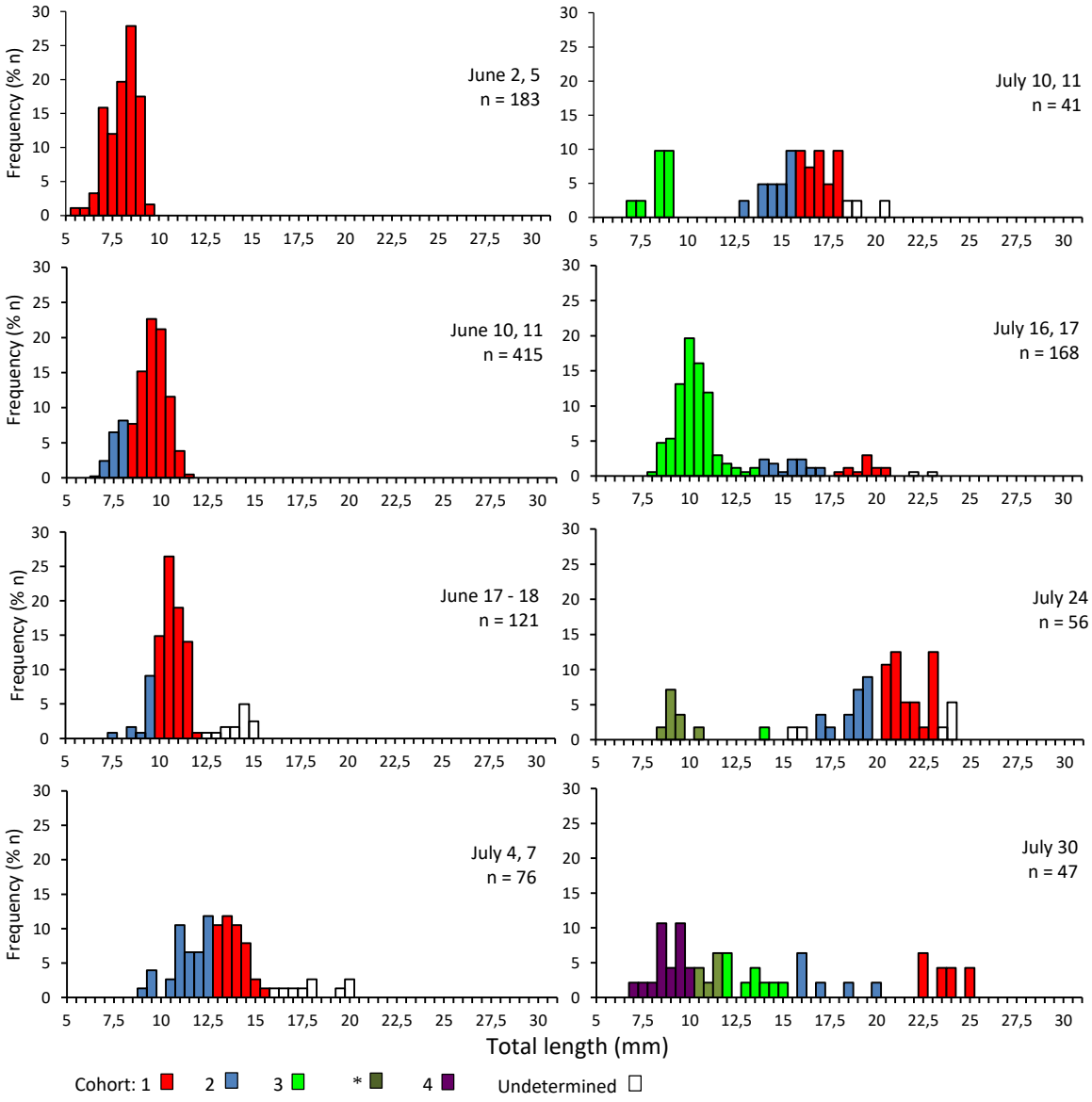


Figure 11. Total length frequency histograms of herring larvae sampled during June and July 2014 in the St. Lawrence Middle Estuary. Total numbers of larvae sampled in each sampling week are indicated (n). Red = cohort 1, blue = cohort 2, green = cohort 3, dark green = cohort *, purple = cohort 4, white = undertermined cohort.

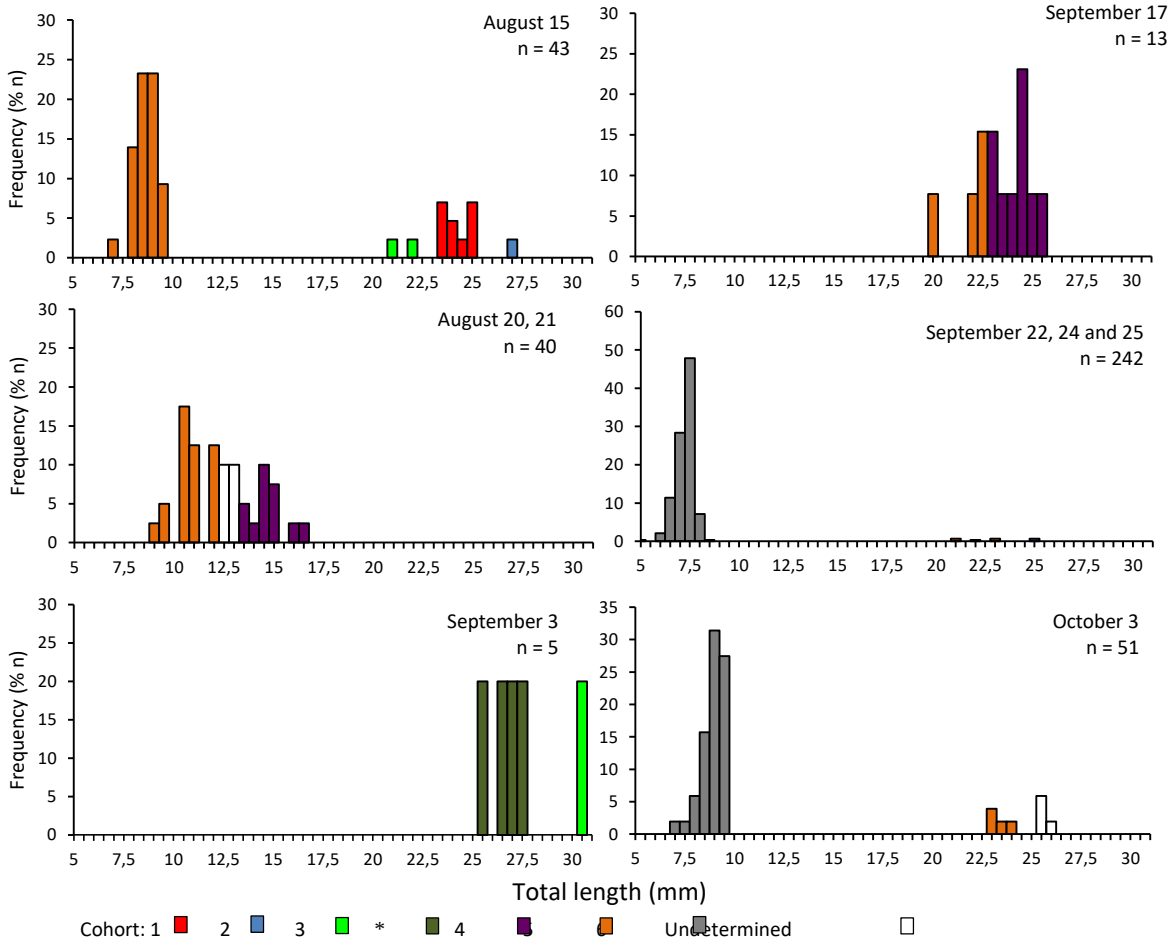


Figure 12. Total length frequency histograms of herring larvae sampled during August, September and October 2014 in the St. Lawrence Middle Estuary. Total numbers of larvae sampled in each sampling week are indicated (n). Red = cohort 1, blue = cohort 2, green = cohort 3, dark green = cohort *, purple = cohort 4, orange = cohort 5, grey = cohort 6, white = undertermined cohort.

1.3.5 Growth rates of different cohorts of herring larvae

Growth rates represented by the slope (α) of the linear regressions of mean total length (TL, mm) on day of the year, were significantly different among cohorts (p = 0.0002*, Table 5, Figure 13). Growth rates of springtime cohorts, namely cohort 1 (0.26 mm d^{-1}, hatched on June 2) and cohort 2 (0.24 mm d^{-1}, hatched on June 10) were significantly lower (Tukey HSD test, $p \leq 0.005$) than the growth rate of summertime cohorts by 11% and 13%, respectively. Cohort 3 (hatched on July 10) showed the highest growth rate of 0.37 mm d^{-1} (Table 5). Only two sampling dates characterized cohort 6 and therefore no linear regression was conducted on these data.

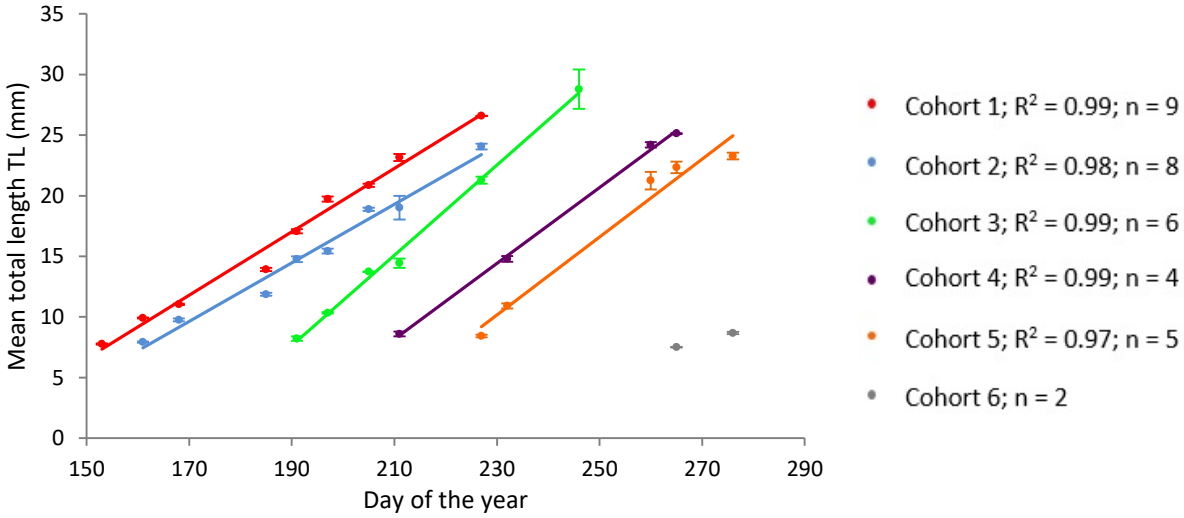


Figure 13. Linear regressions of total length (TL) in function of time for five successive cohorts sampled in 2014 in the St. Lawrence Middle Estuary. Day 150 = May 30 and day 290 = October 17. Numbers of sampling dates for each cohort (n) and regression coefficients (R^2) are indicated in the legend. F and p-values, slopes and intercepts are provided in Table 5.

Table 5. Effect of the time of hatching on the slopes of the linear relationships between total length TL (mm) and day of the year for different cohorts of larval herring sampled in 2014 in the St. Lawrence Middle Estuary presented in Fig. 13. Different letters indicate significantly different slopes (Tukey HSD test, $p \leq 0.005$).

Cohort; range of days	DF	F-Ratio	P-value	Slope (α)	Intercept (β)
1; 74	8	464.21	<0.0001*	0.26; A	-32.6
2; 66	7	296.14	<0.0001*	0.24; B	-31.45
3; 55	5	794.57	<0.0001*	0.37; C	-63.12
4; 54	3	1272.07	<0.0001*	0.31; D	-57.56
5; 49	4	88.87	0.0025*	0.32; E	-63.81

Interaction (Cohort) x (Day of the year) p-value = 0.0002

During growth, each cohort accumulates different total degree-days since they hatched at different moments during the sampling season and thus were exposed for different time periods at different water temperatures. For example, the maximum amount of degree days absorbed per day is seen in cohorts 3 and 4 (Table 6).

Table 6. Amount of degree-days accumulated at the time of last detection of each cohort.

Cohort	Maximum amount of degree-days accumulated (degree-days)	Hatch date (calendar day and day of the year)	Date of last detection (calendar day and day of the year)	Amount of absorbed degree days per day
1	555.04	June 2 (153)	August 15 (227)	7.5
2	500.89	June 10 (161)	August 15 (227)	7.58
3	463.87	July 10 (191)	September 3 (246)	8.43
4	442.07	July 30 (211)	September 22 (265)	8.18
5	350.04	August 15 (227)	October 3 (276)	7.14
6	50.60	September 25 (268)	October 3 (276)	6.33

Relation between total length (TL) and sum of degree-days (SDD) was explored through linear regression. Shapiro-Wilk test was not respected for cohort 1 (SW, p = < 0.0001*) and cohort 2 (SW, p < 0.0001*). However, the comparison between slopes is still robust even though normality is not attained here since the number of samples is almost equal in all cohorts (Quinn and Keough, 2002). All linear regressions were significant (Table 7) and slopes were significantly different from each other (p = 0.0015*, Table 7). A minimal difference of 0.8% was observed between cohorts 1 (α = 0.036) and 3 (α = 0.44) and a maximal difference of 1.5 was observed between cohorts 2 (α = 0.031) and 5 (α = 0.046). For the same amount of degree-days accumulated, cohorts 3 and 5 grew significantly faster than cohorts 1, 2 and 4 (α = 0.031-0.036; Table 7) (Figure 14).

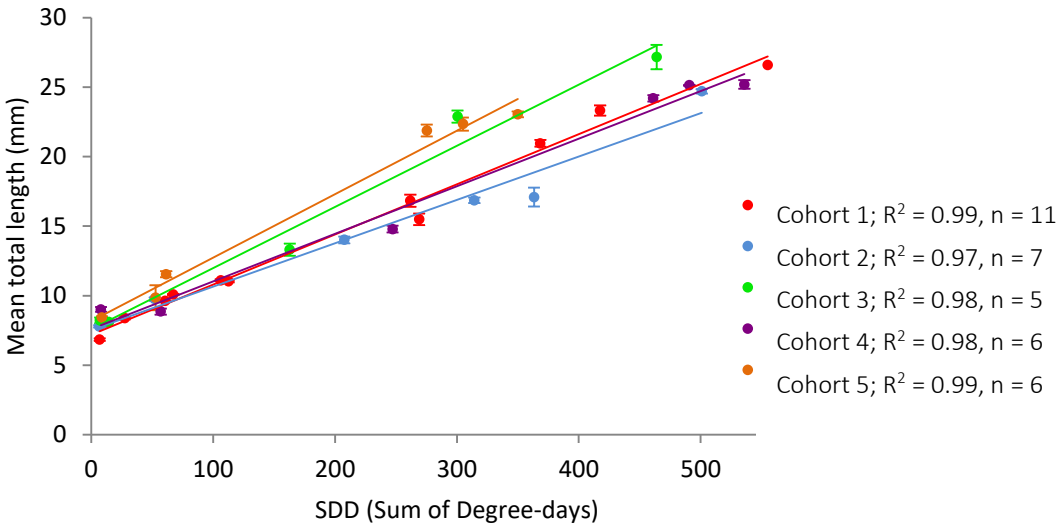


Figure 14. Linear regressions of total length (TL) in function of the sum of degree-days (SDD) for different cohorts of herring larvae sampled in 2014 in the St. Lawrence Middle Estuary. Numbers of sampling dates for each cohort (n) and regression coefficients (R^2) are indicated. F and p-values, slopes and intercepts are provided in Table 7.

Table 7. Effect of the sum of degree-days (SDD) on the slopes of the linear relationships between total length (mm) and SDD for different cohorts of larval herrings sampled in 2014 in the St. Lawrence Middle Estuary. Different letters indicate significantly different slopes (Tukey HSD, $p \leq 0.005$).

Cohort	DF	F-Ratio	P-value	Slope (α)	Intercept (β)
1	10	865.18	<0.0001*	0.036	7.17; A
2	6	177.89	<0.0001*	0.031	7.53; A
3	4	122.08	0.0016*	0.044	7.58; B
4	5	240.88	<0.0001*	0.034	7.59; A
5	5	271.53	<0.0001*	0.046	8.16; B

Interaction (Cohort) x (SDD) p-value = 0.0015*

1.3.6 Larval herring condition

Yolk-sac herring larvae (categories 1a-c)

Slopes of the relationship between height of the eye on head thickness for yolk-sac larvae were parallel (p = 0.50, Table 9) between cohort 1 and 2 during June. Condition of cohorts 1 and 2 were similar during June since there was no significant effect of cohort on head thickness (HT) after controlling for the height of the eye (HE) (ANCOVA, p = 0.24; Table 9; Figure 15-A). Slopes were similar (ANCOVA, p = 0.21, Table 9) among cohorts 1, 2, 5 and 6 during all months (June to October). There was a significant effect of cohort on HT after controlling for HE (ANCOVA, p = <0.0001*, Table 9; Figure 15-B); condition was higher for cohorts 1 and 2 compared to cohort 6, showing a 3 to 4% bigger adjusted mean HT, respectively (Table 9). Condition was higher for cohort 1 compared to cohort 5, with a higher adjusted mean HT of 3.2% (Table 9).

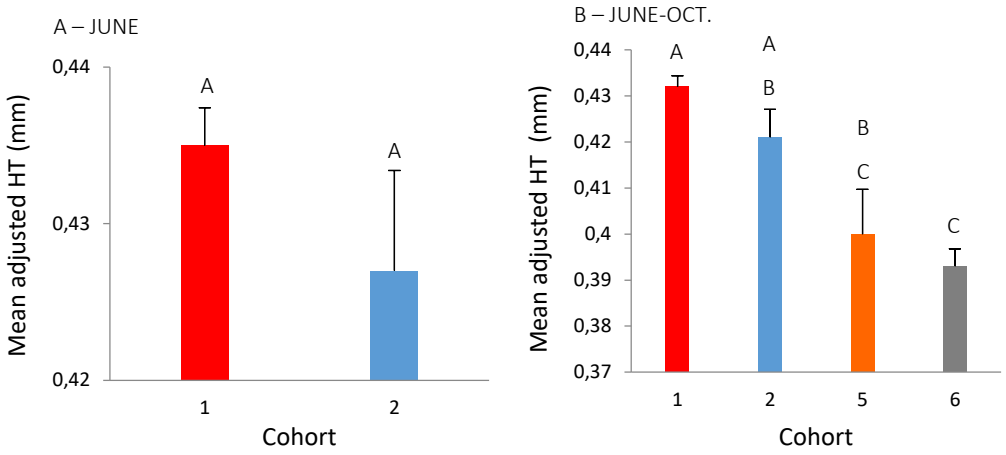


Figure 15. Mean head thickness (HT) adjusted for height of the eye for yolk-sac larval herring of different cohorts sampled in 2014 in the St. Lawrence Middle Estuary in June (A) and from June to October (B) (see Table 9). Different letters represent significant differences among cohorts (ANCOVA, $p \leq 0.005$). Results of linear regression and of ANCOVA analyses are in Tables 8 and 9.

Post yolk-sac herring larvae

Slopes of the relationship between height of the eye on head thickness for post-yolk sac larvae in July were similar ($p = 0.1679$, Table 9, Fig. 16-A) and there was a significant effect of cohort on HT after controlling for HE ($p = <0.0001$*, Table 9). A posteriori Tukey test revealed that differences laid between the y-intercept of each cohort (Table 9). Cohort 3 showed the lowest adjusted mean HT (4.8% less than cohort 2 and 14.6% less than cohort 1) (Table 9). However, the assumption of independence between HT and cohort was not respected for cohort 3; there were more data points for a smaller ratio HE/HT since the majority of larvae from cohort 3 were captured at the beginning of the month near their emergence event (Annex; Figure A1). The number of older larvae for this cohort was

extremely low compared to the number of yolk-sac larvae, so length was biased towards smaller larvae for cohort 3.

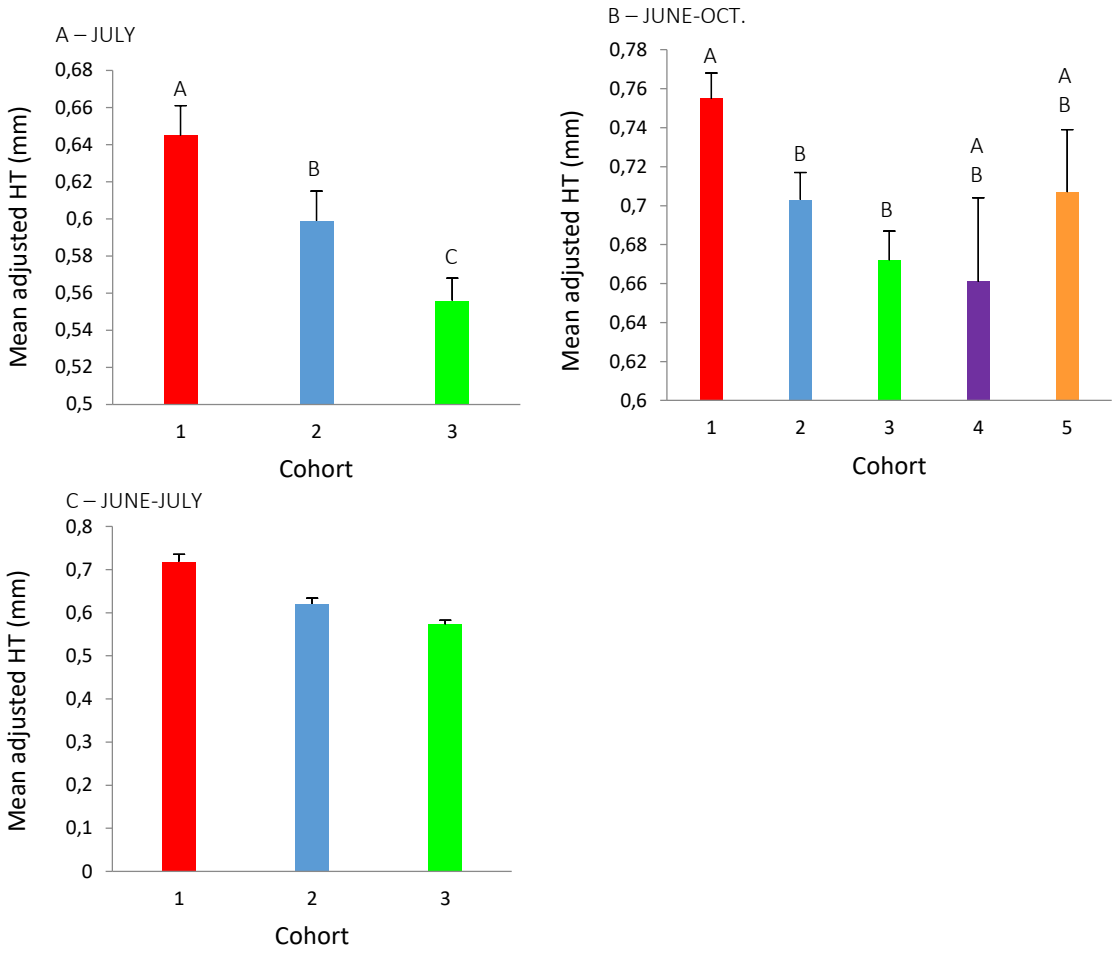


Figure 16. Mean head thickness (HT) adjusted for height of eye for different time periods and different cohorts of post yolk-sac larval herring sampled in 2014 in the St. Lawrence Middle Estuary. Different letters represent significant differences among cohorts (ANCOVA; $p \leq 0.005$). Results of linear regression and of ANCOVA analyses are in Tables 8 and 9.

When post yolk-sac larvae condition across months (June to October) was compared among cohorts, slopes were similar ($p = 0.64$, Table 9, Fig. 16-B). There was a significant effect of cohort on HT after controlling for HE (ANCOVA, $p = 0.0005$*, Table 9). Adjusted mean HT of cohort 1 was higher by 5.2% than that of cohort 2 and 8.3% higher than that of cohort 3, but no difference laid between cohorts 2 and 3 (Table 9).

Again, the assumption of independence between HT and cohort was not respected for cohort 3 since data points were predominantly for small-size larvae only (Annex; Figure A2). Data analysis for June and July was therefore constrained around the majority of data points of cohort 3, with HE ranging from 0.31 to 0.43 mm. Larvae of cohorts 1 and 2 with HE falling in that range were compared to larvae of cohort 3 (Fig. 16-C). Slopes were not parallel ($p = 0.0200$*, Table 9). HT of cohort 1 increased at a greater rate relative to HE during the months of June and July than that of cohort 2 and 3 and HT of cohort 2 increased at a greater rate than cohort 3 ($\alpha = 2.49 > 1.52 > 1.04$, Table 8), which means that condition as well increased (for example, condition of larvae from cohort 1 was getting better than that of cohort 2 and 3 over the same period of time).

Table 8. Linear regressions of head thickness (HT, mm) in function of height of the eye (HE, mm) for different cohorts of herring larvae sampled in SLME in 2014, at the yolk-sac and post yolk-sac larval stages (Figures 15 and 16).

Figure	Cohort	DF	F-Ratio	R^2	P-value	Slope (α)	Intercept (β)
Yolk-sac larvae							
June (Fig. 15-A)	1	561	26.94	0.15	<0.0001*	0.71	0.25
	2	84	99.02	0.26	<0.0001*	0.86	0.2
June to October (Fig. 15-B)	1	542	83.43	0.13	<0.0001*	0.73	0.24
	2	77	22.85	0.23	<0.0001*	1	0.16
	5	30	6.81	0.19	0.0142*	0.52	0.26
	6	223	15.28	0.06	<0.0001*	0.47	0.27
Post yolk-sac larvae							
July (Fig. 16-A)	1	46	18.92	0.3	<0.0001*	1.36	0.2
	2	62	24.78	0.29	<0.0001*	0.95	0.28
	3	126	41.95	0.25	0.0016*	0.81	0.28
June to July (Fig. 16-C)	1	37	41.14	0.53	<0.0001*	2.49	-0.25
	2	37	8.40	0.19	0.0063*	1.52	0.06
	3	69	14.35	0.17	0.0003*	1.04	0.18
June to October (Fig. 16-B)	1	84	111.83	0.57	<0.0001*	1.42	0.14
	2	71	134.39	0.66	<0.0001*	1.38	0.1
	3	75	153.53	0.67	<0.0001*	1.52	0.02
	4	7	77.47	0.93	<0.0001*	1.77	-0.14
	5	13	11.54	0.49	0.0053*	1.34	0.14

Table 9. Analysis of covariance of head thickness (HT, mm) in function of height of eye (HE, mm) and date of hatching (cohort) for herring larvae of the yolk-sac and post yolk-sac stages sampled in the St. Lawrence Middle Estuary in 2014. Tests for homogenized slopes (P_s) and differences in intercepts (P_i) are presented, where significant p-values are indicated in bold. Different letters indicate significant difference of intercepts among different cohorts (ANCOVA, $p \leq 0.005$). Similar results were obtained before and after removing outliers (Annex; Table A3).

Comparison	P_s/P_i	Adjusted mean (HT) of cohort	Slopes (α)	Intercepts (β)	Tukey test results	n
Yolk-sac larvae						
Fig. 15-A						
Cohort 1	0.5/0.24	0.44	0.73	0.24	A	562
Cohort 2		0.43		0.23		85
Fig. 15-B						
Cohort 1	0.21/ **0.0001***	0.43	0.7	0.25	A	543
Cohort 2		0.42		0.24	AB	78
Cohort 5		0.40		0.21	BC	31
Cohort 6		0.39		0.21	C	224
Post yolk-sac larvae						
Fig. 16-A						
Cohort 1	0.17/ **0.0001***	0.72	0.96	0.37	A	47
Cohort 2		0.62		0.27	B	63
Cohort 3		0.57		0.23	C	127
Fig. 16-C						
Cohort 1	**0.0200***/ na	0.65	1.64	0.06		38
Cohort 2		0.6		0.02		38
Cohort 3		0.56		0.03		70
Fig. 16-B						
Cohort 1	0.6438/ **0.0005***	0.76	1.44	0.13	A	85
Cohort 2		0.7		0.08	B	72
Cohort 3		0.67		0.05	B	76
Cohort 4		0.66		0.04	AB	8
Cohort 5		0.71		0.08	AB	14

1.4 DISCUSSION

Areas of emergence of Atlantic herring larvae in 2014 were located close to spawning areas described and recorded 20 years ago, more specifically around Île aux Lièvres, Île Verte and in the southern channel of the SLME in front of the bay of Rivière-du-Loup for the spring population and the latter only for the autumn population. The southern channel also seemed to be a good area of concentration and of retention for older larvae as indicated by the presence of various cohorts of growing post yolk-sac larvae during the whole sampling season. Hatching events also occurred around the same time than recorded 20 years ago as well, for spring and autumn cohorts. Relative proportion of yolk-sac larvae and larval densities of the spring component were larger than that of the autumn component, which matches past studies. However, only one wave of emergence has been recorded in early June in the literature while we recorded two. As for growth and condition of larval herring in the SLME, temperature was an important environmental factor.

1.4.1 Localisations of herring hatching

Île Verte has been recognized as a major spawning ground for the spring component of herring population in the SLME (Côté *et al.*, 1980; Iles and Sinclair, 1982; McQuinn *et al.*, 1983; Fortier and Gagné, 1990; Lacoste *et al.*, 2001). Munro *et al.* (1998) also described an important spawning ground located at the southwest tip of Île aux Lièvres, upstream of Île Verte. Although not used every year, the site was presented as a major spawning ground for herring in the SLME (Munro *et al.*, 1998). The area of the bay of Rivière-du-Loup, along with islands upstream (the archipelago of Îles de Kamouraska and of Îles Pèlerins) were other important spawning areas (Munro *et al.*, 1998). During the spring sampling season of 2014, high concentrations of yolk-sac herring larvae were sampled on the west coast of Île Verte, so this area was still used intensively in 2014. Yolk-

sac larvae were found also at the southwest tip of Île aux Lièvres in June. However, in June 2014, yolk-sac larvae were slightly more abundant around station 15 and offshore from Rivière-du-Loup, in the southern channel. Previous studies have reported herring larval concentrations in the northern channel, from Île aux Lièvres to La Malbaie (Able, 1978; Fortier and Leggett, 1982). In 2014, our sampling effort was limited in the northern channel and therefore, we cannot comment on the current status of herring larvae in this region. As for the autumn component of the population, larvae emerged around the same area as for the 2014 spring component. The utilisation of this same area was recorded in the past for the autumn population (Fortier and Gagné 1990; Lacoste *et al.,* 2001).

1.4.2 Relative densities of herring cohorts

For the springtime cohorts, a major hatching event has been previously documented, around the first two weeks of June (Able, 1978; Fortier and Leggett 1982; McQuinn *et al.*, 1983; Munro *et al.*, 1998). The first two cohorts we identified were so close in time that it was possible that both were taken for one big cohort in former studies. Henri *et al.* (1985) was the only study that sampled as frequently as the present study but they only found one cohort in springtime. However, their sampling started on June 10, so they might have missed the first cohort. Differentiating cohorts afterwards was more difficult if a hatching event was missed, as they grow so closely in time they can be mistaken for one big cohort. Lambert (1984) also described herring cohorts to be as short as 6 days apart. It is also possible that the sampling at different stations biased the results and that the two modes of the size frequency distribution seen on June 10 and 11 were in fact representing one cohort only. For example, those larvae of length of 5-10 mm on June 2-5 and those at 7-12 mm from June 10-11 might be the same larvae according to the growth rate associated with them. Therefore, we cannot conclude to which cohort larvae sampled on June 2-5 and June

10-11 actually would be associated. Morphometric analysis of otoliths could give us the exact date of emergence and resolve this hypothesis.

In the autumn, one cohort was reported in past studies around the third week of September (Fortier and Gagné, 1990; Munro *et al.*, 1998). The present study demonstrated that this hatching event for the autumn population still occurred as a high density of yolk-sac larvae was found on September 25, 2014 in the southern channel. However, during the season, relative abundance varied greatly among hatching events, with the highest (70%) proportion of all yolk-sac larvae hatching during the entire sampling season.

Not only hatching times but also relative abundances of spring and autumn cohorts matched past description by Fortier and Gagné (1990). This result was in contradiction with recent trends observed in relative abundances of spring and autumn spawning stocks in the southern GSL where the spring component have declined since the beginning of the 2000s (MPO, 2005; LeBlanc *et al.*, 2012). If larval densities represent spawner abundances, our results suggest that spring spawners were more abundant than autumn spawners in the SLME in 2014, whereas the autumn component was reported as more abundant than the spring component in the southern GSL in most recent studies (MPO, 2005, LeBlanc *et al.*, 2012). Interestingly, McQuinn (1997b) suggested year-class twinning from herring populations of western Newfoundland, where spring-spawned juveniles that grow faster might become autumn spawners while slow-growing autumn-spawned juveniles might spawn in spring in the following years (three or four years later, when they attain maturation). Therefore, the abundance data obtained on larval herring on one particular season might not necessarily reflect the size of the future adult spring or autumn spawning population in the upcoming years. Possibly intensive mixing between the spring and autumn reproductive units is observed in the SLME. Moreover, studies suggested that 48% of adult herring spawning in spring was composing the ‘pygmy’ herring population (likely originating from larvae hatched in spring in the SLME) (Lambert, 1990). The remaining

part of the spring spawners were likely originating from larvae hatched in the spring or autumn that grew outside the SLME, possibly in warmer waters of the GSL (Lambert, 1990). Data on the present relative proportions of spring and autumn herring adults spawning in the SLME are needed and microchemical analysis of larval and adult otoliths could be used to reveal the location of the origin of the SLME herring spawning units.

As for the summer cohorts, only the first hatching event (sampled on July 10) was noted in the literature. This cohort represented much lower larval densities in the literature (Henri *et al.,* 1985) as observed in the present study compared to the larval densities of June hatching events. It was suggested by McQuinn (1997a) that larger and older individuals spawn earlier while less mature spawning herrings would lay their eggs later in the season. Summer cohorts could arise from those fewer individuals that spawn later. Small cohorts could be explained by the small number of these younger individuals. Moreover, Henri *et al.* (1985) found a positive correlation between small larvae densities and events of spring tides at the time of sampling, suggesting that yolk-sac larvae were displaced vertically in the water column during flow. Spring tides in the summer of 2014 occurred on July 28-29 and August 12-13. It was possible that yolk-sac larvae (July 30) and post yolk-sac larvae (August 15) were present in higher densities during high spring tides events and effectively sampled in the water column at these moments. Concerning emergence events recorded in the spring, sampling dates of high yolk-sac larvae abundances did not match dates of spring tides. However, these emergences were so large that presence of yolk-sac larvae would have been recorded independently of the tidal phase. It is therefore possible that past studies missed the small hatching events during the summertime if they were not timed properly with spring tides. Furthermore, a suprabenthic sled might sample more effectively yolk-sac larvae, as sawtooth tows within the water column sample only a small fraction of the deeper water layer, so we might have underestimated numbers of yolk-sac larvae between events of spring tides. However, even with a suprabenthic sled, Henri *et al.* (1985) did not capture any yolk-sac larvae during the summer, suggesting that summer cohorts

might not have occurred in the past. With climate change, many fish populations could change locations and timing of their spawning. Such shifts in spawning habitat of herring were predicted by models in the North Sea, primarily due to the increase of water temperature, where autumn spawners would spawn earlier, namely in the summer (Tsoukali *et al.* 2015). A slight shift towards summer spawning of the autumn spawners of the SLME might have started only in the past few years since summer hatching events were not recorded in the past. Larvae of summer cohorts had the biggest growth rate and might have a better chance of survival than those hatched in spring and autumn. However, they showed a mediocre condition, which is in contrast to a good survival probability. Annual surveys would be needed to see if there is a real increase of abundance of larvae during the summer.

Post yolk-sac larvae could be tracked through time since bigger larvae were sampled in the same area as yolk-sac larvae over the sampling season. The area comprising the southern channel, BRL and the southeast shore of Île aux Lièvres has been reported as an area of retention by Henri *et al.* (1985). Retention is detected when aggregations of larvae are sampled over time in the same area. Around BRL, residual currents might have brought larvae hatched around Îles Pèlerins and Île aux Lièvres to the southern channel (Munro *et al.*, 1998). Upstream transport is facilitated for yolk-sac herring larvae that are negatively buoyant (Courtois *et al.*, 1982; Couillard *et al.*, 2017). These older larvae can effectuate tidal stream transport (Fortier and Gagné 1990; Fortier and Leggett 1983; Lacoste *et al.*, 2001). Oceanographic conditions could be favorable to the retention of larvae in the southern channel, offshore from Rivière-du-Loup. As they absorb their yolk-sac, larval herring migrate to the surface layer (to feed, for example). At that moment, they could be push into the BRL (when coming from the southwest tip of Île aux Lièvre, for example) with flooding tide and by episodic northwest winds through the mechanism described by Bauer *et al.* (2013) in the Baltic Sea, and therefore retention could occur in BRL where residual circulation is weak (Couillard *et al.*, 2017).

The depth of zero residual current in this area is around 20 m, which corresponds to stations 21 and ES10 in this study (Fig. 3). Henri *et al.* (1985) demonstrated important return of larvae in the area adjacent to stations 6, 21 and ES10 in relation to spring tides. However, in this study, densities decreased significantly as the season progressed, with the highest density in June 2014 (740 larvae per 100 m^3) and the lowest in September 2014 (4 larvae per 100 m^3). Such decrease is expected due to higher predation rates on small larvae, losses by advection out of favorable areas and high declines of larvae when they pass from the yolk-sac to the post yolk-sac stage, when larvae fail to find food adequately at a critical time of their development (Houde, 2008). Several post yolk-sac larvae might have been transported upstream to known retention areas near Île aux Coudres (Able, 1978) or downstream due to strong currents along the southern shore (through the Gaspé current) (Fortier and Gagné, 1990). However, these larger post-yolk sac larvae could have been under sampled due to net avoidance, increasing the bias for larvae over 20 mm (Folkvord *et al.*, 1997).

1.4.3 Length at hatching, growth, and condition of herring yolk-sac larvae

Yolk-sac larvae were predicted to have temperature-dependent growth rates (Hufnagl and Peck, 2011) since they feed endogenously. Larvae hatching in colder waters (< 6°C) are smaller than larvae hatching in warmer waters (Fey, 2001). In contrast, warmer temperatures in the deeper water masses were observed in September 2014, when the larvae of the autumn cohort were significantly smaller. In accordance, Peck *et al.* (2012) also evaluated that herring larvae incubated in 3°C waters hatched at lengths greater than 8 mm and hatched around 7 mm in 6°C waters, which is in accordance to what we observed in our study. Difference of length-at-hatch could be related to the age of embryo, with longer larvae hatched from older embryos (Geffen, 2002). It takes longer time, or more degree-days, for herring larvae to hatch in colder waters (Peck *et al.*, 2012) like those found in the

SLME in spring, so these larvae likely hatched at a greater embryonic age. Other factor(s) could have affected the length at hatch of larvae of the autumn population, like the egg diameter. A decrease in egg diameter has been noted in most northern fishes as the season progressed (Blaxter and Hunter, 1982). Length at hatching was positively correlated with egg size (Bradford and Stephenson, 1992). In North Sea herring, autumn spawners laid more and smaller eggs than winter spawners (van Damme *et al.*, 2009). Both populations of herring start maturation at the same time of the year so the development of the oocytes is the same. However, body condition of the winter population decreases prior to their spawning time. These spawners continue their egg development even though their body condition is lower, giving up bigger eggs (van Damme *et al.*, 2009). Similarly, this has been observed in herring of the 4T unit in southern GSL. A lengthy gonad maturation (7-9 months) has been recorded in the spring reproductive unit compared to the autumn reproductive unit (4 months) (Bradford and Stephenson, 1992). Heavier thus bigger eggs were therefore noted in the spring spawners but the autumn spawnes showed higher fecundity, hence resulting in laying more but smaller eggs. Hence, our results where higher length-at-hatch for the spring unit was found in the SLME might reflect bigger egg size in this unit.

Temperature affected condition on post yolk-sac larvae (Couillard *et al.*, 2017; Diaz *et al.*, 2009). In 2014, the temperature in the SLME surface and deep-water masses in September was much higher than previous years. Therefore, high temperatures might impair condition of yolk-sac from cohort 6. The yolk-sac stage duration is temperature dependent and decreases as temperature increases (Fey, 2001). Westernhagen and Rosenthal (1981) found condition in yolk-sac larvae of Pacific herring (*Clupea pallasii*) to be directly related to the size of the yolk sac. They observed that larvae kept a better condition at the onset of feeding when they had a bigger yolk sac since remnants of this yolk prevented starvation if food resources in the environment was not optimal. Also, in another study, larger larval herring at time of hatching had a bigger yolk sac which allowed

them to survive longer if food availability was not optimal at the time window they hatched (Peck *et al.*, 2012). Larvae from cohorts 1 and 2 were larger and might have a larger yolk sac. Therefore, this could have improved their condition.

1.4.4 Herring post yolk-sac larvae growth in relation to temperature and food availability

The evolution of growth rate values during the sampling season in our study fit those found by Fortier and Gagné (1990). The highest growth rate observed was that of cohort 3 (0.37 mm/day) sampled on July 10 and last detected on September 3. Cohort 3 therefore hatched and grew in water temperatures between 7-13°C, which is the optimal temperature range for viable hatch (Peck *et al.*, 2012). Kiørboe and Munk (1986) reported 0.35 mm/day at 8°C in the laboratory, while Baltic herring larvae (*Clupea harengus* L.) were found to grow at 0.37 mm/day at temperatures of 17.5-17.9°C (Oeberst *et al.*, 2009). Thus growth rate values of around 0.35 – 0.37 mm/day seemed to be in the upper range for this species, where maximal growth rates of 0.58 mm/day have been reported (Fey, 2001). However, overestimation of growth rate might have happened due to size selective predation mortality (smaller larvae that were not well nourished and grew more slowly could be more easily preyed upon) (Hauss and Peck, 2009; Kiørboe and Munk, 1986). Also growth rates were lower at the beginning of the summer, attained higher values in July and August before decreasing in September/October, following the temperature curve over the study area in the SLME. Finally, data was insufficient in autumn to obtain growth rates estimates for cohort 6.

Atlantic herring larval growth has been well studied around the world (Hauss and Peck, 2009; Oeberst *et al.*, 2009; Kobylianski, 2015) but only a handful of studies are found on the component of herring coming to spawn in the SLME (Able, 1978; Fortier and Leggett, 1983; Fortier and Gagné, 1990). In most studies, the temperature was outlined to

be the determinant factor for the growth rate of larval herring (Elliott, 1982; Fortier and Gagné, 1990; Fey, 2001; Hufnagl and Peck, 2011). Most studies have focused on larval herring growth below 12°C, but Oeberst *et al.* (2009) showed that larval Atlantic herring can grow and survive in water temperatures up to 17°C. Stations from ASA and BRL showed similar temperatures (16-18°C) but average temperatures at other stations were situated around 10°C, in a range from 4°C (June) to 14°C (August).

Houde (2008) suggested that more than 50% of variability in the mean daily larval herring growth rate could be attributed to temperature variations. However, adding more explanatory variables, such as salinity, did not explain the remaining variance observed in multiple linear regressions (Oeberst *et al.*, 2009). In the present study, after controlling for the differences in water temperature experienced by the different cohorts during their growth periods (e.g.: differences in growing degree-days), temperature failed to fully explain the observed variability in growth among cohorts. Similar results were found by Neuheimer and Taggard (2007) and they hypothesized that not only temperature but also other environmental variables appeared to influence growth rate.

Growth rate could also be influenced by food quality and availability (Kiørboe *et al.*, 1988; Kiørboe and Munk, 1986). Therefore, it would be important to understand the spatial and temporal distribution of main food items of larval herring in the SLME. Extensive literature exists on particulate matter, phytoplankton and zooplankton distribution around the maximum turbidity zone (MTZ) located around and upstream of Île aux Coudres, but only a handful of studies covered in the region of study around Île aux Lièvres (Courtois *et al.*, 1982; Maranda and Lacroix, 1983; Laprise et Dodson, 1989; Runge and Simard, 1990) and only one in the southern channel (Fortier and Gagné, 1990). *Acartia* spp., *Eurytemora* spp. and *Calanus finmarchicus* represented highest abundant copepod taxa between May and September in the middle Estuary (Runge and Simard, 1990). *Acartia longiremis* and *Eurytemora herdmani* reproduced in the SLME and highest densities were found around Île

aux Coudres and downstream in the deeper channels (Runge and Simard, 1990) while *Eurytemora affinis* is the dominant copepod found around tidal marsh pools of Île Verte (Runge and Simard, 1990). Larval herring are known to feed on copepod eggs, nauplii and copepodite stages C1-C3 following the resorption of yolk sac (Fortier and Gagné, 1990; Arula *et al.*, 2012), and finally prey on bigger copepods when larvae attain 17 mm in length (Hufnagl and Peck, 2011).

The higher growth rates found in cohorts hatched during the summertime could be due to higher temperature coupled with high prey abundance. However, zooplankton densities and gut content were not analyzed in the present study but would have given a much better insight on the differences in growth rates and condition identified between cohorts. Moreover, microstructure analysis of otolith increments and radius reflect somatic growth in larval herring could could improve precision of growth rates (Folkvord *et al.*, 1997). Furthermore, when the same population is sampled through time, it would be possible to assess size-selective growth and mortality (Folkvord *et al.*, 1997).

1.4.5 Condition in herring post yolk-sac larvae of the SLME

Strong and later than usual tributaries freshets (like Rivière-du-Loup) were significantly correlated with higher abundances of larval herring in the SLME possibly because it improves feeding conditions through water quality (Couillard *et al.*, 2017). Freshwater runoff from St. Lawrence tributaries was higher than usual in 2014 (Galbraith *et al.*, 2015). Moreover, higher temperatures, combined with inputs of nutrients and organic carbon from tributaries could possibly promote production of zooplankton becoming available for herring larvae at a good timing (Couillard *et al.*, 2017). This could have impacted positively the condition of the first cohorts hatched at the end of spring (Cohorts 1 and 2). These were in better condition compared to other cohorts. There exists a link

between larval condition and recruitment (Westernhagen and Rosenthal, 1981). Processes like temperature experienced by early larval stages were correlated with year-class success (Margonski *et al.,* 2010). Therefore, condition of yolk-sac larvae can influence condition of post-yolk sac larvae. Fortier and Gagné (1990) determined that zooplankton on which post yolk-sac larvae fed upon were produced in well-mixed, transitional waters of frontal structures that formed due to the St. Lawrence river freshet downstream of Île Verte around the beginning of June. The front migrated upstream, bringing high densities of zooplankton around Île aux Lièvres by the end of June, with persistence of high densities until September (Fortier and Gagné, 1990). St. Lawrence River freshet impacted also the SLME and higher biomass of zooplankton might as well have occurred in the retention areas of larval herring. It might be possible that food density was high enough for larval herring in the SLME in spring 2014, however no zooplankton data was available to confirm this hypothesis.

Abiotic factors such as temperature could also affect larval condition. In a study on condition and growth rate of larval herring from the SLME, Couillard *et al.* (2017) highlighted that the year 2012 was the warmest year of the sampling period, with herring larvae having the highest growth rates and poorer condition compared to larvae from other years that were not as warm. They suggested an "energetic imbalance" (insufficient food ingestion to meet high metabolic demands), in July when water temperatures were high, freshwater flow low and when the larvae were possibly using their body reserves, affecting their condition. In our case, the year of 2014 also represented record high sea surface temperatures, the highest since 1985 in the SSLMP and SLME (Galbraith *et al.,* 2015). Highest temperatures were recorded in mid-July to the end of August (Figure 6) which corresponded to the hatching times of cohorts 4 and 5. Most larvae sampled in cohort 3 came from the coastal station BRL, which is characterized by much higher temperatures (17-20°C). The onset of exogenous feeding is also a critical time and differences in condition among cohorts can arise from that time. Colder temperatures in early spring can

offer a bigger time window to provide a greater feeding success for early post yolk-sac larvae while larvae hatching around summer time have a much shorter time to start feeding, decreasing their success. Thus, it could affect negatively their condition (Peck *et al.*, 2012). This could be a potential explanation for the low condition of cohorts 3 and 4.

Finally, other methods to verify condition on larval fish exist. RNA/DNA ratios have been used, where smaller ratios represent low protein growth characterized by starving/poor condition fish (Folkvord *et al.*, 1997). Analyses of microstructures of otoliths can also reveal if the larvae experienced good feeding conditions (Folkvord *et al.*, 1997). It would be interesting to validate our findings with further analyses to evaluate the condition on larval herring in the SLME.

1.5 CONCLUSION

In 2014, larval herring in the SLME hatched at similar places and time as reported in the last studies on the subject that were conducted almost 20 years ago. Relative abundance in different larval cohorts (spring vs. autumn) did not reflect the changes that occurred in the spring and autumn spawning stocks in the southern GSL since the 2000s. Larval herring hatched in spring 2014 had good growth and condition and therefore did not appear to be limited by food. This study confirmed that the southern channel of the SLME was still highly important for retention, growth and survival of herring larvae. However, unusually high temperatures recorded in the SLME in 2014 might have impaired condition of larvae hatched in the summertime, even though they grew the fastest. It would have been important to analyze stomach contents and zooplankton availability in the environment in order to truly evaluate the food resource that was available for larval herring and how it could have impacted growth rates and conditions. Beluga whales are threatened by many factors but low food abundance such as spring herring in the SLME was outlined to be one

of the causes of their decline. Larval abundances in this study demonstrated that herring still comes spawning in the SLME in the spring, but we cannot evaluate the adult density with that of larval densities. Therefore, evaluation of the adult component must be done to see if it impacts the decline of the beluga whale in the SLME. Morphometric and microchemical analysis of otoliths and yearly surveys of spawning adult herring would be needed to evaluate the sites of origin of the herring spawning in the SLME in spring and autumn and to determine if year-class twinning occurred in the SLME Atlantic herrings. Also, in view of the implementation of a marine protected area focusing on the SLME, any anthropogenic activities in the SLME ecosystem need to be assessed for the risk of disturbing Atlantic herring spawning and larval development from May to October.

DISCUSSION ET CONCLUSION GÉNÉRALE

Cette étude était nécessaire afin de vérifier la persistance des aires et du temps du frai des deux unités reproductives de hareng atlantique (printemps et automne) dans l'estuaire moyen du Saint-Laurent. Puisque les stades embryonnaire et larvaire sont vulnérables chez ce poisson et détermine la survie des adultes, la croissance et la condition larvaires étaient des paramètres importants à évaluer (Cushing, 1990). En effet, le hareng est à la base du réseau alimentaire et donc très important pour beaucoup d'espèces incluant le béluga du Saint-Laurent (*Delphinapterus leucas*) (Lesage et Kingsley, 1995). Le déclin depuis le début des années 2000 de l'unité reproductive de printemps du hareng atlantique de la zone 4T de l'OPANO (dont fait partie le hareng de l'estuaire du Saint-Laurent) venant frayer dans l'EMSL a été proposé comme un facteur pouvant contribuer au déclin du béluga du Saint-Laurent (Plourde *et al.,* 2013). Comme aucune étude sur le hareng atlantique de l'EMSL n'a été effectuée depuis 20 ans, la persistance du frai du hareng de printemps dans l'EMSL était remise en question et l'évaluation de la condition larvaire devenait nécessaire pour comprendre ce stade de vie pour le hareng de l'EMSL. L'étude démontre que la distribution spatio-temporelle des aires d'émergences et de concentration larvaire concordent avec les études précédentes. De plus, les différences entre les taux de croissance et la condition des différentes cohortes étaient liées surtout aux différences de température dans l'environnement. Cependant, l'abondance et la qualité des proies pourraient aussi avoir un impact important qui n'a pas été évalué. Finalement, la cohorte de larve de harengs de printemps dans l'EMSL était plus abondante que celle d'automne. Si l'abondance larvaire reflète l'abondance des géniteurs (ce qui n'a pas été évalué), cette observation indique qu'on n'observe pas dans l'EMSL la chute du ratio entre harengs du printemps et automne qui a été documentée dans le sud du golfe (MPO, 2005; LeBlanc *et al.,* 2012).

2.1 LOCALISATION ET DENSITE RELATIVE DES DIFFERENTES COHORTES DE LARVES DE HARENG ATLANTIQUE

La côte ouest de l'île Verte, la pointe sud-ouest de l'île aux Lièvres et le chenal sud ont été rapportées comme des aires importantes de frai dans le passé (Fortier et Gagné, 1990 ; Munro *et al.,* 1998) et la localisation des épisodes d'émergence larvaire indiquent que ces aires étaient encore utilisées en 2014, et ce pour les unités reproductives de printemps et d'automne. Une abondance de larves a été observée durant tout l'été dans la baie de Rivière-du-Loup et le chenal sud, suggérant qu'il y avait de la rétention larvaire à ces endroits, tel que rapporté dans des études précédentes (Fortier et Gagné, 1990; Fortier et Leggett, 1983), ainsi que récemment (Couillard *et al.,* 2017). Par contre, le biais de l'échantillonnage occasionné par le filet empêchait de récolter les plus grandes larves (> 20 mm) car elles peuvent effectivement l'éviter (Folkvord *et al.,* 1997). Il est possible que la prédation et l'advection diminue le nombre de larves plus âgées, mais on ne peut interpréter comme une diminution d'abondance dans cette étude à cause de l'incapacité à les échantillonner (Fortier et Gagné, 1990). Les mécanismes de rétention discutés dans les études comprennent le transport tidal sélectif, où les larves sans sac vitellin se déplacent dans la colonne d'eau et utilisent la marée montante pour se faire pousser en amont alors qu'elles collent le fond lors du baissant (Fortier et Gagné, 1990; Fortier et Leggett, 1983; Lacoste *et al.,* 2001), et par les épisodes de vents du nord-ouest qui poussent les larves de la couche d'eau supérieure dans le chenal sud et la baie de Rivière-du-Loup (Couillard *et al.,* 2017). Non seulement les zones, mais aussi les moments d'émergences correspondent aussi avec les études précédentes. Notre échantillonnage plus fréquent a permis de déceler deux cohortes très abondantes et proches dans le temps au début juin, suivies d'une troisième cohorte durant la deuxième semaine de juillet (aussi rapportée par Henri *et al.* en 1985), de plus petite abondance cette fois. Cette étude présente la première mention de cohortes durant l'été. Étant donné l'abondance notable de petites larves dans nos échantillons

suivant les événements de marées de vive-eau, il est possible que notre succès de capture ait été influencé par les conditions environnementales durant l'été (Henri *et al.,* 1985) et que les études précédentes aient manqué les cohortes d'été. Il est possible aussi que les aires de frai et le temps de la reproduction changent au cours des années, possiblement à cause des changements climatiques. Par exemple, des changements dans les aires de frai des harengs dans la mer du Nord sont prévus, en raison de à la hausse de température des eaux qui s'en vient progressivement (Tsoukali *et al.,* 2015). Il est possible qu'un changement dans le temps de reproduction des harengs d'automne s'opère depuis les dernières années et soit maintenant rendu visible par notre échantillonnage, où les harengs d'automne se reproduiraient plus tôt, lorsqu'une température optimale est plus rapidement atteinte dans l'eau.

Finalement, la population d'automne a produit une seule cohorte de larve à la fin du mois de septembre (aussi rapportée par Fortier et Gagné en 1990; Munro *et al.* en 1998), d'abondance plus faible relativement aux cohortes du printemps. Les abondances relatives ne semblent pas avoir changées avec les études précédentes (Fortier et Gagné, 1990). Par contre, les méthodes d'échantillonnage ne sont pas les mêmes et donc la comparaison quantitative des abondances larvaires retrouvées dans notre étude avec celles des études passées ne peut se faire objectivement. Par ailleurs, si l'abondance larvaire représente bien l'abondance des adultes, il ne semble pas y avoir de diminution de l'unité reproductive de printemps comparativement à celle d'automne, le contraire de ce qui est observé présentement dans la baie des Chaleurs, où l'unité reproductive d'automne semble désormais plus grande que celle de printemps (MPO, 2005; LeBlanc *et al.,* 2012). Cela pourrait être vérifié par la microchimie des otolithes, où l'origine des reproducteurs et des larves serait retracées. De plus, selon McQuinn (1997b), il peut y avoir des échanges entre populations, où les harengs de la côte ouest de Terre-Neuve qui émergent au printemps grandiraient plus vite et se reproduiraient à l'automne trois ou quatre ans plus tard, une fois l'âge de maturation atteinte, et vice-versa pour les harengs d'automne qui grandiraient plus

lentement. Les populations de hareng de printemps et d'automne de l'île Verte pourraient se mixer à la manière des harengs de Terre-Neuve. Puisque cette étude ne peut démontrer une telle hypothèse, cela pourrait être vérifier par l'analyse morphométrique des otolithes. Alors, l'âge exact des larves de hareng pourrait être déterminé avec précision ainsi que leur date d'émergence, soit au printemps ou à l'automne.

2.2 TAILLE ET CROISSANCE LARVAIRE EN RELATION AVEC LA TEMPERATURE

Les larves avec sac vitellin de la cohorte 6 ont émergé en automne avec une taille moyenne plus petite que celles des cohortes 1 et 2, qui ont émergé au printemps. Les températures plus froides pourraient expliquer en partie cette différence de taille à l'émergence entre cohortes. Les températures plus froides retrouvées dans la couche de fond de l'EMSL au printemps (3°C) font en sorte qu'il faut plus de degrés-jours pour que les larves atteignent un certain stade de développement embryonnaire (Peck *et al.,* 2012). Les larves émergent donc à un âge plus avancé et avec un volume de sac vitellin plus important (Peck *et al.,* 2012); elles sont donc plus grandes à l'émergence de printemps. Par ailleurs, la différence de taille observée entre les larves émergeant au printemps et à l'automne pourrait être liée à la taille des œufs. En effet, différentes stratégies de reproduction ont été documentées entre les harengs de printemps et d'automne. De plus petits œufs, mais plus nombreux sont caractéristiques de la population d'automne de la mer du Nord, alors que le contraire caractérise la population de l'hiver. Les adultes ont alors une moins bonne condition somatique, mais le développement des oocytes continue dans le temps, donnant des œufs plus gros (van Damme *et al.,* 2009). Il est possible que nous observions une stratégie de reproduction similaire dans l'EMSL, où une période plus longue de maturation des gonades a été notée dans l'unité reproductive du printemps du sud du GSL (4T), donnant de plus gros œufs (Bradford and Stephenson, 1992).

La température est le facteur principal influençant le taux de croissance des larves avec sac vitellin car elles ne s'alimentent pas de nourriture exogène, alors qu'elle influence partiellement les larves sans sac vitellin (Westernhagen et Rosenthal, 1981). Les plus hauts taux de croissance caractérisent les cohortes 3, 4 et 5 qui ont émergé dans les eaux les plus chaudes lors de la saison d'échantillonnage de 2014. Lorsque le contrôle pour les différences attribuables à la température a été effectué en utilisant la somme des degrés-jours, la variabilité entre les différents taux de croissance était encore perceptible. L'étude suggère qu'il n'y a pas seulement la température qui peut influencer la croissance, résultat aussi retrouvé dans l'étude de Neuheimer et Taggart (2007). D'autres facteurs comme les différences génétiques, la densité, la prédation, l'abondance et la qualité de la nourriture pourraient être impliqués, mais ils n'ont pas été évalués dans cette étude. La répartition et la présence aux moments opportuns d'œufs, de nauplii et de copépodes des stades C1-C3 et d'adultes d'*Eurytemora affinis* et *Acartia longiremis* peut augmenter les taux de croissance (Kiørboe *et al.*, 1988; Kiørboe et Munk, 1986). Une étude précédente liait le moment d'émergence des larves de hareng et de l'abondance de ces copépodes (Fortier et Gagné, 1990) et il est possible que les conditions de nourriture couplées aux températures plus chaudes aient été favorables aux hauts taux de croissance des cohortes d'été dans l'aire d'étude lors du suivi de 2014. Par contre, la condition amoindrie des larves l'été est peut-être dû à d'autres facteurs. Aussi, l'évaluation des contenus stomacaux permettrait de vérifier l'abondance de nourriture directement dans les larves de hareng, et la morphologie des otolithes permettrait encore une fois de bien déterminer le moment d'émergence.

2.3 CONDITION LARVAIRE DU HARENG ATLANTIQUE

La condition des larves avec et sans sac vitellin des cohortes 1 et 2 était la meilleure alors que la cohorte 6 des larves avec sacs et les cohortes 3 et 4 des larves sans sacs présentaient les moins bonnes conditions. La taille de l'œuf peut avoir une influence sur la condition des larves de la cohorte 1 et 2 puisque la taille à l'émergence était plus élevée

pour ces larves, et donc elles présentaient un plus gros sac vitellin (Bradford et Stephenson, 1992). Les larves avec un sac vitellin plus gros présentaient une meilleure condition chez le hareng du Pacifique (*Clupea pallasii*) (Westernhagen et Rosenthal, 1981). Cela peut aider la condition des larves car il leur reste des vestiges de sac vitellin pour faire face au manque de nourriture possible dans l'environnement (Westernhagen et Rosenthal, 1981). La condition larvaire peut être influencée par des facteurs abiotiques tels que la crue printanière des tributaires de l'EMSL et la température des eaux. En effet, il est suggéré que la crue printanière des tributaires comme Rivière-du-Loup a un impact sur les conditions environnementales du milieu comme l'enrichissement des eaux en nutriments, favorisant la production de phyto et zooplancton (Couillard *et al.*, 2017). Ces auteurs ont démontré une relation positive entre la force des crues printanières des tributaires et l'abondance de larves de harengs en mai dans la baie de Rivière-du-Loup. Les crues des tributaires importants du Saint-Laurent (par exemple, la rivière Malbaie) ont été également fortes en 2014 (Galbraith *et al.*, 2015) et ont probablement aidé à la bonne condition des larves des cohortes 1 et 2, émergées au printemps. Quant à la température, il peut y avoir une baisse de condition lorsqu'elle est trop élevée, comme ce fut observé en 2012 dans l'EMSL (Couillard *et al.*, 2017), si l'abondance des proies est insuffisante pour répondre aux besoins métaboliques accrus. Selon les relevés de température de surface, l'année 2014 fut la plus chaude depuis 1985 dans le PMSSL et l'EMSL (Galbraith *et al.*, 2015). Il est possible que la condition plus faible des cohortes 3, 4 et 5 soit liée à de fortes températures. Finalement, il n'est pas possible de vérifier la quantité de nourriture présente pour les larves de hareng dans cette étude, mais il est possible que la bonne condition des cohortes 1 et 2 soit liée à une densité suffisante de copépodes au moment critique où les larves commencent à se nourrir (Hjort, 1914).

2.4 PERSPECTIVES DE RECHERCHE

Comme cette étude rapporte que le frai du hareng atlantique est toujours présent et que la présence larvaire dans l'aire d'étude persiste jusqu'à l'automne, il serait important de déterminer l'abondance des juvéniles et évaluer si ce serait un bon indicateur de l'abondance des adultes dans l'EMSL. Ainsi, nous pourrions déterminer si réellement la population de hareng de printemps reste plus grande que celle de hareng d'automne, comme c'est le cas dans la baie des Chaleurs, une partie du stock 4T de l'OPANO. Le supposé déclin du hareng de printemps dans l'EMSL était aussi une hypothèse du déclin des bélugas du Saint-Laurent (Plourde *et al.,* 2013). Dans une perspective de conservation, la Loi sur les espèces en péril (LEP) oblige le gouvernement et les organismes à protéger les espèces en danger ainsi que leur habitat et leurs proies (MPO, 2012b). Le hareng atlantique dans l'EMSL est-il réellement en déclin, comme le suggère la population de hareng de la baie des Chaleurs? Les harengs de l'EMSL proviennent-ils réellement de la baie des Chaleurs ou restent-ils dans l'estuaire moyen du Saint-Laurent? Malgré la présence notable de larves de hareng dans l'EMSL au printemps, des mesures d'abondance des géniteurs de printemps et d'automne aux sites de frai de l'EMSL et des analyses microchimiques de leurs otolithes et/ou des études télémétriques de leurs déplacements pourraient mieux répondre à ces questions.

L'analyse par morphologie des otolithes permettraient aussi de retracer avec précision la date d'émergence des larves et ainsi pouvoir différencier les cohortes plus minutieusement et vérifier s'il y a bel et bien un chevauchement dans le temps avec leur proies (bonne abondance de copépodes). De plus, lorsqu'effectuée sur la même population pendant une certaine période de temps, l'analyse des incréments et des rayons des otolithes permettent de déterminer le taux de croissance et la mortalité sélectives selon la taille (Folkvord *et al.,* 1997). Cela permettrait d'attribuer avec précision des taux de croissance propres à nos populations présentes dans l'EMSL au printemps et en automne. Des

analyses génétiques tels que le ratio de ARN/ADN peut déterminer la condition des larves, où un ratio plus élevé représente une croissance somatique également plus élevée et une bonne condition causée par un bon apport nutritif (Folkvord *et al.,* 1997).

Nous ne pouvons pas non plus affirmer qu'il y eu un déclin de l'abondance de larves de hareng atlantique par rapport aux abondances passées, car les méthodes d'échantillonnage sont différentes. De plus, l'évaluation de l'abondance larvaire devrait prendre en compte le biais de l'évitement causé par un filet bongo ou conique de 333 et 500 microns durant la capture des plus grandes larves, qui sont primordiales pour évaluer l'abondance et la croissance des larves qui survivent les premiers stades larvaires critiques. Du côté de la condition larvaire, des échantillons de zooplancton ont été pris avec chaque échantillon larvaire, et combiner l'analyse de ces échantillons avec les contenus stomacaux des larves nous permettrait de mieux interpréter les causes possibles des différences de taux de croissance et de condition larvaire observées entre cohortes. D'autres facteurs environnementaux peuvent avoir un effet sur la condition et la croissance des larves, comme la turbidité et la salinité. Ils pourraient être inclus dans l'analyse des variables environnementales. Finalement, cette étude pourra servir de référence dans le cadre de la création future d'une zone de protection marine incluant tout l'EMSL, car le mandat de protection inclut l'habitat et les proies des mammifères marins comme le hareng atlantique (MPO, 2012b). Non seulement le printemps et l'automne sont des moments importants pour le frai du hareng, mais l'été aussi, car des cohortes ont possiblement émergé à ce moment. Les aires importantes incluent la baie de Rivière-du-Loup, Cacouna, le chenal sud, l'île aux Lièvres et l'île Verte (et toute l'aire entre les îles), car les larves se concentrent par la suite durant toute la saison estivale dans ces aires de rétention, importantes pour la croissance et la survie larvaire. Notre étude fournit de nouvelles informations qui permettront de mieux évaluer les risques d'impacts de différentes activités anthropiques sur de jeunes stades vulnérables d'une espèce clef de l'estuaire moyen du Saint-Laurent.

RÉFÉRENCES BIBLIOGRAPHIQUES

ABLE, K.W., 1978. « Ichthyoplankton of the St. Lawrence Estuary: composition, distribution, and abundance ». *Journal of the Fisheries Research Board of Canada*, 35 (12): 1518-1531.

ARULA, T., KOTTA, J., LANKOV, A., SIMM, M. et S. PÕLME, 2012. « Diet composition and feeding activity of larval spring-spawning herring: Importance of environmental variability ». *Journal of Sea Research*, 68: 33-40.

BAUER, R.K., STEPPUTTIS, D., GRÄWE, U., ZIMMERMANN, C. et C. HAMMER, 2013. « Wind-induced variability in coastal larval retention areas: a case study on Western Baltic spring-spawning herring ». *Fisheries Oceanography*, 22: 388-399.

BÉRUBÉ, S. et J.-D. LAMBERT, 1997. « Suivi ichtyologique dans l'estuaire du Saint-Laurent (1986- 1995) ». *Rapport technique canadien des sciences halieutiques et aquatiques*, 2171 : viii + 57 p.

BECK, G.G., M.O. HAMMILL et T.G. SMITH, 1993. « Seasonal variation in the diet of harp seals (*Phoca groenlandica*) from the Gulf of St. Lawrence and western Hudson Strait ». *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1363-1371.

BLAXTER, J.H.S. et J.R. HUNTER. 1982. The biology of the clupeoid fishes. *Advances in Marine Biology*, 20(C): 1-223.

BOLLENS, S.M. et A. SANDERS, 2004. « Ecology of larval Pacific herring in the San Francisco Estuary: seasonal and interannual abundance, distribution, diet, and condition ». *American Fisheries Society Symposium*, 39: 15-35.

BOURGET, G. et M. BÉLANGER, 2015. « Bilan de l'année 2014 du recrutement des éperlans arc-en-ciel du sud de l'estuaire ». *Ministère des Forêts, de la Faune et des Parcs*. *Direction de la gestion de la faune du Bas-Saint-Laurent*. 3 p.

BOURGET, G. et A. MARQUIS, 2014. « Bilan des trois suivis annuels du recrutement des éperlans arc-en-ciel du sud de l'estuaire, pour l'année 2013 ». *Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs. Direction régionale du Bas-Saint-Laurent, Secteur de la faune.* 47 p.

BRADFORD, R.G. et R.L. STEPHENSON, 1992. « Egg weight, fecundity, and gonad weight variability among northwest Atlantic herring (*Clupea harengus*) populations ». *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2045-2054.

CASINI, M., CARDINALE, M. et J. HJELM, 2006. « Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? ». *Oikos*, 112: 638-650.

CLEARY, L., 1983. « An assessment of the southern Gulf of St. Lawrence herring stock complex ». *Comité Scientifique Consultatif des Pêches Canadiennes dans l'Atlantique*, 83 (69): 40 p.

COMITÉ SUR LA SITUATION DES ESPÈCES EN PÉRIL AU CANADA (COSEPAC), 2009. « Évaluation et Rapport de situation du COSEPAC sur la Plie canadienne *Hippoglossoides platessoides* population des Maritimes, population de Terre-Neuve-et-Labrador et population de l'Arctiqueau Canada ». *Comité sur la situation des espèces en péril au Canada*. Ottawa. x + 80 p.

COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA (COSEWIC), 2014. « COSEWIC assessment and status report on the Beluga Whale *Delphinapterus leucas*, St. Lawrence Estuary population, in Canada ». *Committee on the Status of Endangered Wildlife in Canada*. Ottawa. xii + 64 p.

COSTALAGO, D., STRYDOM, N., FROST, C., et C. CLEMMESEN, 2015. « Preliminary insight into the relationship between environmental factors and the nutritional condition and growth of *Gilchristella aestuaria* larvae in the upper reaches of South African estuaries ». *Environmental Biology of Fishes*, 98: 2367-2378.

CÔTÉ, G., LAMOUREUX, P., BOULVA, J. et G. LACROIX, 1980. « Séparation des populations de hareng atlantique (*Clupea harengus harengus*) de l'estuaire du Saint-Laurent et de la péninsule gaspésienne ». *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 66-71.

COUILLARD, C.M., OUELLET, P., VERREAULT, G., SENNEVILLE, S., ST-ONGE-DROUIN, S. et D. LEFAIVRE, 2017. « Effect of decadal changes in freshwater flows and temperature on the larvae of two forage fish species in coastal nurseries of the St. Lawrence Estuary ». *Estuaries and Coasts*, 40 (1): 268-285.

COURTOIS, R. et J.J. DODSON, 1986. « Régime alimentaire et principaux facteurs influençant l'alimentation des larves de capelan (*Mallotus villosus*), d'éperlan (*Osmerus*

mordax) et de hareng (*Clupea harengus harengus*) dans un estuaire partiellement mélangé ». *Canadian Journal of Fisheries and Aquatic Sciences*, 43: 968-979.

COURTOIS, R., SIMONEAU, M. et J.J. DODSON, 1982. « Interactions multispécifiques: répartition spatio-temporelle des larves de capelan (*Mallotus villosus*) d'éperlan (*Osmerus mordax*) et de hareng atlantique (*Clupea harengus harengus*) au sein de la communauté planctonique de l'estuaire moyen du Saint-Laurent ». *Canadian Journal of Fisheries and Aquatic Sciences*, 39: 1164-1174.

CUSHING, D.H., 1967. « The grouping of herring populations ». *Journal of the Marine Biological Association of the UK*, 47:193-208.

CUSHING, D.H., 1990. « Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis ». *Advances in Marine Biology*, 26: 249-293.

D'ANGLEJEAN, B.,1981. « On the advection of turbidity in the Saint Lawrence middle Estuary ». *Estuaries*, 4(1): 2-15.

D'ANGLEJEAN, B. et R.G. INGRAM. 1976. « Time-depth variations in tidal flux of suspended matter in the Saint Lawrence Estuary ». *Estuarine and Coastal Marine Science*, 4(4): 401-16.

DAUVIN, J. C. et J.J. DODSON, 1990. « Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed Estuary ». *Marine Ecology Progress Series*, 60: 1-12.

DAWE, E.G., KOEN-ALONSO, M., CHABOT, D., STANSBURY, D.et D. MULLOWNEY, 2012. « Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change ». *Marine Ecology Progress Series*, 469: 233-248.

DE LAFONTAINE, Y., 1990. « Ichthyoplankton communities in the St. Lawrence Estuary: composition and dynamics. In El-Sabh, M. I. et N. Silverberg (éds). Oceanography of a Large-Scale Estuarine System: The St. Lawrence, Coastal and Estuarine Studies, vol. 39, Springer-Verlag, p.321-343.

DIAZ, M.V., PÀJARO, M., OLIVAR, M.P., MARTOS, P. et G.J. MACCHI, 2011. « Nutritional condition of Argentine anchovy *Engraulis anchoita* larvae in connection with nursery grounds properties ». *Fisheries Research*, 109: 330-341.

DIAZ, M.V., PÀJARO, M., et R.P. SÀNCHEZ, 2009. « Employment of morphometric variables to assess nutritional condition of argentine anchovy larvae Engraulis anchoita Hubbs & Marini, 1935 ». *Revista De Biología Marina y Oceanografia*, 44(3): 539-549.

DOYLE, M.J., 1977. « A morphological staging system for the larval development of the herring *Clupea harengus* L. ». *Journal of the Marine Biological Association of the UK*, 57: 859-867.

DU, J., 2002. « Combined Algorithms for Fitting Finite Mixture Distributions ». McMaster University, unpublished M.Sc. project.

EHRLICH, K.F., BLAXTER, J.H.S. et R. PEMBERTON, 1976. « Morphological and histological changes during the growth and starvation of herring and plaice larvae ». *Marine Biology*, 35: 105-118.

ELLIOTT, J.M., 1982. « The effects of temperature and ration size on the growth and energetics of salmonids in captivity ». *Comparative Biochemistry and Physiology*, 73B: 81-91.

EL-SABH, M.I. et T.S. MURTY, 1990. « Mathematical modelling of tides in the St. Lawrence Estuary ». In El-Sabh, M. I. et N. Silverberg (éds). Oceanography of a Large-Scale Estuarine System: The St. Lawrence, Coastal and Estuarine Studies, vol. 39, Springer-Verlag, p.10-50.

FAHAY, M.P., 2007. « Early Stages of Fishes in the Western North Atlantic Ocean (Davis Strait, Southern Greenland and Flemish Cap to Cape Hatteras) ». Volume One: Northwest Atlantic Fisheries Organization, 931 p.

FISHERIES AND AQUACULTURE SOFTWARE, 2006. « FISAT II - FAO-ICLARM Stock Assessment Tool ». En ligne. <http://www.fao.org/fishery/topic/16072/en>. Fisheries and Aquaculture Department (FAO). Rome. Updated 28 November 2013.

FEY, D.P., 2001. « Differences in temperature conditions and somatic growth rate of larval and early juvenile spring-spawned herring from the Vistula Lagoon, Baltic Sea manifested in the otolith to fish size relationship ». *Journal of Fish Biology*, 58: 1257-1273.

FOLKVORD, A., RUKAN, K., JOHANNESSEN, A., et E. MOKSNESS, 1997. « Early life history of herring larvae in contrasting feeding environments determined by otolith microstructure analysis ». *Journal of Fish Biology*, 51(sA): 250-263.

FORTIER, L., et J.A. GAGNÉ, 1990. « Larval herring (*Clupea harengus*) dispersion, growth, and survival in the St. Lawrence Estuary: match/mismatch or membership/vagrancy? ». *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1898-1912.

FORTIER, L., LEVASSEUR, M.E., DROLET, R. et J.-C. THERRIAULT, 1992. « Export production and the distribution of fish larvae and their prey in a coastal jet frontal region ». *Marine Ecology Progress Series*, 85: 203-218.

FORTIER, L., et W.C. LEGGETT, 1982. « Fickian transport and the dispersal of fish larvae in estuaries ». *Canadian Journal of Fisheries and Aquatic Sciences*, 39 (8): 1150-1163.

FORTIER, L., et W.C. LEGGETT, 1983. « Vertical migrations and transport of larval fish in a partially mixed Estuary ». *Canadian Journal of Fisheries and Aquatic Sciences*, 40: 1543-1555.

FOX C. J., HARROP, R. et A. WIMPENNEY, 1999. « Feeding ecology of herring (*Clupea harengus*) larvae in the turbid blackwater Estuary ». *Marine Biology*, 134(2): 353-365.

GALBRAITH, P.S., CHASSÉ, J., NICOT, P., CAVERHILL, C., GILBERT, D., PETTIGREW, B., LEFAIVRE, D., BRICKMAN, D., DEVINE, L., and C. LAFLEUR, 2015. « Physical Oceanographic Conditions in the Gulf of St. Lawrence in 2014 ». *DFO Canadian Science Advisory Secretariat, Research Document*, 2015/032: v + 82 p.

GAYANILO, F.C, SPARRE, P. et D. PAULY, 2005. « FAO-ICLARM stock assessment tools II, User's Guide ». Worldfish Center – Food and Agriculture Organization of the United Nations. Rome. 164 p.

GEFFEN, A.J., 2002. « Length of herring larvae in relation to age and hatching order ». *Journal of Fish Biology*, 60: 479-485.

GRÉGOIRE, F. et J.-L. BEAULIEU, 2011. « Atlantic herring (*Clupea harengus harengus* L.) on the Quebec North Shore (NAFO Division 4S) in 2010 ». *DFO Canadian Science Advisory Secretariat, Research Document*, 2011/019: vi + 102 p.

GRÉGOIRE, F., BEAULIEU, J.-L. et I.H. MCQUINN, 2013. « Les stocks de hareng (*Clupea harengus harengus* L.) de la côte ouest de Terre-Neuve (Division 4R de l'OPANO) en 2011 ». *Secrétariat canadien de consultation scientifique du MPO, Document de recherche*, 2012/121 : iv + 70 p.

HAEDRICH, R.L, 1983. « Estuarine fishes ». In B.H. Ketchum (Ed.), Ecosystems of the World, Estuaries and Enclosed Seas, vol. 26, Elsevier Scientific Publishing Co., Oxford, p. 183-207.

HAEGELE, C.W. et J.F. SCHWEIGERT, 1985. « Distribution and characteristics of herring spawning grounds and description of spawning behavior ». *Canadian Journal of Fisheries and Aquatic Sciences*, 42 (Suppl. I): 39-55.

HARVEY V., HAMMILL M.O., SWAIN D.P., BREED G.A., LYDERSEN C.et K.M. KOVACS, 2012. « Winter foraging by a top predator, the grey seal *Halichoerus grypus*, in relation to the distribution of prey ». *Marine Ecology Progress Series*, 462: 273-286.

HAUSS, H.M. et M.A. PECK, 2009. « Comparing observed and modelled growth of larval herring (*Clupea harengus*): Testing individual-based model parameterisations ». *Advances in early life history study of fish, Scientia Marina*, 73S1: 37-45.

HENRI, M., J.J. DODSON et H. POWLES, 1985. « Spatial configurations of young herring (*Clupea harengus harengus*) larvae in the St. Lawrence Estuary: importance of biological and physical factors ». *Canadian Journal of Fisheries and Aquatic Sciences*. 42 (Suppl. 1): 91-104.

HJORT, J., 1914. « Fluctuation in the great fisheries of northern Europe reviewed in the light of biological research ». *ICES*, 20: 1-228.

HOUDE, E.D., 2008. « Emerging from Hjort's shadow ». *Journal of Northwest Atlantic Fisheries Science*, 41: 53-70.

HUFNAGL, M. et M.A. PECK, 2011. « Physiological individual-based modelling of larval Atlantic herring (*Clupea harengus*) foraging and growth: insights on climate-driven life-history scheduling ». *ICES Journal of Marine Science*, 68(6): 1170-1188.

ILES T.D. et M. SINCLAIR, 1982. « Atlantic herring: Stock discreteness and abundance ». *Science*, 215(4533): 627-633.

KETCHUM, B.H., 1952. « Circulation in estuaries ». *Coastal Engineering Proceedings*, 1(3): 65-76.

KIØRBOE, T. et P. MUNK, 1986. « Feeding and growth of larval herring, *Clupea harengus*, in relation to density of copepod nauplii ». Environmental Biology of Fishes,

17(2): 133-139.

KIØRBOE, T., MUNK, P., RICHARDSON, CHRISTENSEN, K.V. et H. PAULSEN, 1988. « Plankton dynamics and herring larval growth, drift and survival in a frontal area ». *Marine Ecology Progress Series*, 44: 205-219.

KIRKLEY, J. E., WALDEN, J., et R. FÄRE, 2011. « A general equilibrium model for Atlantic herring (Clupea harengus) with ecosystem considerations ». *ICES Journal of Marine Science*, 68: 860–866.

KOBYLIANSKI, S. G., DRITS, A.V., EVSEENKO, S.A., SEMENOVA, T.N. et A.V. MISHIN, 2015. « Effect of trophic conditions on the growth and abundance of larvae herring *Clupea pallasii marisalbi* in areas of their mass aggregations in Kandalaksha and Onega Bays of the White Sea ». *Journal of Ichthyology*, 55(4): 540-548.

KORNFIELD, I., SIDELL, B.D. et P. S. GAGNON, 1982. « Stock definition in Atlantic herring (*Clupea harengus harengus*): genetic evidence for discrete fall and spring spawning Populations ». *Canadian Journal of Fisheries and Aquatic Sciences*, 39: 1610-1621.

LACOSTE, K.N., MUNRO, J., CASTONGUAY, M., SAUCIER, F. J., et J.A. GAGNÉ, 2001. « The influence of tidal streams on the pre-spawning movements of Atlantic herring, *Clupea harengus* L., in the St Lawrence Estuary ». *ICES Journal of Marine Science*, 58: 1286-1298.

LAMBERT, J., 1990. « Structure de population et stratégie de reproduction du hareng de l'estuaire du Saint-Laurent ». MSc thesis, Univ. du Québec, Rimouski. 118 p.

LAMBERT, T.C., 1984. « Larval cohort succession in herring (*Clupea harengus*) and capelin (*Mallotus villosus*) ». *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 1552-1564.

LAMBERT, T.C. et D.M. WARE, 1984. « Reproductive strategies of demersal and pelagic spawning fish ». *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 1565-1569.

LAPRISE, R. et J.J. DODSON, 1989. « Ontogenetic changes in the longitudinal distribution of two species of larval fish in a turbid well-mixed estuary ». Journal of Fish Biology, 35: 39-47.

LAPRISE, R. et J.J. DODSON, 1990. « The mechanism of retention of pelagic tomcod, *Microgadus tomcod*, larvae and juveniles in the well-mixed part of the St. Lawrence Estuary ». *Environmental Biology of Fishes*, 29(4): 293-302.

LEBLANC, C.H., MALLET, A., MACDOUGALL, C., BOURQUE, C. et D. SWAIN, 2012. « Assessment of the NAFO Division 4T southern Gulf of St. Lawrence herring stocks in 2011 ». *DFO Canadian Science Advisory Secretariat, Research Document*, 2012/111. vi + 167 p.

LEFEBVRE, S.L., MICHAUD, R., LESAGE, V. et D. BERTEAUX, 2012. « Identifying high residency areas of the threatened St. Lawrence beluga whale from fine-scale movements of individuals and coarse-scale movements of herds ». *Marine Ecology Progress Series*, 450: 243-57.

LEGGETT, W.C., et E. DEBLOIS, 1994. « Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? ». *Netherlands Journal of Sea Research*, 32(2): 119-134.

LESAGE, V. et M.C.S. KINGSLEY, 1995. « Bilan des connaissances de la population de bélugas (*Delphinapterus leucas*) du Saint-Laurent ». *Rapport technique canadien des sciences halieutiques et aquatiques*, 2041: vii+44p.

MARANDA, Y. et G. LACROIX, 1983. « Temporal variability of zooplankton biomass (ATP content and dry weight) in the St. Lawrence Estuary: advective phenomena during neap tide ». *Marine Biology*, 73(3): 247-255.

MARGONSKI, P., HANSSON, S., TOMCZAK, M.T., et R. GRZEBIELEC, 2010. « Climate influence on Baltic cod, sprat and herring stock-recruitment relationships ». *Progress in Oceanography*, 87: 277–288.

MCGURK, M.D., 1989. « Advection, diffusion and mortality of Pacific herring larvae *Clupea harengus pallasi* in Bamfield Inlet, British Columbia ». Marine Ecology Progress Series 51:1–18.

MCGURK, M.D., PAUL, A.J., DOYLE, K.O., ZIEMANN, D.A. et L. J. HALDORSON, 1993. « Relationships between prey concentration and growth, condition, and mortality of Pacific herring, *Clupea pallasi*, larvae in an Alaskan subarctic embayment *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 163-188.

MCQUINN, I.H., FITZGERALD, G.J. et H. POWLES, 1983. « Environmental effects on embryos and larvae of the Isle Verte stock of Atlantic herring (*Clupea harengus harengus*) ». *Naturaliste canadien, (Rev. Écol. Syst.)*, 110(3): 343-355.

MCQUINN, I.H., 1997a. « Metapopulations and the Atlantic herring ». *Reviews in Fish Biology and Fisheries*, 7(3): 297-329.

MCQUINN, I.H., 1997b. « Year-class twinning in sympatric seasonal spawning populations of Atlantic herring, *Clupea harengus* ». *Fishery Bulletin US*, 95: 126-136.

MINISTÈRE DE PÊCHES ET OCÉANS CANADA (MPO), 2005. « Stock Assessment Report on Southern Gulf of St. Lawrence (4T) Herring ». *DFO Canadian Science Advisory Secretariat, Science Advisory Report,* 2005/021: 11 p.

MINISTÈRE DE PÊCHES ET OCÉANS CANADA (MPO), 2010. « Avis sur la désignation de l'habitat essentiel des bélugas du Saint-Laurent (*Delphinapterus leucas*) ». *Secrétariat canadien de consultation scientifique du MPO, Avis scientifique*, 2009/070: 187 p.

MINISTÈRE DE PÊCHES ET OCÉANS CANADA (MPO), 2012a. « Programme de rétablissement du béluga (*Delphinapterus leucas*), population de l'estuaire du Saint-Laurent au Canada », *Série de Programmes de rétablissement de la Loi sur les espèces en péril*, MPO, Ottawa, 93 + XI p.

MINISTÈRE DE PÊCHES ET OCÉANS CANADA (MPO), 2012b. « Développement d'un plan de suivi écologique de la zone de protection marine de l'estuaire du Saint-Laurent ». *Secrétariat canadien de consultation scientifique du MPO, Avis scientifique*, 2012/039: 26 p.

MINISTÈRE DE PÊCHES ET OCÉANS CANADA (MPO). 2014. Situation du béluga (*Delphinapterus leucas*) de l'estuaire du fleuve Saint-Laurent. *Secrétariat canadien de consultation scientifique du MPO, Avis scientifique*, 2013/076.

MOSNIER, A., DONIOL-VALCROZE, T., GOSSELIN, J.-F., LESAGE, V., MEASURES, L., et M.O. HAMMILL, 2014. An age structured Bayesian population model for St. Lawrence Estuary beluga (*Delphinapterus leucas*). *DFO Canadian Science Advisory Secretariat, Research Document*, 2013/127. v + 39 p

MUNRO, J., GAUTHIER, D., et J.A. GAGNÉ, 1998. « Description d'une frayère de hareng (*Clupea harengus* L.) à l'île aux Lièvres dans l'estuaire moyen du Saint-Laurent ». *Rapport technique canadien des sciences halieutiques et aquatiques*, 2239: vi + 34 p.

NEUHEIMER, A.B. et C.T. TAGGART, 2007. « The growing degree-day and fish size-at-age: the overlooked metric ». *Canadian Journal of Fisheries and Aquatic Sciences*, 64(2): 375-385.

OEBERST, R., DICKEY-COLLAS, M. et R.D.M. NASH, 2009. « Mean daily growth of herring larvae in relation to temperature over a range of 5–208C, based on weekly repeated cruises in the Greifswalder Bodden ». *ICES Journal of Marine Science*, 66: 1696-1701.

OUELLET, P., BUI, A.O.V., LAVOIE, D., CHASSÉ, J., LAMBERT, N., MÉNARD, N. et P. SIROIS, 2013. « Seasonal distribution, abundance, and growth of larval capelin (*Mallotus villosus*) and the role of the lower Estuary (Gulf of St. Lawrence, Canada) as a nursery area ». *Canadian Journal of Fisheries and Aquatic Sciences*, 70(10): 1508-1530.

PAULSEN, M., HAMMER, C., MALZAHN, A.M., POLTE, P., VON DORRIEN, C. et C. CLEMMESEN, C. 2014. « Nutritional situation for larval Atlantic herring (*Clupea harengus* L.) in two nursery areas in the western Baltic Sea ». *ICES Journal of Marine Science*, 71(4): 991-1000.

PECK, M.A., KANSTINGER, P., HOLSTE, L. et MARTIN, M. 2012. « Thermal windows supporting survival of the earliest life stages of Baltic herring (*Clupea harengus*) ». *ICES Journal of Marine Science*, 69 (4): 529-536.

PLOURDE, S., GALBRAITH, P., LESAGE, V., GRÉGOIRE, F., BOURDAGE, H., GOSSELIN, J.-F., MCQUINN, I. and M. SCARRATT, 2013. « Ecosystem perspective on changes and anomalies in the Gulf of St. Lawrence: a context in support to the management of the St. Lawrence beluga whale population ». *DFO Canadian Science Advisory Secretariat, Research Document*, 2013/032. vi + 82 p.

POLTE, P., KOTTERBA, P., HAMMER C. et T. GRÖHSLER, 2013. « Survival bottlenecks in the early ontogenesis of Atlantic herring (*Clupea harengus*, L.) in coastal lagoon spawning areas of the western Baltic Sea ». *ICES Journal of Marine Science*, 71: 982-990.

POWLES, H., AUGER, F. et G.J. FITZGERALD, 1984. « Nearshore ichthyoplankton of a north temperate estuary ». *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 1653-1663.

QUINN, G.P. et M.J. KEOUGH, 2002. « Experimental design and data analysis for biologists ». Cambridge University Press, Cambridge, United Kingdom. 541pp.

R CORE TEAM, 2015. « R: A language and environment for statistical computing ». R Foundation for Statistical Computing, Vienna, Austria. En ligne. <http://www.R;project.org/>.

RUNGE, J.A., et Y. SIMARD, 1990. « Zooplankton of the St. Lawrence Estuary: the imprint of physical processes on its composition and distribution ». In El-Sabh, M. I. et N. Silverberg (éds). Oceanography of a Large-Scale Estuarine System : The St. Lawrence, Coastal and Estuarine Studies, vol. 39, Springer-Verlag, p. 296-320.

SCHNUTE, J.T., BOERS, N. et R. HAIGH, 2015. « PBSmapping: Mapping Fisheries Data and Spatial Analysis Tools ». R package version 2.69.76. En ligne: <http://CRAN.R;project.org/package=PBSmapping>.

SIROIS, P. et J.J. DODSON, 2000. « Influence of turbidity, food density and parasites on the ingestion and growth of larval rainbow smelt (*Osmerus mordax*) in an estuarine turbidity maximum ». *Marine Ecology Progress Series*, 193: 167-179.

TSOUKALI, S., CHRISTENSEN, A., TIAN T., VISSER, A. et B. MACKENZIE, 2015. « Predicting future shifts in herring spawning habitat in the North Sea ». Abstract from ICES Annual Science Conference 2015, Copenhagen, Denmark.

VAN DAMME, C.J.G., DICKEY-COLLAS, M., RIJNSDORP, A.D. et O.S. KJESBUC, 2009. « Fecundity, atresia, and spawning strategies of Atlantic herring (*Clupea harengus*) ». *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 2130-2141.

WESTERNHAGEN, H.V. et H. ROSENTHAL, 1981. « On condition factor measurements in Pacific herring larvae ». *Helgoländer Meeresunters*, 34: 257-262.

WHITEHEAD, P.J.P., 1985. FAO Species Catalogue. Vol. 7. « Clupeoid fishes of the world (suborder *Clupeioidei*). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings ». *FAO Fisheries Synopsis*, Rome: FAO, 125(7/1): 1-303.

WINTERS, G.H. et J.P. WHEELER, 1994. « Length-specific weight as a measure of growth success of adult Atlantic herring (*Clupea harengus*) ». *Canadian Journal of Fisheries and Aquatic Science*, 51: 1169-1179.

WRIGHT, B.D. et M.H. STONE, 1999. « Measurement essentials. 2nd edition ». Wilmington, DE: Wide Range, Inc. 221 p. En ligne. <http://www.rasch.org/measess/me-all.pdf>

ANNEXE

Table A1. Total body length (TL) means and standard deviations (SD) computed by the software FiSAT II and expected from previous growth rates (Fortier and Gagné, 1990) used to identify the ranges (minimum-maximum) of lengths used to delimitate cohorts of herring larvae, standard deviations and separation index. Undefined data (und.) comprise cohorts and computed means that could not be calculated by the software.

Sampling date	Cohort	Computed mean TL (mm)	Expected mean TL (mm)	TL SD (mm)	Separation index	Range (± 1-2 mm)
June 2	1	7.52		0.81	0	4.8-9.3
June 10	2	7.78		0.49	0	6.5-8.5
	1	9.68		0.67	3.26	8.5-11.3
June 17	2	und.	9.25			8.3-10.0
	1	10.06	10.11	0.92	n.a.	10.0-12.3
	und.	14.31		0.58	5.67	
July 4	2	12.23		1.58	0	10.5-13.0
	1	und.	13.51			13.0-16.0
	und.	17.93		1.30	3.96	
July 10	3	7.95		0.65	n.a.	6.0-9.0
	2	14.97		1.26	7.35	12.8-16.0
	1	16.35		1.57	0.98	16.0-18.0
July 16	3	10.08		0.8	n.a.	7.8-12.0
	2	15.66		3.14	2.83	14.0-17.0
	1	19.59		0.25	2.32	18.0-21.0
July 24	*	8.75		0.56	n.a.	7.8-10.01
	2	18.74		0.26	24.37	17.5-19.5
	1	20.13		2.31	1.08	19.5-23.0
July 30	4	8.53		0.97	n.a.	6.0-10.0
	*	und.	10.69			10.0-12.0
	3	12.59	13.59	2.68	2.22	12.0-16.0
	2	19.5		0.25	4.72	17.0-20.0
	1	23.11		0.94	6.07	22.0-24.6
August 15	5	8.14		0.56	n.a.	6.0-10.0
	3	20.9		0.49	24.3	19.0-22.5
	2	23.89		1.13	3.69	22.5-25.0
	1	27.55		1.08	3.31	26.0-28.0
	und.	28.11		1.8	0.36	
August 20	5	11.81	10.82	1.8	n.a.	8.0-12.0
September 3	4	15.88		0.25	3.97	14.0-17.0
	und.	25.44		3.75	0	
	*	25.99		0.76	0.24	24.0-27.0
	und.	29.02		1.12	3.23	
	3	29.61		7.68	0.13	27.0-30.0
September 17	5	22.54	18.88	1.84	n.a.	19.0-23.0
	4	25.82		2.96	1.37	23.0-26.0
	und.	31.59		9.25	0.95	
	und.	37.42		15.92	0.46	
September 22	6	7.67		0.63	n.a.	5.0-9.0
	5	22.3	20.11	2.21	10.3	19.0-23.5
	4	27.06		4.27	1.47	23.5-27.5
	und.	32.83		19.7	0.48	
October 3	6	8.42		0.58	n.a.	6.0-10.0
	5	24.01	21.8	1.17	17.82	21.0-24.5
	und.	24.5		17.24	0.05	

Table A2. Shapiro-Wilk test results and potential outliers for linear regressions of head thickness (HT, mm) in function of height of the eye (HE, mm) for different cohorts of herring larvae sampled in SLME in 2014, at the yolk-sac and post yolk-sac larval stages (Figures 15 and 16).

Regression	W	P-value	Cook's D Influence of potential outliers
Graph 15-A - Length Cat. 1a-c - JUNE - Cohort 1 before removing potential outliers	0.9679	0.0001*	Har 4 (2-6 st.4): 0.018 – Har 28 (2-6 st. 4): 0.038 – Har 27 (18-6 st.2) : 0.03 – Har 33 (18-6 st.5) : 0.007 – Har 10 (10-6 st.2) : 0.012
Graph 15-A - Length Cat. 1a-c - JUNE - Cohort 1 after removing potential outliers	0.9952	0.0842	na
Graph. 15-B - Length Cat. 1a-c – All months – Cohort 1 filtered Before removing potential outliers	0.9672	0.0001*	Har 4 (2-6 st.4): 0.01 – Har 28 (2-6 st.4): 0.03 – Har 10 (10-6 st.2): 0.006 – Har 33 (18-6 st.5): 0.003 – Har 27 (18-6 st.2): 0.02
Graph. 15-B - Length Cat. 1a-c – All months – Cohort 1 filtered After removing potential outliers	0.9952	0.0982	na
Graph. 15-B - Length Cat. 1a-c – All months – Cohort 6 filtered Before removing potential outliers	0.985	0.0180*	Har 32 (24-9 st.20R): 0.003 – Har 50 (24-9 st.5): 0.006 – Har 16 (25-9 st.ES10): 0.008
Graph. 15-B - Length Cat. 1a-c – All months – Cohort 6 filtered After removing potential outliers	0.9926	0.3375	na
Graph. 16-C - Length 2 – All months – Only cohorts 1-2-3 – Cohort 1 filtered Before removing potential outliers	0.942	0.0485*	Har 46 (4-7 st.ASA-04): 0.03 – Har 55 (4-7 st.ASA-04):0.04 – Har 45 (7-7 st.RDL-08): 0.03
Graph. 16-C - Length 2 – All months – Only cohorts 1-2-3 – Cohort 1 filtered After removing potential outliers	0.9704	0.4541	na
Graph 16-B - Length 2 - All months - Cohort 4 filtered Before removing potential outliers	0.7585	0.0101*	Har 38 (21-8 st.25R) :0.06
Graph 16-B - Length 2 - All months - Cohort 4 filtered After removing potential outliers	0.9293	0.5448	na

Table A3. Analysis of covariance of head thickness (HT, mm) in function of height of eye (HE, mm) and date of hatching (cohort) for herring larvae of the yolk-sac and post yolk-sac stages sampled in the St. Lawrence Middle Estuary in 2014 after removing potential outliers. Tests for homogenized slopes (P_s) and differences in intercepts (P_i) are presented, where significant p-values are indicated in bold.

Comparison	P_s/P_i	Adjusted mean (HT)	Slope	Intercepts	Tukey test results	n
Fig. 15-A **Cohort 1 vs. Cohort 2 after removing potential outliers**	0.54/0.32	C. 1 = 0.44 C. 2 = 0.43	α = 0.73	C. 1 : β = 0.24 C. 2 : β = 0.23	A A	C. 1 = 557 C. 2 = 85
Fig. 15-B **Cohorts 1, 2, 5, 6 after removing potential outliers**	0.07/**0.0001***	C. 1 = 0.43 C. 2 = 0.42 C. 5 = 0.40 C. 6 = 0.39	α = 0.7	C. 1 : β = 0.25 C. 2 : β = 0.24 C. 5 : β = 0.21 C. 6 : β = 0.21	A AB BC C	C. 1 = 538 C. 2 = 78 C. 5 = 31 C. 6 = 221

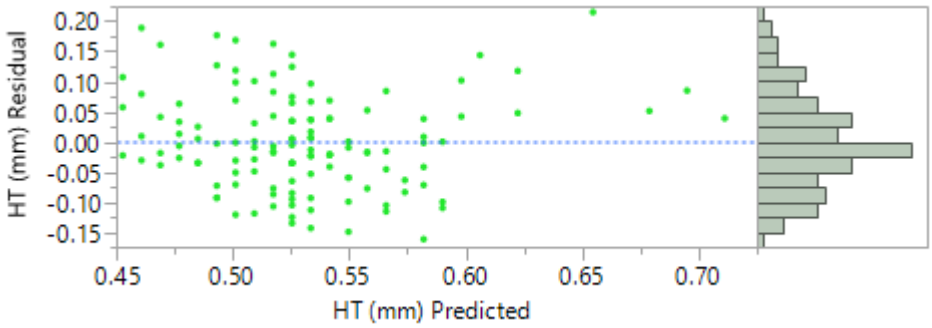


Figure A1. Scatterplot of residuals and predicted values for head thickness (HT) for cohort 3 in July to check for the homogeneity of variance.

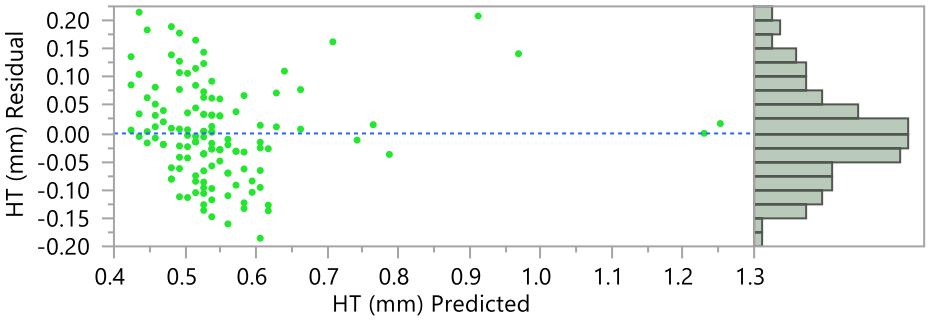


Figure A2. Scatterplot of residuals and predicted values for head thickness (HT) for cohort 3 in June-September to check for the homogeneity of variance.