Université du Québec
à Rimouski

Régime alimentaire, croissance, et facteurs de recrutement des larves de sébaste (*Sebastes mentella*) dans la golfe du Saint-Laurent

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To my parents, Robert and Lois Burns, who always fanned the flames of my scientific curiosities and encouraged me to kiss every fish that I ever caught. Now I can claim that I am an expert at it.

« *…I made it up to Music Row, Lordy don't the wheels turn slow, still I wouldn't trade a minute, I wouldn't have it any other way, just show me to the stage…* » - Alan Jackson

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#GoNicsGo

RÉSUMÉ

La surpêche et des décennies de faible recrutement ont provoqué l'effondrement du stock de sébaste du golfe du Saint-Laurent (GSL), *Sebastes mentella*, et sa biomasse est restée faible jusqu'au milieu des années 2010. Le recrutement sans précédent de la cohorte de 2011, ainsi que le fort recrutement de la cohorte de 2013, ont permis aux populations de sébaste de rebondir à une biomasse record estimée à 2,8 millions de tonnes en 2021, et des discussions sur la réouverture de la pêche sont actuellement en cours. On sait peu de choses sur le cycle biologique du sébaste dans la région. De plus, le sébaste est catégorisé comme une espèce à recrutement spasmodique, qui produit de fortes cohortes en moyenne une fois tous les 10 ans. Cette caractéristique de reproduction rend difficile la collecte d'un échantillon suffisant d'années de fort recrutement pour permettre d'identifier des relations empiriques entre les conditions environnementales et le recrutement. Chez les poissons marins, le succès du recrutement est souvent régulé par l'ampleur de la mortalité par différents agents qui affectent la survie des individus au stade larvaire. Une meilleure compréhension des facteurs qui régulent la survie des larves de sébaste et le recrutement subséquent des sébastes dans la région permettrait aux équipes d'évaluation des stocks de mieux prévoir la dynamique future du stock.

L'objectif principal de ce projet était d'identifier les conditions environnementales susceptibles d'influencer la survie des larves de sébaste. Pour ce faire, j’ai d'abord dû identifier les sources d'énergie et de nutriments en détaillant la composition du régime alimentaire des larves de sébaste, ainsi que l'étendue et les moyens par lesquels le régime alimentaire influence la croissance larvaire. Ensuite, j’ai pu commencer à reconstituer mécaniquement les processus dans lesquels le recrutement des larves de sébaste pourrait potentiellement être influencé par l'océanographie physique et biologique. Dans le Chapitre 1, j’ai identifié, catégorisé et quantifié les proies dans le régime alimentaire des larves de sébaste afin de déterminer les préférences alimentaires. À l'aide de ces données, j’ai identifié d'importants taxons de proies et des stades de développement dont les larves de sébaste se nourrissent préférentiellement afin d'éviter la famine. Au Chapitre 2, j'ai déterminé l'âge et les patrons de croissance des larves de sébaste en mesurant les accroissements quotidiens formés sur l’otolithe. À l'aide des données sur la microstructure des otolithes et de l'analyse du régime alimentaire, j’ai décrit la relation entre le succès alimentaire récent, la composition du régime alimentaire, et la condition et la croissance des larves. Au Chapitre 3, j'ai utilisé une approche fondée sur le poids de la preuve pour identifier les variables océanographiques physiques et biologiques qui expliquent le mieux la variabilité du recrutement du sébaste. J’ai utilisé des ensembles de données environnementales à long terme compilés par Pêches et Océans Canada pour décrire les relations entre plusieurs variables environnementales et la force du recrutement annuel.

J'ai constaté que les larves de sébaste se nourrissent de façon généraliste et que le régime alimentaire est dominé par les stades d'œufs et de nauplii du copépode calanoïde, *Calanus finmarchicus*, avec certaines années présentant l'évidence d'une préférence alimentaire pour les œufs de *C. finmarchicus*. Lorsque j'ai étudié le rôle de la composition du régime alimentaire sur la croissance des larves de sébaste, j'ai constaté qu'il existe une période critique autour de 8 jours après l'extrusion au cours de laquelle les patrons de croissance diffèrent de ceux immédiatement après l'extrusion. Cela correspond vraisemblablement au début de l'alimentation exogène. J'ai constaté que le type de proie, plutôt que la quantité totale de carbone consommée, est important pour favoriser une croissance rapide des larves de sébaste se nourrissant de manière exogène. Les larves qui consommaient du carbone de proies mobiles, en particulier les stades nauplii de *C. finmarchicus*, étaient en meilleure condition et avaient récemment grandi plus rapidement que les larves qui consommaient du carbone de proies immobiles, tel que les œufs de *C. finmarchicus*. Ces résultats suggèrent une grande importance de la variabilité interannuelle entre le moment de l'extrusion larvaire et le moment de la saison de reproduction de *C. finmarchicus* afin d'assurer un chevauchement spatio-temporel entre l'émergence des larves de sébaste et les nauplii de *C. finmarchicus*. Au final, j'ai identifié 4 caractéristiques environnementales pouvant être responsables de la variabilité dans le recrutement du sébaste : la phénologie tardive de *C. finmarchicus*, l'abondance élevée de *C. finmarchicus*, le faible volume de la couche intermédiaire froide et la faible biomasse du stock reproducteur. Mes résultats suggèrent que des conditions environnementales appropriées pour chaque facteur doivent être réunies afin de favoriser un fort recrutement du sébaste, et chacune de ces conditions était présente lors des récents événements de fort recrutement en 2011 et 2013. Ces résultats fournissent aux gestionnaires des pêches une base de conditions environnementales qui peut être suivie annuellement afin de mieux prédire les fluctuations naturelles des populations de sébaste du GSL.

Mots clés : recrutement, larves de poissons, processus ascendants, océanographie, copépodes, trophodynamique, croissance

ABSTRACT

Overfishing and decades of poor recruitment caused Gulf of St. Lawrence (GSL) redfish, *Sebastes mentella*, populations to crash in the early 1990s and stock biomass remained low until the mid-2010s. Unprecedentedly high recruitment of the 2011 cohort, along with strong recruitment of the 2013 cohort, have allowed redfish populations to rebound to a record high estimated biomass of 2.8 million tons in 2021, and talks of reopening the fishery are currently underway. Little is known about the life history of redfish in the region. In addition, redfish are categorized as a spasmodically-recruiting species, which produce strong recruitment cohorts on average once every 10 years. This reproductive characteristic makes it difficult to gather a large sample size of strong recruitment years in order to identify empirical relationships linking recruitment to environmental conditions. In marine fishes, recruitment success is often regulated by the magnitude of mortality by different agents that affect the survivorship of individuals during the larval stage. A better understanding of the factors that affect larval redfish survival, and ultimately drive redfish recruitment in the region, would allow stock assessment teams to better predict and monitor survival of early life stages of redfish in the future.

The overarching objective for this project was to identify likely environmental conditions that drive recruitment success of larval redfish. In order to accomplish this, I had to first understand the sources of energy and nutrients in the larval redfish diet, and the extent to, and means by which diet influences larval redfish growth. Then, I was able to begin to mechanistically piece together the processes in which larval redfish recruitment could potentially be influenced by physical and biological oceanography. In Chapter 1, I identified, categorized, and quantified prey in the larval redfish diet in order to determine feeding preferences. Using these data, I identified important prey taxa and developmental stages that larval redfish preferentially prey upon in the environment in order to avoid starvation. In Chapter 2, I determined age and growth patterns of redfish larvae by measuring daily otolith increments. Using otolith microstructure data and diet analysis, I described the relationship between recent feeding success, diet composition, and larval condition and growth. In Chapter 3, I used a weight-of-evidence approach to identify physical and biological oceanographic variables that best explain redfish recruitment variability. I used long-term environmental data sets compiled by Fisheries and Oceans Canada to describe the relationships between multiple environmental variables and annual recruitment strength.

I found that larval redfish are generalist feeders, and frequently multiple prey taxa commonly found within the GSL. The majority of carbon in the diet is contributed egg and naupliar stages of the calanoid copepod, *Calanus finmarchicus*, with larvae in some years demonstrating a feeding preference for *C. finmarchicus* eggs. When I investigated the role of diet composition on larval redfish growth, I found that there is a critical period around 8 days post-extrusion at which growth patterns differ from those immediately post-extrusion. This likely corresponds with the onset of exogenous feeding. I found that prey type, rather than the total amount of carbon consumed, is important to drive fast growth in exogenously feeding larval redfish. Larvae that consumed carbon from mobile prey, such as *C. finmarchicus* nauplii, were in better condition and had recently grown faster than larvae that consumed carbon from immobile prey, such as *C. finmarchicus* eggs. These results inferred the importance between the timing of larval extrusion and the timing of the *C. finmarchicus* reproduction season in order to ensure that larval redfish overlapped in space and time with *C. finmarchicus* nauplii. I identified 4 likely environmental drivers of redfish recruitment: late *C. finmarchicus* phenology, high *C. finmarchicus* abundance, low volume of the cold intermediate layer, and low spawning stock biomass. These results suggest that suitable environmental conditions for each driver must be met in order to promote a strong redfish recruitment event, and each of these conditions were present during the recent strong recruitment events of 2011 and 2013. These findings provide fishery managers with a conceptual framework of environmental effects on recruitment, and a suite of conditions that can be monitored annually in order to better predict natural population fluctuations in GSL redfish.

Keywords: recruitment, larval fish, bottom-up processes, oceanography, copepods, trophodynamics, growth

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GSL	Gulf of St. Lawrence
SL	Standard length
BD	Body depth at anus
P(X | Y)	Percentile score of a larva’s performance of measured variable X given Y
CIL	Cold intermediate layer
SRS	Spasmodically-recruiting stock

INTRODUCTION GÉNÉRALE

After the collapse of the Atlantic cod (*Gadus morhua*) fishery in 1994, fishermen in the Northwest Atlantic began to target redfish in order to maintain an income (Duplisea et al. 2016, Duplisea 2018). This resulted in overfishing, which caused Gulf of St. Lawrence (GSL) deepwater redfish, *Sebastes mentella*, populations to crash and a moratorium was placed on the fishery in 1995 (Duplisea et al. 2016). Poor annual recruitment since 1981 prevented the population from recovering even in the absence of fishing pressure throughout the late 1990s and early 2000s. Unprecedentedly high recruitment of the 2011 cohort, along with strong recruitment of the 2013 cohort, have allowed redfish populations to rebound to a record high estimated biomass of 2.8 million tons in 2021, and talks of reopening the fishery are presently underway. Little is known about the life history of redfish in the region, and the ecological impacts of the resurgence of redfish populations in the GSL are unknown. In marine fishes, recruitment success is often regulated by the magnitude of mortality by different agents that affect the survivorship of individuals during the larval stage (Hjort 1914, Cushing 1975, 1990, Houde 1987). Understanding the factors that drive redfish recruitment in the region will allow stock assessment teams to better predict and monitor recruitment success of redfish in the future.

1.1 RECRUITMENT

Understanding drivers of recruitment variability of commercially-important species has been one of the most important goals in fisheries science for more than 100 years (Houde 2008). Fish experience extremely high mortality during early life stages that is strongly linked with the success of recruitment for cohorts of individuals (Houde 1987, Legget and Deblois 1994). Mortality rate is the greatest during the larval stage for most marine fishes

(Houde 1987). Recruitment is defined as the entry of a cohort into the exploited component of the population. For species like the redfish, annual recruitment can usually be predicted by the year-class strength of the cohort, the number of individuals that survive the larval stage and through the first year of life. There are three primary agents of mortality that shape recruitment success during the larval stage: starvation, predation, and advection. Multiple hypotheses were proposed over the past century in order to explain the drivers behind recruitment variability for marine fish species based on these three primary mortality agents. Risk of advection for redfish outside of the GSL is low due to the relatively closed nature of the system, therefore we believe redfish recruitment in this region is primarily driven by factors relating to starvation and predation.

Johan Hjort's (1914) Critical Period Hypothesis was the catalyst for scientists to begin investigating recruitment variability. Hjort (1914) hypothesized that year-class success was determined by mortality due to starvation during a short "critical period" at the onset of exogenous feeding. Cushing (1975, 1990) expanded on Hjort's work by proposing the Match-Mismatch Hypothesis, where recruitment success of a cohort is dependent on the temporal overlap between exogenously-feeding larvae and the peak of prey abundance in the environment throughout the larval stage. In years when there is little to no overlap between feeding larvae and prey items, larvae would starve, leading to recruitment failure. Contrarily, in years when larvae and peak prey abundance overlap temporally in the environment, recruitment would be high. A species' dependence on environmental cues for reproductive events can determine annual match or mismatch. Species should evolve to reproduce at a time when newly-hatched larval offspring encounter abundant prey in order to maximize fitness. Larval fishes prey upon zooplankton, which quickly increase in biomass following seasonal phytoplankton blooms. The timing of primary productivity, and ultimately zooplankton (secondary production), are determined by changes in abiotic environmental factors such as temperature, photoperiod, and freshwater inflow (nutrient flux). Therefore, both natural annual weather variability as well as long-term climatic shifts change the phenology of regional plankton blooms. A fish species' evolutionary dependence on a zeitgeber for reproductive events plays a role in determining the degree of "match" or "mismatch" between larvae and prey to avoid starvation, and ultimately annual recruitment success.

Predation has been argued as being the greatest cause of mortality to larval fishes and strongly shapes recruitment success (Bailey and Houde 1989, Houde 2008). Mortality within larval populations has been shown to be size dependent, with smaller larvae at a greater risk of being preyed upon relative to larger larvae (Bigger is Better hypothesis, Bailey and Houde 1989). Larval size is often strongly coupled with developmental stage. Large larvae are usually more developed than smaller conspecifics of the same age, and will reach the juvenile stage in a shorter time span, decreasing the time spent in the larval stage where mortality risk is highest (Stage Duration hypothesis, Chambers and Leggett 1987).

Starvation and predation mortality are strongly linked by larval growth rate. Larval growth is positively related to the amount of organic material consumed by larval fish, also referred to as feeding success (Ware 1975). Increased larval feeding success results in faster growth, but the strength of this relationship is species dependent (Pepin et al. 2015). If predation is the main source of mortality during the larval stage, and predation risk is related to larval size, then larval survival is strongly determined by the effect of feeding success on growth rate (Growth-Mortality hypothesis, Anderson 1988). Temperature also influences larval growth to a secondary degree by altering metabolic processes, but feeding success is the primary limiting factor of growth in larval fishes. Growth-rate driven selection by predation has been documented among larvae of similar size characterized by variable growth rates. Larval Japanese anchovy (*Engraulis japonicus*) with slower growth rates were preyed upon more often by some predator species (including conspecifics via cannibalism) than faster-growing individuals of a similar size (Growth-Selective Predation hypothesis, Takasuka et al. 2003, 2004). Overall, larval feeding success is related to survival through two of the three agents of larval mortality: directly against starvation, and indirectly against predation by strongly influencing larval growth and size.

Fishes undergo intense cell differentiation, organogenesis, and somatic growth during embryonic and larval life stages. It is assumed that the nutrient composition of the yolk is optimal, or near-optimal, for proper embryonic and endogenously-feeding larval development, but the transition from endogenous to exogenous feeding separates larvae from this beneficial maternal investment (Watanabe and Kiron 1994). At the onset of exogenous feeding, larvae must successfully detect and capture suitable prey in the environment in order to survive. Prey must be smaller than larval mouth gape width for successful capture and consumption and prey should also provide larvae with the necessary suite of nutrients to continue with proper development. Various potential prey taxa occur within a zooplankton community, but in order to optimize growth and survival, larvae should preferentially prey upon taxa that are abundant, easy to capture, and provide the highest net gain of energy and essential nutrients (Schoener 1971, Werner and Hall 1974). Prey size is often used as a proxy for energetic content, therefore it is advantageous for larvae to prey upon the largest consumable taxa, although nutritional content of copepods can fluctuate dramatically across space and time (Bergvik et al. 2012). Finally, this process must be repeated throughout the entire larval stage in a timely fashion in order to avoid starvation, while evading predation (Blaxter 1986). Sensory and swimming capabilities, as well as mouth gape width, of larval fishes increase throughout ontogeny, therefore larval feeding abilities change quickly and dramatically from the early to late larval stage.

The occurrence of larval fishes and potential prey taxa of a consumable size within an environment has historically resulted in a weak, or an absence of a relationship between prey abundance and larval survival in the literature (ie. Brander 1992, Pershing et al. 2005, Agostini et al. 2007). Until recently, species-specific prey identification was not performed in larval diet analyses. Studies where larval stomach content was identified to the species-level concluded that larval fishes prefer to feed on certain planktonic species relative to others (Anderson 1994, Robert et al. 2008, Voss et al. 2009, Murphy et al. 2012, Llopiz and Cowen 2014). Consumption of the preferred prey species results in higher larval growth rates, and ultimately survival (Robert et al. 2009, Sponaugle et al. 2010, Murphy et al. 2013). The concept of preferential feeding by larval fishes, and differences in growth and survival potentials as a result of successful preferred prey consumption, opens the door to investigate the importance of prey quality during the larval stage, in addition to potential prey abundance.

Larval fish feeding success can be measured in two ways representing relatively short- and long-time scales: directly using stomach content analyses and indirectly using daily otolith increment measurements that represent larval growth, respectively. Larval fishes have high metabolism and fast gut evacuation time, therefore stomach content is representative of food consumption within hours of capture. Zooplankton blooms are not homogenously distributed throughout the ocean, and occur in small area patches, so it is important to consider the patchiness of the environment when analyzing stomach content. Plankton samples taken concurrently with larval fish collections aim to provide a measure of the density and composition of potential prey available to larvae at that moment in time. Measurements of daily otolith increments depict lifelong larval growth history, which is related to the individual’s daily feeding success (Dower et al. 2009, Robert et al. 2014, Pepin et al. 2015). Relationships between otolith increment width and stomach content demonstrate the degree to which growth is determined by feeding success in each species. High feeding success during species-specific “critical periods” of larval development has been shown to permanently increase larval growth rates in an individual for the remainder of its larval stage in some species (Pepin et al. 2015). Successful feeding over a moderate timespan can also be measured using larval condition, which can be estimated by the ratio of larval body depth to standard length. Larval condition has been shown to be a better indicator of long-term feeding success than larval growth in some species (Robert et al. 2014b). When used together, these methods provide data to connect feeding success to larval condition and growth during the larval stage, in addition to uncovering the amount of variability between individual larvae over time and space.

1.2 DEEPWATER REDFISH, *Sebastes mentella,* LIFE HISTORY

Long-lived fish species, such as redfish, characteristically have spasmodic recruitment events with strong cohorts occurring on average once per decade. Extreme longevity of individuals allows these species to have multiple reproductive events where eventually one cohort may encounter a suitable environment, produce a strong year-class, and go forth to compose the majority of the stock’s biomass until the next strong year-class (Longhurst 2002). It is because of this spasmodic nature that researchers have hypothesized that a “perfect storm” of conditions is necessary in order to produce a strong year-class (Sysoeva 2000; Gascon 2003). Redfish, as for all species in the genus *Sebastes*, are ovoviviparous. Female redfish in the Gulf of St. Lawrence extrude offspring in the early summer months (May-June), which are capable of feeding exogenously at the time of expulsion (St-Pierre and de Lafontaine 1995). Little is known about the larval ecology of redfish, but it is hypothesized that recruitment success is determined through the larval stage. Even less is known about larval redfish feeding preferences in the region. By understanding the trophodynamics of larval redfish, fisheries scientists, managers, and stock assessment biologists may begin to understand what environmental parameters drove the strong recruitment classes of 2011 and 2013, and identify important environmental variables that can be annually monitored to predict strong recruitment events in the future.

Previous work identifying the diet of larval redfish species (*S. mentella* and *Sebastes fasciatus*) in the northwest Atlantic region concluded that larval redfish feed primarily on copepod eggs and *Spiratella* larvae (Einarsson 1960, Bainbridge 1965). Ichthyoplankton and zooplankton samples collected in 1963 around the Flemish Cap in the northern Atlantic were used to provide a more extensive look at larval redfish diet throughout the summer months. The majority of the biomass of the larval redfish (6 – 11 mm) diet from April to May consisted of copepod eggs, specifically *Calanus finmarchicus* eggs, with a dietary shift to *C. finmarchicus* nauplii in June and July across all larval sizes. *Oithona* spp. nauplii and copepodites were the second most prevalent copepod species, contributing more weight to the diet in larger larvae and later in the summer months. Bainbridge and McKay (1968) identified differences in feeding success and growth rates between 3 adjacent oceanographic regions around the Flemish Cap, highlighting the importance of investigating trophodynamics and growth of *Sebastes* spp. within specific, local regions for management purposes. Anderson (1994) identified preferred prey species of *Sebastes* spp. over the Flemish Cap by comparing larval stomach content with the proportions of copepods occurring in the surrounding zooplankton community at the time of collection (Chesson's α-selectivity index; Chesson 1978). Larval redfish stomach content and prey preference are seasonally and annually variable. Prey selectivity changes during the larval stage as larvae grow and zooplankton community composition changes. Newly extruded larvae (April-May 1980, 1981) showed no feeding preference for any prey item in the environment, but avoided large prey such as *C. finmarchicus* copepodites, whether by choice or due to physical inability to ingest large prey. Older larvae (June 1981) preferentially preyed on calanoid eggs and cyclopoid nauplii, and still avoided copepodites. Zooplankton collections in 1981 were characterized by relatively high proportions of cyclopoid copepods, dominated by *Oithona* spp. The diet of larval redfish in 1981 was composed of a larger proportion of cyclopoid prey than the 3 other collection years, and larvae were in significantly poorer condition, with slower development relative to larvae from 1980. These data support Cushing's (1990) Match-Mismatch hypothesis and may indicate that among prey species consumed, the quality of the diet is important for larval *Sebastes* spp. condition, growth, and recruitment success.

One study has been performed in the Gulf of St. Lawrence on the diet of larval *Sebastes* spp. Runge and de Lafontaine (1996) measured the temporal and spatial overlap of *Calanus* copepod species and larval redfish species. They concluded that larval redfish fed predominantly on *Calanus* eggs from the point of first-feeding throughout the larval period (> 13 mm larval length), and > 80% of stomach content biomass was from the consumption of *Calanus* eggs (assumed to be *C. finmarchicus* based on the reported dominance of this species in the environment at the time of collection) until larvae reached 12 mm in length, when the proportion of biomass in the diet from copepodite consumption began to increase. This paper did not report on other copepod species other than *Calanus* sp. present in the redfish diet. Whether this is because no other species were found in the stomachs, or these data were not reported because of the study scope's focus primarily on *Calanus*, is unknown. This paper also did not calculate feeding selectivity indices to identify whether larval *Sebastes* spp. passively or selectively preyed upon *Calanus* eggs in the environment.

Some hypotheses describing drivers of *S. mentella* recruitment were formed following research in the Barents Sea. Sysoeva (2000) proposed that there is a positive relationship between sea surface temperatures throughout the mid- to late larval stage and larval growth and recruitment success. Redfish recruitment was also negatively related to the number of storms that occurred during the larval stage; an increase in the occurrence of storms resulted in water mixing and a decrease in sea surface temperatures which demonstrates the complex relationships between environmental variables. Lastly, in agreeance with Anderson (1994) and Runge and de Lafontaine (1996), Sysoeva (2000) proposed that there was a strong relationship between the timing and abundance of *C. finmarchicus* and larval redfish survival and recruitment.

Work on recruitment variability in other species within the genus *Sebastes* comes from the northeast Pacific Ocean along upwelling regions in the California current. Wheeler (2015) found that growth and survival of larval *Sebastes* spp. were dependent on the temporal overlap of larvae with secondary production blooms as a result of upwelling events. While Anderson (1994) found that growth and survival of *Sebastes* spp. in the Flemish Cap region was positively correlated with sea surface temperatures, Wheeler (2015) found a negative correlation between growth and sea surface temperature in Pacific *Sebastes* spp. This is likely a result of colder temperatures from upwelling events driving productivity in the region, and higher growth rates of larvae resulting from increased feeding success despite slower metabolism. Other studies have attempted to relate physical oceanographic conditions to recruitment success of *Sebastes* in the Pacific. Upwelling indices and sea surface temperature appear to influence recruitment success of *Sebastes* in the California current (Field and Ralston 2005, Wilson et al. 2008, Markel et al. 2017). Inconclusive results and weak relationships may be a result of late season data collection while larvae are in the latter portion of the larval stage. At this stage, larvae may be more resistant to variability in environmental conditions, suggesting that larval mortality of *Sebastes* species due to physical oceanography may occur early in the larval stage (Wilson et al. 2008).

1.3 PROJECT OBJECTIVE

The overarching objective for this project was to identify environmental variables that drive recruitment success of larval redfish in the GSL. The Match-Mismatch hypothesis proposes that year-classes of redfish that overlap temporally with preferred prey items will feed successfully and have higher recruitment than year-classes where a mismatch occurs. In Chapter 1, I identified, categorized, and quantified prey in the larval redfish diet in order to determine feeding preferences. Morphometric measurements such as standard length, anal body depth, and mouth gape width were used to compare the condition and developmental stages of larvae across multiple locations within the GSL and across multiple years. Using these data, I identified important prey taxa and developmental stages that larval redfish preferentially preyed upon in the environment. In Chapter 2, I determined age and growth history of larvae by measuring daily otolith increments. The Growth-Mortality (Anderson 1988) hypothesis states that it is advantageous for recruitment success to be large and grow quickly. Using otolith microstructure data and larval diet analyses, I found a relationship between recent larval feeding success and recent larval growth. In Chapter 3, I utilized a weight-of-evidence approach and identified 4 physical and biological oceanographic variables that best explained redfish recruitment variability. The Match-Mismatch hypothesis is rooted in abiotic environmental variables that strongly influence the phenology of potential planktonic prey species and fish reproductive events. Therefore, physical variables, such as temperature, salinity, and water stratification, can positively or negatively affect larval physiology and growth. In addition, as previously stated, the quantity and quality of the available potential prey likely also drive recruitment success during the larval stage, and physical environmental conditions can mediate the abundance and community composition of larval prey fields. Using data on key prey taxa collected in Chapter 1, in addition to condition and growth results collected in Chapter 2, I tested individual hypotheses that potentially influenced recruitment success to determine the effect of specific physical and biological parameters on the annual year-class success of redfish in the GSL.

CHAPITRE 1

VARIABILITE INTERANNUELLE DE LA COMPOSITION DU REGIME ALIMENTAIRE ET PREFERENCE ALIMENTAIRE DES PROIES DES LARVES DE SEBASTE DANS LE GOLFE DU SAINT-LAURENT

1.1 RESUME EN FRANÇAIS

Le chevauchement spatio-temporel entre les larves de poissons et leurs proies planctoniques est une source importante de variabilité du recrutement. Au cours de la dernière décennie, une espèce de sébaste, *Sebastes mentella*, du golfe du Saint-Laurent (GSL) a produit plusieurs cohortes fortes après des décennies de faible recrutement, ce qui a suscité un vif intérêt pour l'identification des facteurs potentiels de survie des larves. La présente étude fournit la première évaluation pluriannuelle détaillée de la trophodynamique larvaire du sébaste (*Sebastes* spp.). La variabilité interannuelle de la composition du régime larvaire du sébaste et de la sélectivité des proies a été évaluée à l'aide de l'identification à haute résolution des proies du contenu stomacal des larves et des champs de proies *in situ*. Les œufs du copépode calanoïde *Calanus finmarchicus* représentaient la proie la plus fréquemment consommée au cours de 3 des 4 années de collecte et ont constitué la plus grande proportion de carbone ingéré par les larves de sébaste au cours de toutes les années. La forte consommation d'œufs de *C. finmarchicus* par les larves, combinée à des preuves de sélection positive pour ce taxon pendant certaines années, confirme l'hypothèse d'un lien trophique fort entre les larves de sébaste et un copépode calanoïde clé dans l'écosystème du GSL. Nos résultats indiquent que les futures étude des processus de recrutement du sébaste du GSL devraient tenir compte de la variabilité environnementale de la phénologie de la reproduction et de l'abondance de *C. finmarchicus*.

Cet article a été accepté pour publication dans sa version finale en août 2020 par les éditeurs du *Journal of Plankton Research*. Cet article a reçu le « 2021 David Cushing Prize » du *Journal of Plankton Research* pour la meilleure publication dans la revue par un scientifique en début de carrière lors de l'année précédente. En tant que première autrice, j'ai effectué la majorité de la collecte des données, des analyses statistiques, de l'interprétation des résultats et de la rédaction du manuscrit. Le deuxième auteur, Félix Lauzon, a participé à la collecte des données et aux analyses préliminaires des données. Les auteurs Stéphane Plourde, Pascal Sirois et Dominique Robert ont tous contribué aux interprétations biologiques et écologiques de ces résultats. Tous les auteurs ont participé à la révision de l'article. Cet article a été présenté en personne à la *43rd Annual Larval Fish Conference* à Palma, Majorque, Espagne (mai 2019), à *Ressources Aquatiques Québec* à Rimouski, Québec, Canada (novembre 2019) et à la *Canadian Conference for Fisheries Research* à Halifax, Nova Scotia, Canada (janvier 2020).

1.1.1 Summary in English

Spatiotemporal overlap between fish larvae and their planktonic prey is an important source of recruitment variability. Over the past decade, one species of redfish, *Sebastes mentella*, from the Gulf of St. Lawrence (GSL) produced multiple strong cohorts following decades of low recruitment which has generated strong interest in identifying potential drivers of larval survival. The present study provides the first detailed, multi-year assessment of larval redfish (*Sebastes spp.*) trophodynamics. Interannual variability in larval redfish diet composition and prey selectivity was assessed using high-resolution prey identification of larval gut contents and *in situ* prey fields. Eggs from the calanoid copepod *Calanus finmarchicus* represented the most frequently consumed prey in 3 of the 4 collection years, and contributed the largest proportion of carbon ingested by redfish larvae in all years. The high consumption of *C. finmarchicus* eggs by larvae, combined with evidence of positive selection for this taxon in some years, supports the hypothesis of a strong trophic link between larval redfish and a key calanoid copepod in the GSL ecosystem. Our results indicate that future efforts investigating GSL redfish recruitment processes should consider environment-driven variability in the reproductive phenology and abundance of *C. finmarchicus*.

This article titled “Interannual variability of diet composition and prey preference of larval redfish (*Sebastes* spp.) in the Gulf of St. Lawrence” was accepted for publication in its final version in August 2020 by the editors of the *Journal of Plankton Research*. This article was awarded the 2021 *David Cushing Prize* by the *Journal of Plankton Research* for the best publication in the journal by an early-career stage scientist in the previous year. As first author, I performed a majority of the data collection, statistical analyses, interpretation of results, and writing of the manuscript. Second author, Félix Lauzon, assisted in data collection and preliminary data analyses. Authors Stéphane Plourde, Pascal Sirois, and Dominique Robert all contributed to the biological and ecological interpretations of these results. All authors participated in the revision of the article. This article was presented in-person at the *43rd Annual Larval Fish Conference* in Palma, Mallorca, Spain (May 2019), *Ressources Aquatiques Québec* in Rimouski, Québec, Canada (November 2019), and the *Canadian Conference for Fisheries Research* in Halifax, Nova Scotia, Canada (January 2020).

1.2 INTRODUCTION

Understanding recruitment variability of commercially-important fish species has been one of the most important goals in fisheries science for more than 100 years (Houde, 2008). Johan Hjort's (1914) seminal hypotheses on recruitment variability were the catalysts for scientists to further investigate drivers of larval fish survival and mortality. Hjort's (1914) primary hypothesis, known as the Critical Period, stated that variability in year-class success is determined by mortality due to starvation during a short period at the onset of exogenous feeding. Cushing (1975, 1990) expanded on Hjort's concept by proposing the Match-Mismatch hypothesis, where recruitment success of a cohort is dependent on the temporal overlap between exogenously-feeding larvae and sufficient planktonic prey abundance in the environment throughout the entire larval stage. Years characterized by little to no overlap between larvae and their prey would result in recruitment failure driven by slow growth and starvation mortality. On the contrary, years with matching peaks in larval emergence and prey abundance would result in strong year classes through optimal larval feeding and growth. These trophic hypotheses on the control of recruitment variability have shaped the current Growth-Survival paradigm (e.g. Chambers and Leggett, 1987; Miller et al., 1988), which links variability in year-class strength to variability in larval feeding, growth and survival.

A majority of studies that attempted to demonstrate the dependence of larval survival on the temporal overlap with peak plankton abundance have either failed to detect any link or only found weak relationships (e.g. Brander, 1992; Pershing et al., 2005; Agostini et al., 2007). Until recently, detailed identification of planktonic prey items was not commonly performed in the analysis of larval fish diet composition. However, studies in which prey have been identified to the species level revealed that larval fishes exhibit strong species-specific preferences within their potential prey field (e.g. Anderson, 1994; Robert et al., 2008; Voss et al., 2009; Demontigny et al., 2012; Murphy et al., 2012; Llopiz and Cowen, 2008). Successful feeding on preferred prey species generally results in high larval growth and survival (Robert et al., 2009; Sponaugle et al., 2010; Murphy et al., 2013). Given the importance of preferred prey taxa in driving variability in growth and survival potential, it is essential to investigate prey selectivity during the larval stage as a first step towards the robust assessment of recruitment-relevant bottom-up processes in a given population (Robert et al., 2014).

Deepwater redfish, *Sebastes mentella* and *S. fasciatus*, are long-lived, ovoviviparous species found in the Gulf of St. Lawrence (GSL). Following a 30-year period of consecutive weak year classes and a collapse of the fishery, strong recruitment events in 2011-2013 resulted in rapid stock recovery of *S. mentella*. Little is known about the drivers of recruitment dynamics in the species, and knowledge of larval ecology is particularly scarce. Furthermore, there is no known morphological criterion to discriminate between these two redfish species during the larval stage, and literature investigating early life history of these two species often groups them together as “redfish”. Females are known to extrude offspring in spring and early summer (May-July) that are capable of feeding exogenously at the time of expulsion (St-Pierre and de Lafontaine, 1995). Length-at-extrusion is highly variable but averages 6 mm (Taning, 1961; Penney and Evans, 1985). Little is known about larval redfish feeding requirements in the GSL. A previous study that described larval diet of the 1989 year-class concluded that eggs of the calanoid copepod *Calanus finmarchicus* strongly dominated dietary prey composition (Runge and de Lafontaine, 1996). On the Flemish Cap, redfish larvae have also been reported to mainly feed on *C. finmarchicus* eggs, but the proportion of eggs in the diet relative to another frequently consumed prey taxon, the nauplii of the cyclopoid copepod *Oithona* spp., varied among years during the period 1979-81 (Anderson, 1994). While interannual variability in plankton community composition resulted in significant differences in the larval redfish diet on the Flemish Cap, the links between variability in prey field composition and larval redfish diet remain to be assessed in the GSL.

The objective of the present study was to identify key planktonic prey taxa and feeding preferences of larval redfish in the GSL using a 4-year dataset. In particular, we aimed to describe changes in diet composition through early ontogeny and among year-classes. We measured prey selectivity by comparing high-resolution taxonomical composition of prey within individual larval stomachs to that of the potential prey field at time of capture. These results expand on the findings of Runge and de Lafontaine (1996) by describing the diet of larval redfish in the GSL with a higher taxonomic resolution and a multi-year dataset. Detailed knowledge of larval trophodynamics constitutes a necessary first step in identifying and understanding the environmental drivers responsible for shifting recruitment dynamics of GSL redfish.

1.3 METHODS

1.3.1 Sampling of redfish larvae and their prey

The Gulf of St. Lawrence (GSL) is an enclosed sea connected to the Northwest Atlantic Ocean through the Belle-Isle and Cabot straits. Ichthyoplankton and zooplankton were sampled over a grid of 27 fixed stations located throughout redfish spawning areas at the junction of the Laurentian and Esquiman channels in the Northeast sector of the GSL between June 12-17 in each of the years 1997-2000 (Figure 1). Ichthyoplankton were collected using a 61 cm diameter bongo sampler equipped with 333 µm mesh nets deployed obliquely in the upper 50 m of the water column. To assess the prey field of larval fish, concurrent zooplankton tows (filtered water volume: 34 to 131 m^3) were carried out at each station using a second bongo frame equipped with 63 µm mesh nets. All ichthyoplankton and zooplankton samples were immediately preserved in a 4% buffered formaldehyde solution onboard the vessel. Following each annual survey, larval *Sebastes* spp. were identified, sorted, and stored in scintillation vials using 4% buffered formaldehyde solution.

Extrusion events for both *S. mentella* and *S. fasciatus* occur within the GSL during late spring and early summer. Due to the impossibility of relying on genetic identification as a result of formalin preservation, and a lack of morphological criterion for species identification, we could not directly confirm species identity of our samples. However, our survey directly targeted *S. mentella* based on known spatial and temporal larval occurrence of both species in the GSL derived from a genetic assessment (Sévigny et al., 2000). Relying on extensive larval sampling achieved during two consecutive years (1991-1992) over the Laurentian, Esquiman and Anticosti channels, Sévigny et al. (2000) concluded that *S. mentella* larvae are extruded over the deep Laurentian and southern Esquiman channels in mid-June, while *S. fasciatus* larvae are extruded over the shallower Anticosti and northern Esquiman channels from late June to early July. Given that our sampling was carried out over the Laurentian and southern Esquiman channels in mid-June, we contend that our larval collections are strongly dominated by *S. mentella*.

1.3.2 Laboratory analyses

A subsample of 10 larvae from each station (when available) were photographed and measured for standard length (SL) to the nearest 0.01 mm at 16× magnification under a stereoscopic microscope connected to the Olympus cellSens® software. Larvae were grouped into 3 size classes (< 7 mm, 7 to < 8 mm, and ≥ 8 mm).

The hindgut and foregut of each larva were dissected at 120× magnification and individual prey were photographed, identified to the lowest taxonomic level, developmentally staged, and measured for total length or prosome length to the nearest 0.1 µm. Prey measurements were used to convert stomach contents to carbon weight using previously determined equations from the literature (Table I in Robert et al., 2008). Prey that were too damaged to be accurately measured were assigned measurements based on the average length of the taxon and corresponding developmental stage, when identifiable, in the collection year. Copepod eggs were categorized by size classes: < 135 µm, 135 – 165 µm, 165-195 µm, and > 195 µm. Eggs < 135 µm correspond to a multitude of species such as *Oithona similis*, *Pseudocalanus* spp. and *Temora longicornis* (McLaren et al., 1988; Castellani et al., 2005; Demontigny et al., 2012). Copepod eggs of size ranging between 135 – 165 µm correspond with average *C. finmarchicus* egg size, 165 – 196 µm to *C. glacialis and Metridia longa* (Plourde and Joly, 2008), and > 195 µm to *C. hyperboreus*. Free egg yolks lacking a membrane were assumed to be partially-digested eggs and the original egg diameter was estimated. Digested eggs were randomly assigned an original egg diameter in proportions that corresponded to the frequency of each egg size class at each collection station. Unidentifiable digested material was not measured or converted to carbon content.

Aliquots of each potential prey sample for prey field identification correspond to a known fraction of the total sample that contained at least 300 copepods, not including copepod eggs. All individual organisms were identified to the lowest taxonomic level, developmentally staged, and counted using a stereomicroscope at 120× magnification.

1.3.3 Prey selectivity analysis

To measure variability in consumed prey sizes, diet niche breadth was calculated for each larva by calculating the standard deviation of the log-transformed mean prey length (Pearre, 1986). Diet niche breadth values were averaged between larvae in the same size-class for each year.

Prey preference for each larva was calculated using Chesson's α-selectivity index (Chesson, 1978), which is recognized as one of the most stable and robust indices to measure prey selectivity (Pearre, 1982; Govoni et al., 1986):

$$\alpha_j = \frac{d_j/p_j}{\sum \frac{d_i}{p_i}}$$

where d_j is the proportion of prey taxon j by occurrence in the larval diet and p_j is the proportion of prey taxon j in the prey field. Prey taxa that represented more than 2% of the larval diet by number in each size class were used in this equation. Neutral selectivity is calculated as an α value of $1/n$, where n is the number of prey taxa used in the Chesson's equation. An α value higher than $1/n$ indicates positive selection for a given prey taxon as it was ingested in higher proportion than its relative frequency in the surrounding environment, while an α value lower than 1/*n* indicates selection against that prey. In the present study, we defined positive selection as 'strong' when Chesson's α was > 2/*n*, meaning that the proportion of the taxon in the larval diet was at least double that of its proportion in the potential prey field. Alternatively, negative selection was defined as strong when Chesson's α was < 1/2*n*, meaning that the proportion of the taxon in larval diet was less than half of its proportion within the potential prey field. Chesson's α was averaged among larvae within the same size class in the same year to determine differences in preference throughout larval development, as well as among years.

1.4 RESULTS

1.4.1 Larval redfish

Redfish larvae were found at 15 stations in 1997, 9 stations in 1998, 23 stations in 1999, and 9 stations in 2000. The highest mean densities of larvae were observed in 1999 (1.32 ind. m^{-3} ± 1.59), followed by stations in 1998 (0.68 ind. m^{-3} ± 0.83), 2000 (0.30 ind. m^{-3} ± 0.24), and 1997 (0.19 ind. m^{-3} ± 0.13).

Larvae dissected in this study averaged 7.18 mm ± 1.01 (range: 4.61 – 10.21 mm), with the largest larvae on average collected in 1999 and the smallest larvae on average in 1997 (Table 1). Over half of the larvae sampled in 1997 and 1998 were yolk-sac larvae, and none of the larvae sampled in these years were undergoing flexion. In contrast, over half of larvae collected in 1999 and 2000 were undergoing flexion, identified here as the presence of one or more hypural plates at the end of the notochord. Larvae collected in 1998 were on average larger than larvae at the same developmental stage in other years.

1.4.2 Potential prey field

Potential copepod prey (egg, naupliar, and copepodite stages) densities were the lowest in 2000, with an average combined density of 5,700 individuals m^{-3}. Combined potential prey densities were higher than in 2000 by coefficients of 2.7, 2.6 and 1.9 in 1997, 1998, and 1999. A similar trend was observed in the densities of *Pseudocalanus* spp. and *Oithona* spp. nauplii densities, while the density of copepodite and egg stages did not follow this pattern (Figure 2A). Among copepod egg size classes, the density of eggs comprised within the 135 – 165 µm size class, attributable to *Calanus finmarchicus*, was characterized by particularly low densities in 1999 compared to the three other years, during which densities were about 7 times higher.

Naupliar and copepodite stages of *Oithona* spp. were the most prevalent taxa in 1997 (34.7 % of total potential prey field), 1998 (37.3%), and 1999 (50.4%) (Figure 2B). In 2000, copepod eggs composed the highest proportion of potential prey taxa (50.3%); *C. finmarchicus* eggs (135 – 165 µm size class) represented 36.7% of all prey by numbers. The proportion of copepod eggs within the potential prey field dropped to < 20% in 1997 and 1998, and to < 10% in 1999, the only year where the majority of eggs belonged to the < 135 µm size class. *Pseudocalanus* spp. nauplii and copepodites made up similar proportions (11.5-16.7%) of the prey field in all years. *C. finmarchicus* nauplii occurred in the highest proportions in 1997 (7.7%), and 2000 (5.4%), and similar low proportions in 1998 and 1999 (2.3% and 2.5%, respectively). *Calanus* spp. copepodites composed less than 2.0% of the total prey field in 1997 and 1998, but its proportion increased to 3.4% of the prey field in 1999, and to 6.4% in 2000.

Other prey taxa that occurred frequently (> 2.0% of all organisms) in one or more of the sampling years, but not all 4 years, were nauplii of *Centropages* spp. (1998 – 7.0%) and *Temora longicornis* (1997 – 2.9%, 1998 – 5.9%, 1999 – 6.8%), copepodites of *C. hyperboreus* (2000 – 2.3%), *Triconia borealis* (1997 – 2.2%, 1998 – 2.8%) and *Temora longicornis* (1998 – 2.4%), and bivalve larvae (1999 – 2.3%, 2000 – 3.7%).

1.4.3 Larval diet

The mean number of prey ingested increased with larval length: 11.7 prey by larvae < 7 mm, 25.8 prey by larvae 7 to < 8 mm, and 38.8 prey by larvae ≥ 8 mm (Table 2). Larvae captured in 1999 consumed the most prey on average throughout all size classes, while the greatest proportion of larvae with an empty gut was observed in 1997. In all years, the proportion of larvae with empty guts decreased as larval size increased. Copepod eggs were the most frequently consumed prey taxa by numbers in 1997, 1998, and 2000 across all larval size classes, comprising at least 25.0% of the total diet (Figure 3). The contribution of copepod eggs was highest in 2000, when they made up more than 50% of items consumed by numbers. Among copepod egg size classes, eggs within the 135-165 µm size range were the most frequently ingested in all size classes each year. Larvae collected in 1999 fed most frequently on *Oithona* spp. nauplii, which composed between 37.6% and 45.1% of the larval diet by prey number (Table 2). The second most consumed nauplii of a species was *Pseudocalanus* spp. (7.0-21.4%), with a contribution to proportion of prey by numbers that remained relatively constant across all larval size classes and years. The contribution of *Calanus* spp. nauplii (predominantly *C. finmarchicus*) to diet composition by numbers was relatively small, except in 1997 when they represented up to 17.5% of the prey consumed by larvae in the 7 to < 8 mm size class. Copepodites were rarely consumed overall, with the exception of *Oithona similis*, which showed an increasing contribution to the larval diet with increasing larval size (Table 2).

Mean amount of carbon ingested increased with larval length from 2.6 µg C in larvae < 7 mm to 6.8 µg C in larvae ≥ 8 mm, and was highest in larvae collected in 1999 (Table 3). In general, the contribution in carbon of the different taxa to diet composition was relatively similar to that by prey numbers (Table 3, Figure 4). Copepod eggs (all size classes) contributed the greatest amount of carbon of any prey taxa across all larval size classes and all years, except for the 7 to < 8 mm size class in 1997, where nauplii of *C. finmarchicus* was the dominant taxon (Figure 4). Among copepod eggs, the size class ranging between 135 – 165 µm, corresponding to *C. finmarchicus*, contributed the greatest proportion of carbon by far to redfish diet across larval size classes and years.

1.4.4 Prey preference and selectivity

Diet niche breadth of redfish larvae did not change with increasing larval standard length, with the exception of 1997, when a modest increase was noted between the two smallest size classes (Figure 5). Variability in prey size was lower in 2000 compared to the three other years. In all years, larvae ingested small prey dominated by copepod eggs across all larval size classes (Figure 6). There was no change in mean prey size or carbon content consumed across larval size classes (Table 4).

Seven prey taxa contributed at least 2% to the larval diet by prey numbers across all larval size classes and were used for the Chesson’s α selectivity analysis: copepod eggs < 135 µm, 135 – 165 µm, and 165 – 195 µm, nauplii of *C. finmarchicus*, *Pseudocalanus* spp. and *Oithona* spp., as well as copepodites of *O. similis*. The threshold for neutral selectivity was calculated to 0.142, while those for strong positive and negative selection were determined as 0.284 and 0.071, respectively. Larvae collected in 1997 and 1998 did not exhibit strong positive preference for any of the commonly consumed prey taxa (Figure 7). Moderate positive selection for copepod eggs smaller than 135 µm was observed in all larval size classes in 1998. Strong positive selection for copepod eggs in the 135-165 µm size class was observed in 1999, which increased with larval size. Larvae collected in 2000 positively selected for copepod eggs in the 135 – 165 µm and 165 – 195 µm size classes, but there were no clear trends through ontogeny. Larvae across all size classes and years demonstrated a strong negative selection against *O. similis* copepodites. Prey taxa that did not contribute at least 2% to the larval diet by prey number but represented > 2% of the potential prey field in one or more collection years can also be considered strongly selected against by larval redfish. Those potential prey taxa avoided by larval redfish were the nauplii of *Temora* *longicornis* (1997, 1998, 1999) and *Centropages* spp. (1998), copepodites of *Microsetella* spp. (all years), *Triconia borealis* (1997, 1998) and *Temora longicornis* (1998), as well as bivalve larvae (1998, 1999).

1.5 DISCUSSION

Knowledge of larval redfish trophodynamics in the GSL prior to this study comes from previous work by Runge and de Lafontaine (1996), who concluded that larval redfish strongly select for eggs of the copepod *C. finmarchicus* throughout early ontogeny, based on the high relative frequency of copepod eggs observed in the diet of the 1989 cohort. However, this conclusion was formulated in the absence of quantitative analyses of potential prey field and prey selectivity. Even though particularly high proportions of *C. finmarchicus* eggs were consumed during that year, an assessment of diet composition of larval redfish from the Flemish Cap revealed the existence of significant interannual variability in the proportion of main prey taxa ingested (Anderson, 1994). In order to characterize potential food web effects on larval survival and recruitment of redfish in the Gulf of St. Lawrence, it is important to test Runge and de Lafontaine's hypothesis using a multi-year dataset. In the present study, we relied on a 4-year dataset of larval gut contents and potential prey assemblages, both characterized at high taxonomic resolution to assess interannual variability in larval redfish diet composition and prey selectivity. Results from our comprehensive assessment of larval redfish trophodynamics can aid us in identifying potential bottom-up drivers of early-life survival, which will provide key information for future investigations into recruitment dynamics of the stock.

The diet composition of larval fish from boreal marine environments is generally dominated by the naupliar and copepodite stages of calanoid copepods (e.g. Hunter, 1981; Pepin and Penney, 1997; Llopiz, 2013). Copepod species that are reported as main prey in North Atlantic ecosystems commonly include *Pseudocalanus* spp. and *C. finmarchicus*. In Atlantic cod (*Gadus morhua*), a widely-distributed species across the Northeast and

Northwest Atlantic Ocean, a large body of literature has shown that larvae from the numerous stocks demonstrate feeding preferences for these two copepod species (Kane, 1984; Heath and Lough, 2007; Robert et al., 2011). Naupliar and/or copepodite stages of *C. finmarchicus* and *Pseudocalanus* spp. have also been identified as key prey for larval Atlantic mackerel (*Scomber scombrus*) (Ringuette et al., 2002, Robert et al., 2008), haddock (*Melanogrammus aeglefinus*) (Kane, 1984; Economou, 1991), whiting (*Merlangius merlangus*) (Fortier and Harris, 1991), pollock (*Pollachius virens*) (Economou, 1991), and silver hake (*Merluccius bilinearis*) (Reiss et al., 2005).

As they grow and develop, most larval fish species display rapid dietary shifts from small copepod nauplii during the first-feeding stage, to larger copepodites during the late-larval stage (Hunter, 1981; Robert et al., 2008; Reiss et al., 2005). Contrary to the majority of species which exhibit dietary shifts in the 5-10 mm size range, our results provide evidence that there was no apparent ontogenetic change in larval redfish diet within the early larval stage. Redfish larvae continued to ingest large numbers of *C. finmarchicus* eggs throughout early ontogeny, and in general, they foraged on a suite of relatively small prey taxa throughout early development. This is reflected by a particularly narrow niche breadth that remained constant with increasing larval size. Even though our results support previous conclusions from Runge and de Lafontaine (1996) that *C. finmarchicus* eggs constitute the most frequent prey taxon within the larval redfish diet, the proportion of the diet composed of eggs across the 4-year period, both by number and carbon content, was significantly smaller than that reported in the 1989 year class. Within the 5-10 mm larval size range, Runge and de Lafontaine (1996) estimated that copepod eggs contributed >85% of gut content by biomass, while in our study, total egg carbon contribution was estimated to range between 31.4% and 68.7% across size classes and years, pointing to a more flexible diet composition in which naupliar stages of the calanoid copepods *C. finmarchicus* and *Pseudocalanus* spp., as well as early stages of the cyclopoid copepod *Oithona similis*, accounted for significant but variable proportions among years.

1.5.1 Larval redfish feeding preferences

There is increasing evidence that many fish species exhibit strong prey preference and selectivity during the larval stage (Robert et al., 2008). In selective species, larvae that feed successfully on preferred prey are characterized by faster growth, which increases their probability of survival (Robert et al., 2009; Sponaugle et al., 2010; Murphy et al., 2013). Various potential consumable prey taxa occur within a given zooplankton assemblage, but in order to optimize growth and survival, larvae should preferentially feed on taxa that are abundant, easily captured, and provide the highest net gain of energy and essential nutrients (Schoener, 1971; Werner and Hall, 1974). Carbon content of zooplankton prey typically increases with prey size following an allometric relationship, making it advantageous for larvae to prey upon the largest consumable prey taxa. As larvae grow, sensory system capabilities (visual, mechanical, chemoreception, etc.) develop and/or improve, swimming abilities strengthen, and mouth gape width increases; these developmental changes increase prey detection capabilities, prey encounter rate, and potential consumable prey size range, respectively (Hunter, 1981). Well-developed, late-stage larvae are, in theory, better suited for effectively foraging on large, motile prey taxa within the environment relative to their less-developed, first-feeding conspecifics.

Within the GSL region, larvae of several fish species exhibit a quick shift in preferred prey size from small to large taxa during early larval development. Within the size range of redfish larvae in the present study, larval striped bass inhabiting Eastern Canadian estuaries transition in feeding preference at the size of 10 mm from rotifers to the adult stage of the calanoid copepod *Eurytemora* spp. (Chesson's $\alpha = 0.9$) in coastal habitats (Robichaud-Leblanc et al., 1997); larval Atlantic cod shift feeding preferences at the size of 6 mm from *Pseudocalanus* spp. and *Calanus* spp. nauplii to adult stages of the same species (Chesson's $\alpha = 0.53$) (Robert et al., 2011); and larval Atlantic mackerel switch selectivity at the size of 7 mm from *Pseudocalanus* spp., *Oithona* spp. and *Temora* spp. nauplii to fish larvae (Chesson's $\alpha = 0.65$) and cladocerans (Chesson's $\alpha = 0.5$) (Robert et al., 2008; Paradis et al., 2012). Using mean lengths of zooplankton taxa reported by Robert et al. (2008) for Atlantic mackerel, mean preferred prey size increased from 0.19 mm (*Pseudocalanus* spp. nauplii) to 0.46 mm (cladocerans) and 3.30 mm (fish larvae), a 242% and 1,736% increase in preferred prey size by 7.0 mm Atlantic mackerel larvae relative to smaller size classes. Contrary to these species, larval redfish in the present study did not demonstrate an increase in mean prey size over a similar larval size range, nor did they exhibit increased preference or selectivity for larger taxa. The only occurrences of strong prey selectivity across the four annual cohorts concerned *C. finmarchicus* eggs, one of the smallest frequently consumed prey taxa, and the maximum Chesson's ɑ value of 0.45 in redfish larvae ≥ 8 mm in 1999 remains modest relative to selectivity of other species described so far in the GSL. Even though the strong annual variability in selectivity observed in this study may be partly attributable to the short sampling window within each year, our results for GSL redfish are in line with those reported by Anderson (1994) for recently-extruded Flemish Cap redfish, which showed high interannual variability in selection for copepod eggs, ranging from moderately positive to neutral.

The lack of strong trends in prey selectivity during early ontogeny of larval redfish is counter-intuitive given the similar developmental morphologies, and therefore apparent foraging capacities, among larval redfish, Atlantic mackerel and Atlantic cod. All three species are characterized by an anteriorly deep bodied shape with large mouth gape width relative to body length, and segmented guts. However, instead of showing increasing preference for larger prey along development as predicted by the optimal foraging theory, and as observed in mackerel and cod, the feeding strategy displayed by larval redfish appears closer to that of larval sandlance, *Ammodytes* spp., based on the prevalence of small egg prey (Demontigny et al., 2012). Sandlance are characterized by small mouth gape width relative to total body length, and a linear gut morphology. It is possible that, regardless of similar morphologies to larval fish species with strong foraging skills, young redfish larvae are ineffective predators of mobile prey. However, this is unlikely considering that diet composition of larvae < 7 mm in 1997 was dominated by *C. finmarchicus* and *Pseudocalanus* spp. naupliar stages *N*3-6. Instead, based on the combination of a constant diet composition through early ontogeny and relatively weak positive prey selectivity, we argue that eggs were frequently consumed because redfish larvae exhibit a more generalist feeding strategy relative to several other GSL species, and thus consume frequently occurring prey taxa in similar proportions relative to that in the surrounding environment.

1.5.2 Revisiting the redfish—*Calanus* reliance

Based on the massive contribution of *C. finmarchicus* egg biomass to diet of the 1989 larval redfish cohort, Runge and de Lafontaine (1996) hypothesized that a strong, "provocative" link existed between larval redfish survival and the abundance and reproductive timing of *C. finmarchicus* in the GSL. Our results support this hypothesis to a certain extent. We have shown that larval redfish did not systematically exhibit strong preference for *C. finmarchicus* eggs across size classes and years, and that diet composition was characterized by relatively high interannual variability. However, our results also indicate that copepod eggs dominated the ingested prey biomass in all collection years, albeit not in the large proportions reported by Runge and de Lafontaine (1996). Even though we observed important differences in the diet composition between the 1997-2000 and the 1989 year classes, we consider, based their general dominance in the proportion by prey numbers and by carbon ingested, that *C. finmarchicus* eggs should be considered as a key prey taxon for larval redfish feeding success, growth and survival.

There are several potential advantages for redfish larvae to consume copepod eggs instead of other potential prey in the environment. A large proportion (69.1%) of the eggs identified in larval guts in the present study were partially digested. Unlike many marine fish species, *Sebastes* spp. demonstrate the ability to digest copepod eggs during the larval stage (Bainbridge and McKay, 1986; Runge and de Lafontaine, 1996; Mitsuzawa et al., 2017, this study). It is possible that there is less competition within the GSL for copepod eggs relative to other frequently consumed prey taxa, such as calanoid copepod nauplii, which presents an open feeding niche for larval redfish to occupy. In addition, eggs are highly concentrated with energy and essential nutrients and require less foraging and capture effort than mobile prey. *C. finmarchicus* eggs contain, on average, greater amounts of carbon per unit of volume than abundant naupliar stages of other species that are characterized by similar sizes (e.g. *Oithona* spp. and *Pseudocalanus* spp. nauplii), and even taxa of larger sizes (e.g. *O. similis* copepodites). Most importantly, copepod eggs contain up to 2 orders of magnitude more essential fatty acids than later copepod life stages of similar sizes (Fuiman et al., 2015). Essential fatty acids, such as docosapentaenoic acid (DHA; 22:6 *n-3*) and eicosapentaenoic acid (EPA; 20:5 *n-3*), must be consumed since they cannot be biosynthesized in the body in physiologically relevant quantities. These essential fatty acids are crucial for proper larval fish growth and survival, especially in cold water species (Sargent, 1997). Runge and de Lafontaine (1996) discussed the role of primary producers in the development and reproductive season of *C. finmarchicus*. Primary producers such as diatoms, some dinoflagellate species, and some heterotrophic flagellates synthesize essential fatty acids, so that the composition and abundance of primary producer communities can alter the concentrations of fatty acids available within an ecosystem, as well as reproductive viability of adult *C. finmarchicus* (Starr et al., 1999). Variability in phytoplankton community composition can influence the timing and rate of egg production, as well as egg fatty acid composition and concentration, all of which directly affect egg consumers (Hirche and Kattner, 1993). Additionally, we cannot overlook the potential direct energy and essential fatty acid contributions from primary producers to the larval diet via consumption. There is a possibility that we were unable to identify some primary producers, as well as small, soft-bodied protozoa, through visual identification of prey items found in the guts due to rapid digestion of these prey, and long-term formalin preservation (Montagnes et al., 2010). This multi-trophic level connection places emphasis on the importance of primary productivity and bottom-up processes within the pelagic ecosystem for the survival of many commercially-important fisheries species that rely on early *Calanus* spp. stages, such as GSL Atlantic redfish.

Environmental conditions in the GSL that control primary productivity and secondary productivity differed between the Runge and de Lafontaine (1996) study performed in 1989 and the 1997-2000 collection years examined in the present study, and these conditions continue to shift as of 2020. The GSL underwent an environmental regime shift during 1997, where surface and deep-water temperatures increased, and winter sea ice area and duration decreased relative to pre-1997 (Plourde et al. 2014). While an earlier sea ice retreat often leads to an earlier onset of peak primary productivity un sub-arctic regions (i.e. Brosset et al., 2019), these physical oceanographic changes in the GSL also corresponded with an earlier timing of the spring cohort abundance peak and decreased mean prosome length of *C. finmarchicus* (Plourde et al., 2014). Warmer surface waters are associated with increased abundance of small calanoid copepods such as *Pseudocalanus* spp.*,* whereas the abundance of large calanoid copepods such as *C. finmarchicus* is negatively associated with surface and deep-water temperatures (Blais et al. 2019). Even though total copepod abundance has remained relatively stable following the regime shift, the increasing dominance of small copepod species in the GSL has resulted in a marked decrease in total available copepod biomass. Since the early 2010s, the trend of increasing surface and deep-water temperature has accelerated, accentuating the ecological shift affecting *C. finmarchicus* reproductive phenology (earlier reproductive seasons) and abundance (decreasing) (Blais et al., 2019, Galbraith et al., 2019, Sorochan et al., 2019). Given that the period 2011-2013 generated strong redfish, specifically *S. mentella*, recruitment events, while *C. finmarchicus* abundance was low relative to previous decades, we hypothesize that the reproductive phenology of *C. finmarchicus* could be more important than its absolute abundance for the feeding success of larval redfish. The early reproduction of *C. finmarchicus* may increase the duration of temporal overlap with larval redfish extrusion in the GSL, optimizing redfish growth and survival, as predicted by the Match-Mismatch Hypothesis (Cushing, 1975). Moreover, the larval diet composition of redfish is primarily composed of small zooplankton taxa, therefore the shift in copepod communities from large to small species observed in recent years may constitute a foraging advantage for larval redfish.

1.6 CONCLUSIONS

Results from the present study providing the first multi-year assessment of larval redfish diet composition lay the initial groundwork for the further identification of potential bottom-up recruitment drivers for this species in the Gulf of St. Lawrence redfish. We showed strong evidence that eggs of the calanoid copepod *Calanus finmarchicus* constitute the main component of larval redfish diet composition in the GSL. Variability in abundance and reproductive phenology in this key copepod, linked to the ongoing warming of surface and deep water temperatures within the system, should be considered in future investigations of larval redfish growth and survival potential.

1.7 ACKNOWLEDGEMENTS

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1.8 FUNDING

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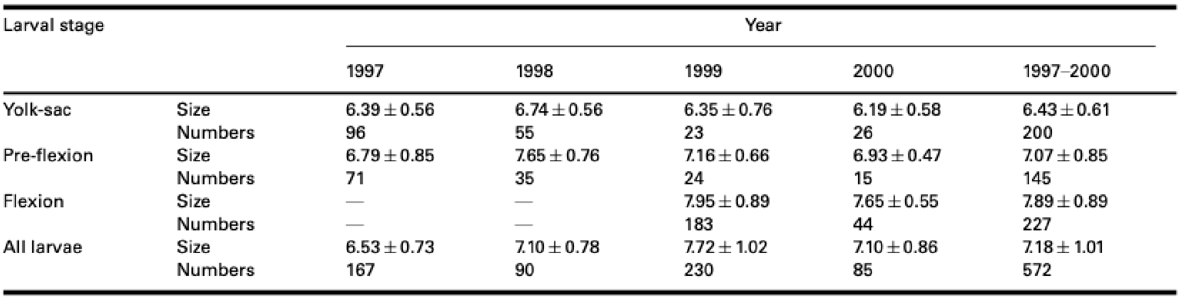
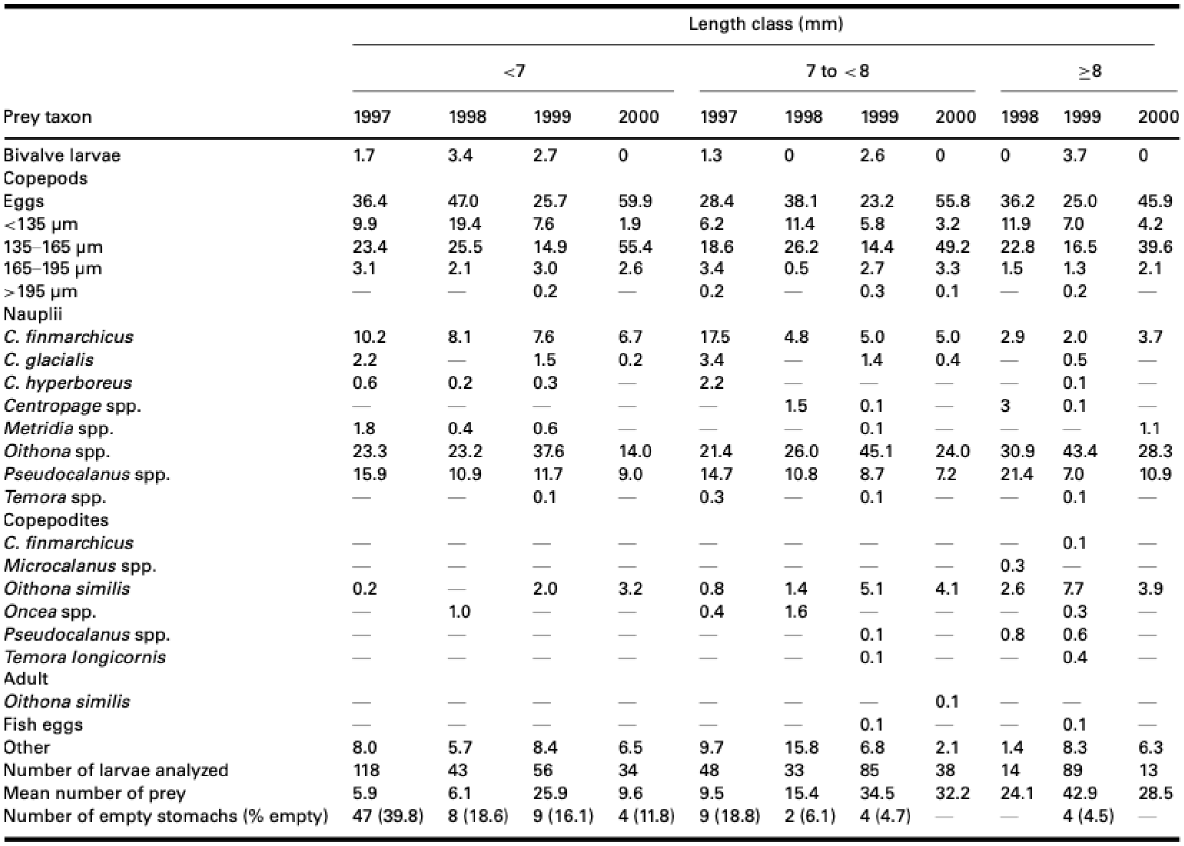
1.9 TABLES



Larval stage		Year				
		1997	1998	1999	2000	1997–2000
Yolk-sac	Size	6.39 ± 0.56	6.74 ± 0.56	6.35 ± 0.76	6.19 ± 0.58	6.43 ± 0.61
	Numbers	96	55	23	26	200
Pre-flexion	Size	6.79 ± 0.85	7.65 ± 0.76	7.16 ± 0.66	6.93 ± 0.47	7.07 ± 0.85
	Numbers	71	35	24	15	145
Flexion	Size	—	—	7.95 ± 0.89	7.65 ± 0.55	7.89 ± 0.89
	Numbers	—	—	183	44	227
All larvae	Size	6.53 ± 0.73	7.10 ± 0.78	7.72 ± 1.02	7.10 ± 0.86	7.18 ± 1.01
	Numbers	167	90	230	85	572

Tableau 1. Size (SL) and number of larvae per developmental stage used for each year in the present study. The measure of error represents the standard deviation on SL.

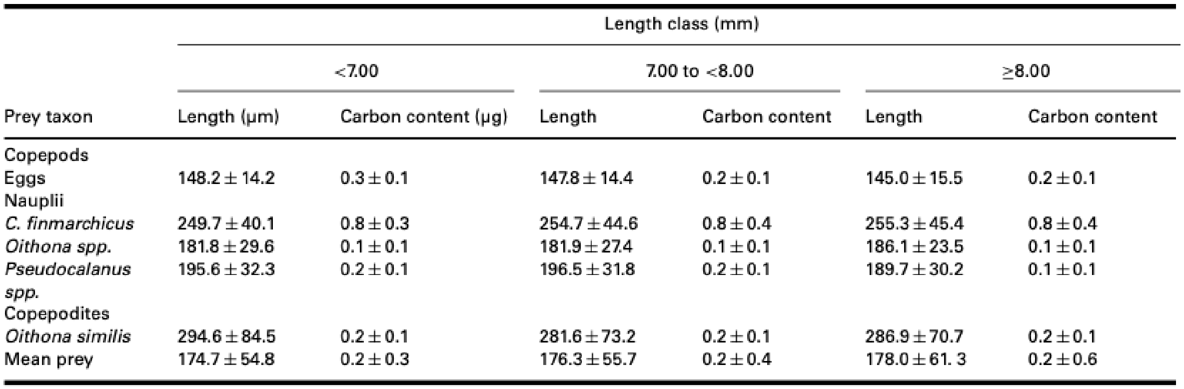


	Length class (mm)										
	<7				7 to <8				≥8		
Prey taxon	1997	1998	1999	2000	1997	1998	1999	2000	1998	1999	2000
Bivalve larvae	1.7	3.4	2.7	0	1.3	0	2.6	0	0	3.7	0
Copepods											
Eggs	36.4	47.0	25.7	59.9	28.4	38.1	23.2	55.8	36.2	25.0	45.9
<135 μm	9.9	19.4	7.6	1.9	6.2	11.4	5.8	3.2	11.9	7.0	4.2
135–165 μm	23.4	25.5	14.9	55.4	18.6	26.2	14.4	49.2	22.8	16.5	39.6
165–195 μm	3.1	2.1	3.0	2.6	3.4	0.5	2.7	3.3	1.5	1.3	2.1
>195 μm	—	—	0.2	—	0.2	—	0.3	0.1	—	0.2	—
Nauplii											
C. finmarchicus	10.2	8.1	7.6	6.7	17.5	4.8	5.0	5.0	2.9	2.0	3.7
C. glacialis	2.2	—	1.5	0.2	3.4	—	1.4	0.4	—	0.5	—
C. hyperboreus	0.6	0.2	0.3	—	2.2	—	—	—	—	0.1	—
Centropage spp.	—	—	—	—	—	1.5	0.1	—	3	0.1	—
Metridia spp.	1.8	0.4	0.6	—	—	—	0.1	—	—	—	1.1
Oithona spp.	23.3	23.2	37.6	14.0	21.4	26.0	45.1	24.0	30.9	43.4	28.3
Pseudocalanus spp.	15.9	10.9	11.7	9.0	14.7	10.8	8.7	7.2	21.4	7.0	10.9
Temora spp.	—	—	0.1	—	0.3	—	0.1	—	—	0.1	—
Copepodites											
C. finmarchicus	—	—	—	—	—	—	—	—	—	0.1	—
Microcalanus spp.	—	—	—	—	—	—	—	—	0.3	—	—
Oithona similis	0.2	—	2.0	3.2	0.8	1.4	5.1	4.1	2.6	7.7	3.9
Oncea spp.	—	1.0	—	—	0.4	1.6	—	—	—	0.3	—
Pseudocalanus spp.	—	—	—	—	—	—	0.1	—	0.8	0.6	—
Temora longicornis	—	—	—	—	—	—	0.1	—	—	0.4	—
Adult											
Oithona similis	—	—	—	—	—	—	—	0.1	—	—	—
Fish eggs	—	—	—	—	—	—	0.1	—	—	0.1	—
Other	8.0	5.7	8.4	6.5	9.7	15.8	6.8	2.1	1.4	8.3	6.3
Number of larvae analyzed	118	43	56	34	48	33	85	38	14	89	13
Mean number of prey	5.9	6.1	25.9	9.6	9.5	15.4	34.5	32.2	24.1	42.9	28.5
Number of empty stomachs (% empty)	47 (39.8)	8 (18.6)	9 (16.1)	4 (11.8)	9 (18.8)	2 (6.1)	4 (4.7)	—	—	4 (4.5)	—

Tableau 2. Diet composition by length classes and year of redfish larvae expressed as the percent contribution in numbers of the different prey taxa.

	Length class (mm)										
	<7				7 to <8				≥8		
Prey taxon	1997	1998	1999	2000	1997	1998	1999	2000	1998	1999	2000
Bivalve larvae	1.6	3.5	3.1	—	0.5	—	2	—	—	3.0	—
Copepods											
Eggs	39.1	51.0	32.5	68.7	31.4	49.7	34.7	62.4	43.2	35.0	55.6
<135 μm	9.3	17.9	7.1	1.2	5.1	11.2	5.5	2.4	9.0	6.3	2.9
135–165 μm	24.2	29.3	18.6	63.4	21.4	37.5	23.1	54.9	31.1	25.1	48.4
165–195 μm	5.6	3.8	6.2	4.1	4.6	1.0	5.3	5.0	3.1	2.4	4.3
>195 μm	—	—	0.6	—	0.3	—	0.8	0.1	—	1.2	—
Nauplii											
C. finmarchicus	19.5	17.4	21.1	12.3	34.2	13.3	14.7	15.5	10.6	8.1	12.7
C. glacialis	4.7	—	5.4	1.1	9.6	—	4.6	2.0	—	2.6	—
C. hyperboreus	0.6	1.6	1.6	0	4.4	—	0.2	—	—	0.5	—
Centropage spp.	—	—	—	—	—	1.7	—	—	2.8	0.1	—
Metridia spp.	1.4	0.2	0.7	—	0.6	—	0.1	—	—	—	1.8
Oithona spp.	16.1	17.7	19.6	5.7	8.8	21.1	24.8	9.9	20.4	26.6	18.4
Pseudocalanus spp.	16.9	8.2	9.3	6.9	9.3	11.2	7.1	5.3	20.0	6.8	7.9
Temora spp.	—	—	0.1	—	0.6	—	0.3	—	—	0.1	—
Copepodites											
C. finmarchicus	—	—	—	—	—	—	—	—	—	1.1	—
Microcalanus spp.	—	—	—	—	—	—	—	—	0.1	—	—
Oithona similis	0.1	—	1.9	2.7	0.4	1.5	5.9	3.8	2.3	10.4	3.6
Oncea spp.	—	0.5	—	—	0.4	1.4	—	—	—	0.4	—
Pseudocalanus spp.	—	—	—	—	—	—	0.1	—	0.5	1.8	—
Temora longicornis	—	—	—	—	—	—	0.3	—	—	1.2	—
Adult											
Oithona similis	—	—	—	—	—	—	—	0.2	—	—	—
Fish eggs	—	—	0.7	—	—	—	1.6	—	—	0.6	—
Number of larvae analyzed	69	35	47	29	39	28	80	38	14	86	13
Mean C ingested (μg)	1.4	1.4	5.2	2.5	3.5	3.1	6.6	7.3	3.9	7.4	6.0

Tableau 3. Diet composition by length classes and year of redfish larvae expressed as the percent contribution in carbon of the different prey taxa.



	Length class (mm)					
	<7.00		7.00 to <8.00		≥8.00	
Prey taxon	Length (μm)	Carbon content (μg)	Length	Carbon content	Length	Carbon content
Copepods						
Eggs	148.2 ± 14.2	0.3 ± 0.1	147.8 ± 14.4	0.2 ± 0.1	145.0 ± 15.5	0.2 ± 0.1
Nauplii						
C. finmarchicus	249.7 ± 40.1	0.8 ± 0.3	254.7 ± 44.6	0.8 ± 0.4	255.3 ± 45.4	0.8 ± 0.4
Oithona spp.	181.8 ± 29.6	0.1 ± 0.1	181.9 ± 27.4	0.1 ± 0.1	186.1 ± 23.5	0.1 ± 0.1
Pseudocalanus spp.	195.6 ± 32.3	0.2 ± 0.1	196.5 ± 31.8	0.2 ± 0.1	189.7 ± 30.2	0.1 ± 0.1
Copepodites						
Oithona similis	294.6 ± 84.5	0.2 ± 0.1	281.6 ± 73.2	0.2 ± 0.1	286.9 ± 70.7	0.2 ± 0.1
Mean prey	174.7 ± 54.8	0.2 ± 0.3	176.3 ± 55.7	0.2 ± 0.4	178.0 ± 61. 3	0.2 ± 0.6

Tableau 4. Mean size and carbon content for each prey taxa, and overall mean prey size and carbon content, of prey consumed within each larval size class averaged across all collection years.

1.10 FIGURES

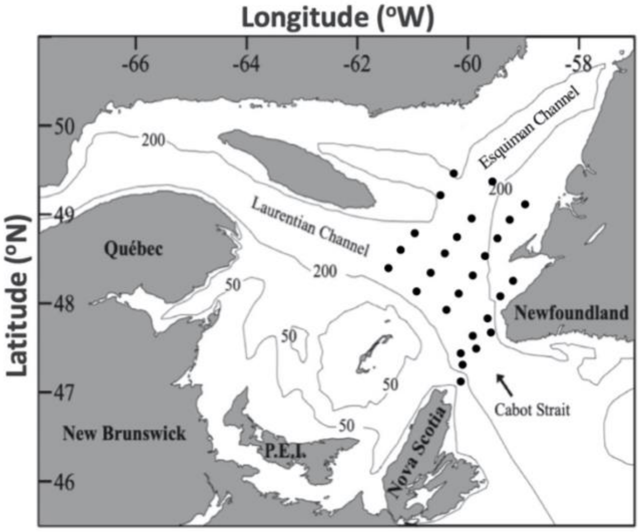


Figure 1. Map of 27 fixed sampling stations where ichthyoplankton and zooplankton samples were collected in 1997-2000.

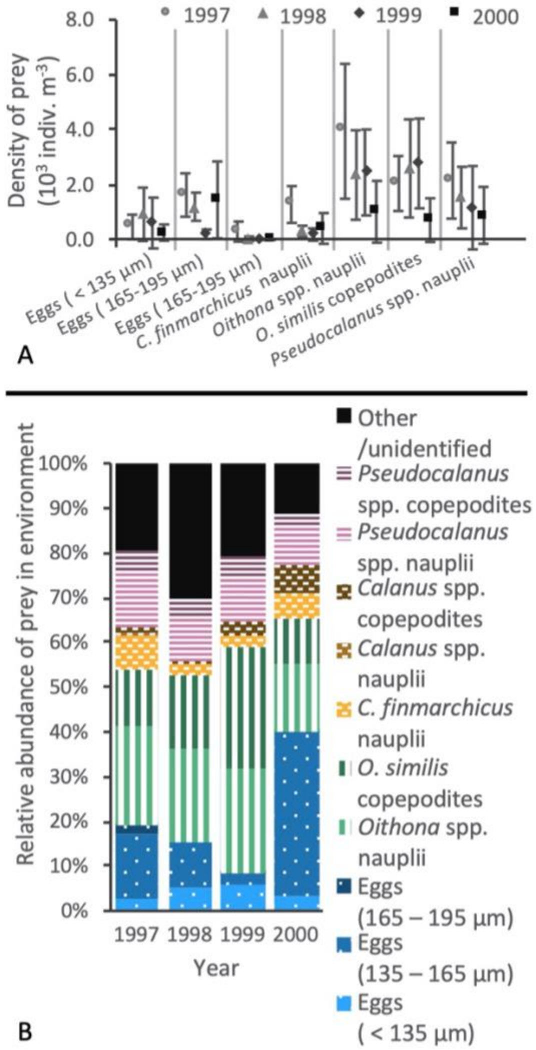


Figure 2. A. Densities (± SD) of frequently consumed prey taxa at collection stations for each year. B. Mean proportions of common prey field taxa in the environment by prey number across collection years.

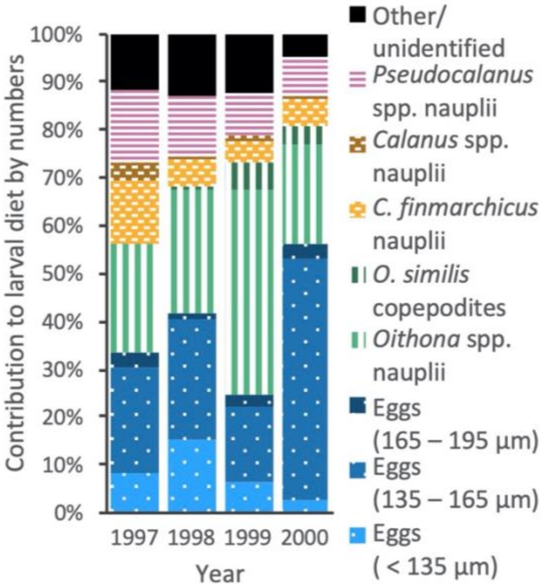


Figure 3. Mean percent contribution of prey taxa in larval diet by number across collection years.

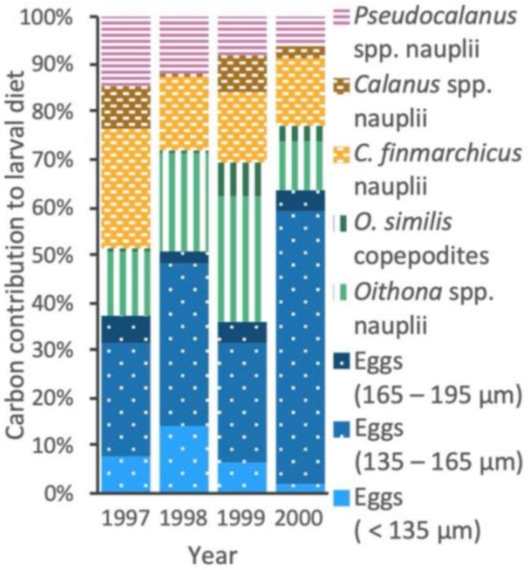


Figure 4. Mean percent of carbon contribution by prey taxa to larval diet across collection years.

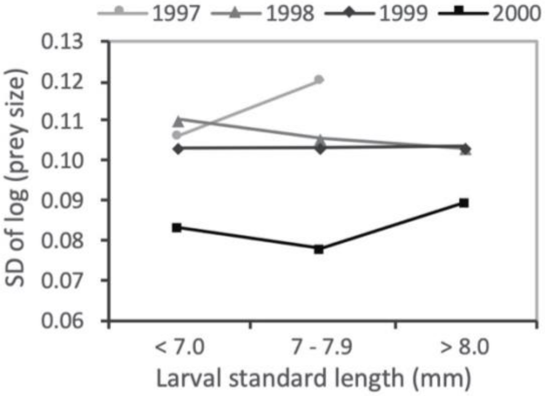


Figure 5. Diet niche breadth, measured as the SD of log-transformed prey size averaged across all larvae within the same size class (x-axis) in a collection year. There is no change in diet niche breadth throughout early development.

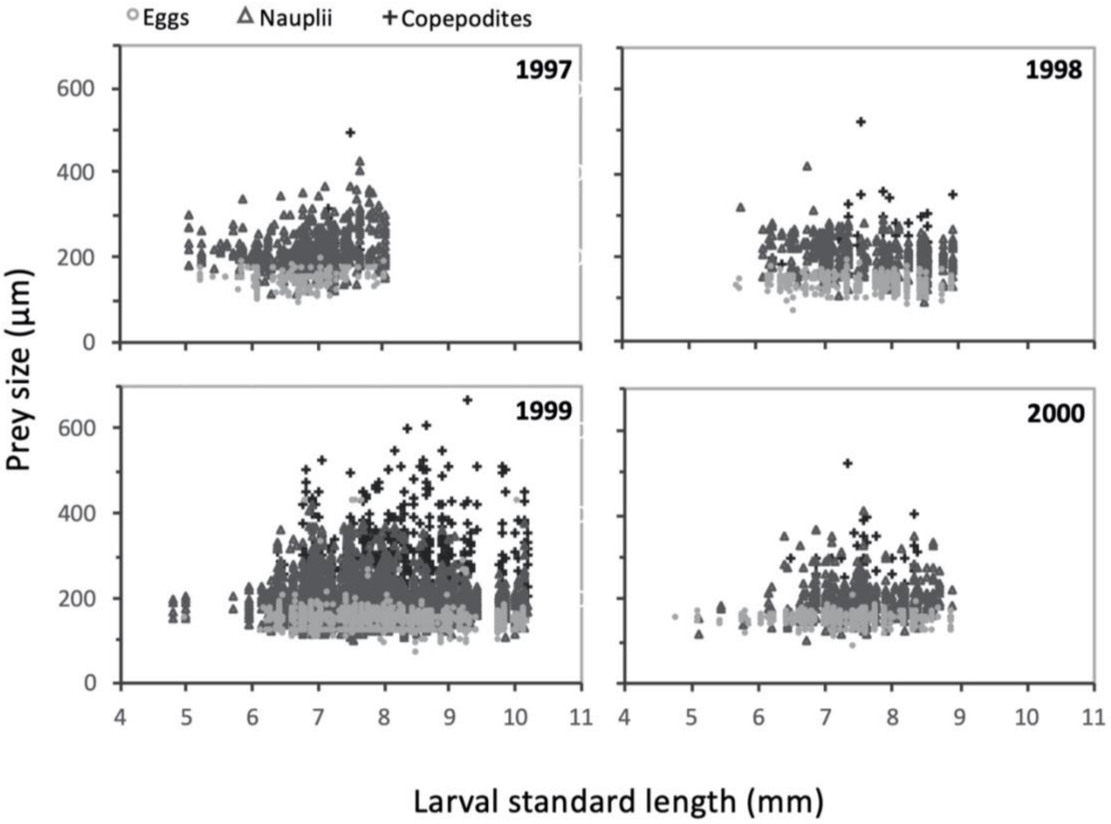


Figure 6. Size and developmental stage of prey consumed by individual larvae by year. Light grey circles represent copepod eggs, medium grey triangles represent copepod nauplii, and dark grey crosses represent copepodites. Copepod eggs are consumed throughout each of the early development sizes collected for this study.

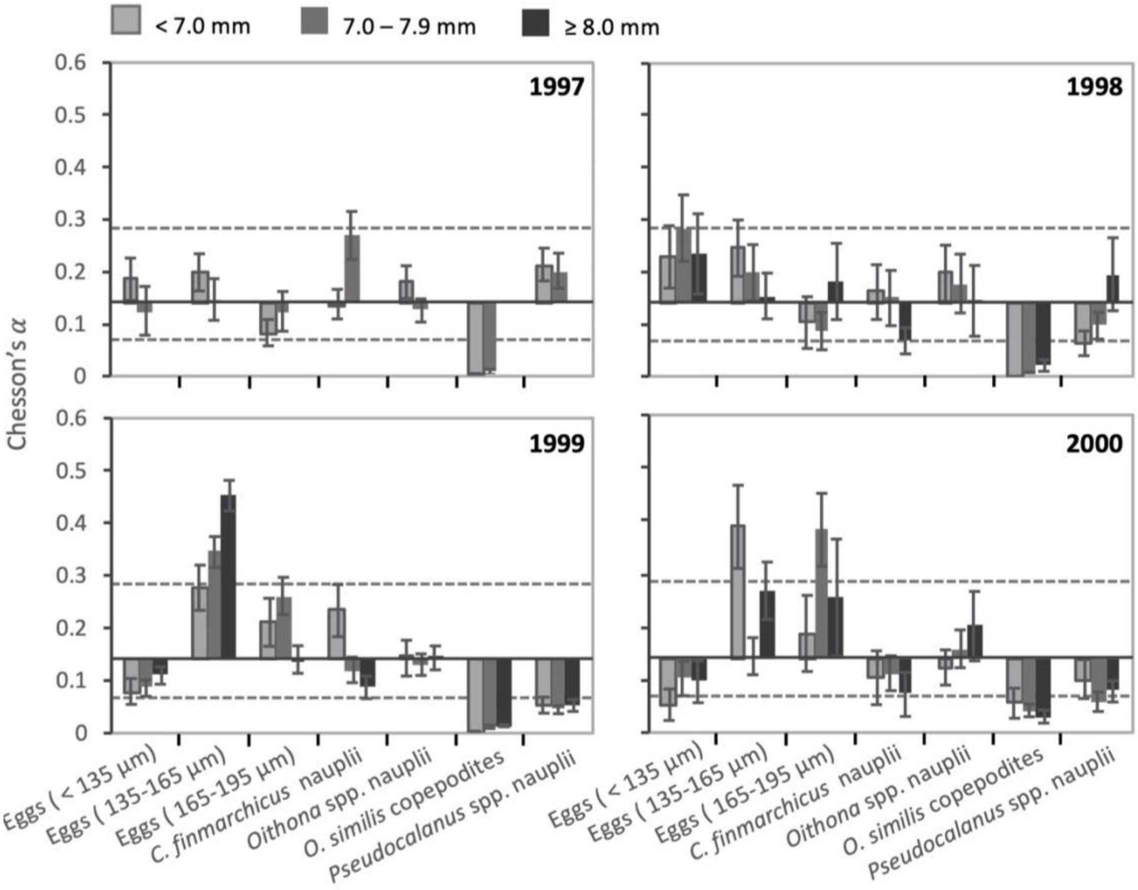


Figure 7. Chesson's alpha-selectivity indices (± SE) for the 7 most frequently consumed prey taxa in the larval redfish diet across the 3 larval size classes (< 7.00 mm, 7.00 – 7.99 mm, and ≥ 8.00 mm) : A – Copepod eggs < 135 µm, B – Copepod eggs 135 – 165 µm, C – Copepod eggs 165 – 195 µm, D – *C. finmarchicus* nauplii, E – *Oithona* spp. nauplii, F – *O. similis* copepodites, G – *Pseudocalanus* spp. nauplii. The neutral alpha value, 0.1428 (1/7), has been subtracted from the mean alpha values so a Chesson's alpha value of 0 is complete neutral selection, positive values represent positive selection, and negative values represent negative selection. In 1997, only 1 larva was ≥ 8.00 mm, therefore Chesson's alpha for this size class was not calculated.

CHAPITRE 2

REVELER LA RELATION ENTRE L'ALIMENTATION ET LA CROISSANCE DES LARVES DE SEBASTE (*SEBASTES* SP.) DANS LE GOLFE DU SAINT-LAURENT

2.1 RESUME EN FRANÇAIS

La force des classes d'âge des stocks de poissons est souvent établie lors du stade larvaire, une croissance rapide étant un facteur favorable menant à un fort recrutement. Après 30 ans de faible recrutement, le sébaste (*Sebastes* sp.) du golfe du Saint-Laurent (GSL) a produit des classes d'âge sans précédent en 2011-2013. La relation entre le régime alimentaire des larves et la croissance qui a potentiellement conduit à ces forts événements de recrutement est inconnue. Le contenu stomacal et la microstructure des otolithes de larves de sébaste capturées dans le GSL en 1999 et 2000 ont été analysés afin de comprendre la relation entre le succès alimentaire et la croissance récente des larves de sébaste et d'identifier les comportements alimentaires associés à une croissance rapide. La croissance était positivement corrélée avec la profondeur du corps des larves, qui a été utilisée comme proxy morphologique pour la croissance. Le type et la taille des proies étaient les meilleures variables explicatives de la profondeur corporelle des larves après la première alimentation obligatoire. Les larves qui consommaient de grands stades nauplii de taxons de copépodes fréquemment consommés avaient un corps plus profond et se développaient plus rapidement que les larves qui consommaient la proie préférée du sébaste, les œufs de *Calanus finmarchicus*. Le réchauffement des eaux du GSL a modifié la phénologie des taxons de proies couramment consommés plus tôt dans la saison, ce qui peut augmenter le chevauchement entre les sébastes et les proies nauplii qui favorisent une croissance rapide, la survie, et potentiellement le succès du recrutement.

Cet article a été accepté pour publication dans sa version finale en octobre 2021 par les éditeurs du *ICES Journal of Marine Science*. En tant que première autrice, j'ai effectué la majorité de la collecte des données, des analyses statistiques, de l'interprétation des résultats et de la rédaction du manuscrit. Le deuxième auteur, Pierre Pepin, a aidé à l'exécution des analyses statistiques et l'interprétation des résultats. Le quatrième auteur, Guillaume Veillet, a participé aux dissections en laboratoire et à la collecte et aux analyses préliminaires des données. Les auteurs Pierre Pepin, Stéphane Plourde, Pascal Sirois et Dominique Robert ont tous contribué aux interprétations biologiques et écologiques de ces résultats. Tous les auteurs ont participé à la révision de l'article. Cet article a été présenté virtuellement au *1st Virtual Larval Fish Town Hall* (juin 2020), à *l'American Fisheries Society Virtual Meeting* (septembre 2020), à la *Réunion Annuelle de Ressources Aquatiques Québec* (novembre 2020) et à *Avenir Maritime* (juin 2021).

2.1.1 Summary in English

Year-class strength of fish stocks is often set during the larval stage, with fast growth being a favorable factor leading to strong recruitment. Following 30 years of poor recruitment, redfish (*Sebastes* sp. in the Gulf of St. Lawrence (GSL) produced unprecedentedly strong year classes in 2011-2013. The relationship between larval diet and growth that potentially drove these successful recruitment events is unknown. Gut content and otolith microstructure of redfish larvae collected from the GSL in 1999 and 2000 were analyzed in order to understand the relationship between recent feeding success and growth in larval redfish and identify feeding behaviors that are associated with fast growth. Growth was positively correlated with larval body depth, which was used as a morphological proxy for growth. Prey type and size were the best explanatory variables of larval body depth after obligatory first-feeding. Larvae that consumed large naupliar stages of frequently consumed copepod taxa were deeper-bodied and grew more quickly than larvae that consumed redfish's preferred prey, *Calanus finmarchicus* eggs. Warming GSL waters have shifted the phenology of commonly consumed prey taxa earlier in the season, which may increase the overlap between redfish and naupliar prey that drive fast growth, survival, and potentially recruitment success.

This article titled “Revealing the relationship between feeding and growth of larval redfish (*Sebastes* sp.) in the Gulf of St. Lawrence” was accepted for publication in its final version in October 2021 by the editors of *ICES Journal of Marine Science*. As first author, I performed a majority of the data collection, statistical analyses, interpretation of results, and writing of the manuscript. Second author, Pierre Pepin, assisted in the execution of statistical analyses and interpretation of results. Fourth author, Guillaume Veillet, assisted in laboratory dissections and preliminary data collection and analyses. Authors Pierre Pepin, Stéphane Plourde, Pascal Sirois, and Dominique Robert all contributed to the biological and ecological interpretations of these results. All authors participated in the revision of the article. This article was presented virtually at the *1st Virtual Larval Fish Town Hall* (June 2020), the *American Fisheries Society Virtual Meeting* (September 2020), the *Réunion Annuelle of Ressources Aquatiques Québec* (November 2020), and *Avenir Maritime* (June 2021).

2.2 INTRODUCTION

The fine-scale understanding of recruitment variability in commercially-exploited fish stocks has continued to evade fisheries scientists since Hjort's (1914) early hypotheses on potential sources of variability in North Sea fish populations. It is generally accepted that year-class strength of a stock is set during the first year of life, a period which encompasses the larval and early juvenile stages (Leggett and DeBlois 1994). Variability in year-class strength is attributable to small interannual variations in mortality rates during these early life stages, which frequently result in 10 to 100-fold differences in the number of individuals recruited into the fishery (Pepin 2016). The Growth-Mortality hypothesis (Anderson 1988) states that the probability of a larva's survival to recruitment is positively correlated with its growth rate through the larval stage, which is explained by three complementary mechanisms: the 'bigger-is-better' mechanism predicts that at a given age, larger individuals are vulnerable to a lower number of gape-limited ichthyoplankton predators relative to their smaller counterparts (e.g. Bailey and Houde 1989); the 'stage duration' mechanism proposes that, by metamorphosing at a younger age, fast-growing larvae take advantage of a shorter period of high pre-metamorphosis predation mortality (e.g. Chambers and Leggett 1987); and the 'growth-selective predation' mechanism stipulates that at a given size, younger, fast-growing individuals present a better physiological condition linked to an enhanced capacity to escape a predator (e.g. Takasuka et al. 2003, 2004). Based on this conceptual framework, interannual variability in individual larval growth rates constitutes an important determinant of year-class strength.

A larva's ability to feed successfully is a primary pillar of its growth performance (Werner and Gilliam 1984, Fortier and Harris 1989, Leggett and Deblois 1994, Sysoeva 2000). Feeding success, often defined as the amount of prey carbon consumed, is generally considered a key determinant of somatic growth. Beyond total carbon ingested, a proxy for energy intake, feeding success is also modulated by the capacity of ingested prey taxa to provide the suite of essential nutrients, such as amino acids and fatty acids, that are necessary for proper larval development (Rønnestad et al. 1999; Sargent et al. 1999). The larval prey field is composed of various taxa characterized by differences in potential to fulfill requirements relative to energy and essential nutrient intake, which likely explains why several larval fish species have been shown to selectively consume prey taxa that result in their optimal growth (Robert et al. 2009, Sponaugle et al. 2010, Murphy et al. 2013). These considerations make it important to identify larval fish prey to the lowest taxonomic resolution possible.

A common measure of short-term larval feeding success is derived through gut content analysis, which represents the last few hours of feeding prior to capture (Llopiz and Cowen 2008). Longer-term feeding success indices can also be derived through larval morphometrics. For example, the ratio of larval body depth to standard length or age, constitutes a mid-term feeding success index often used as a proxy for condition (Ferron and Leggett 1994). Given the positive relationship between feeding success and growth, measuring the width of daily otolith increments can also provide an estimate of the history of feeding success achieved over the entire life of individuals (Pepin et al. 2001; Dower et al. 2009). Because these various indices rely on different measurements and represent different time scales, few previous studies have looked into the relationships linking them in the same individual larvae (but see Pepin et al. 2015). However, detailed knowledge of the links among short- to longer-term feeding indices and growth is needed to refine our understanding of processes driving recruitment variability in commercially-exploited species.

Redfish (*Sebastes* sp.) are long-lived, ovoviviparous species distributed throughout the North Atlantic. In the Gulf of St. Lawrence (GSL), strong recruitment events in 2011-2013 after 30 years of low productivity have led to the recovery of the deepwater redfish *Sebastes mentella*. The specific mechanisms driving variability in larval growth, survival, and year-class strength for this species remain unknown. In addition, the uncommon ovoviviparous reproductive strategy of redfish likely results in different patterns of early life growth and potential critical periods relative to what is previously described in the literature about more commonly researched, oviparous fishes (e.g. Pepin et al. 2015). Previous studies on GSL larval redfish diet composition and prey selectivity have clearly highlighted the prevalence, preference, and hypothesized importance, of the eggs of the calanoid copepod *Calanus finmarchicus* as a primary food source during the early and mid-larval stage (Runge and de Lafontaine 1996; Burns et al. 2020). However, the level of benefit of *C. finmarchicus* egg consumption for larval redfish growth remains to be tested.

The objective of the present study is to describe the roles of diet composition and feeding success on growth of recently extruded redfish larvae. The daily growth trajectory of larval redfish was estimated based on the otolith microstructure, and a recent otolith growth index was compared to indices of feeding success based on gut content and body depth at age. We hypothesize that the measures of recent daily larval growth and body depth at age were positively related to the amount of carbon contributed to gut content by the redfish's preferred prey, *C. finmarchicus* eggs. An understanding of the linkage between the larval redfish diet and growth performance will facilitate the robust investigation of the role of environmental drivers on redfish recruitment dynamics.

2.3 METHODS

2.3.1 Sampling area

Redfish larvae were collected in an area of the Gulf of St. Lawrence spanning the junction of the Laurentian and Esquiman channels, known for being the primary larval extrusion area (Figure 8). Details on collection methods were provided in Burns et al. (2020). Briefly, ichthyoplankton were collected over a grid of 27 stations using a bongo net sampler between June 12 and June 17 during the years 1997 to 2000. At 11 stations sampled in 1999 and 2000, larval fish were preserved in a 95% ethanol solution to preserve otoliths, making them available for the present study. Zooplankton samples were collected concurrently at each sampling station and preserved in a 4% formalin-seawater solution to identify and quantify prey field at the time of larval capture. Depth, water volume filtered, and GPS coordinates were measured for each tow at each location.

2.3.2 Laboratory analyses

In the laboratory, larval fish collections were sorted and identified to the lowest taxonomical level possible. In redfish, there are no morphological differences between *S. mentella* and *S. fasciatus* larvae, so larvae were identified as *Sebastes* sp. However, the narrow temporal window of larval collection specifically targeted *S. mentella* (Sévigny et al. 2000), which we assume make up the bulk of *Sebastes* sp. larvae captured in the present study. Individual larvae were photographed under a stereoscopic microscope at 16× magnification and measured for standard length (SL) and body depth at anus (BD) to the nearest 0.1 mm using Olympus cellSens software. SL was measured from the tip of the snout to the end of the notochord; BD was measured as a perpendicular line from the dorsal edge of the notochord down to the anus.

The hindgut and foregut from each larva were dissected at 120× magnification and individual consumed prey were photographed, prey length was measured to the nearest 0.1 µm and identified to the lowest taxonomic level using methods previously described in Burns et al. (2020) following GSL copepod identification guides assembled for internal use by the Department of Fisheries and Oceans Canada. Carbon content of each prey item was calculated using carbon-length relationship equations from the literature for each prey taxa (Table I in Robert et al. 2008) and allowed for comparison of redfish feeding success relative to other diet studies (ie. Robert et al. 2008, Pepin et al. 2015). Larvae with empty guts were excluded from statistical analyses. Feeding success (total carbon consumed) was calculated for each individual larva.

Both left and right sagittal otoliths were extracted under a stereoscopic microscope and fixed to a slide using Crystalbond 509 thermoplastic cement. When necessary, otoliths were polished using 3 µm metallurgical lapping film for adequate reading. Photographs of otoliths were taken under an Olympus BX50 oil immersion microscope at 1000× magnification. Previous work has confirmed the absence of differences in microstructure between left and right sagittal otoliths in *S. mentella* (Penney and Evans 1985), therefore the best otolith photo from each individual larva, regardless of side, was used for otolith readings (Penney and Evans 1985). Otolith microstructure was measured using the ObjectJ plugin in ImageJ software. Daily increment banding is often not clear around the entirety of the otolith, therefore a measurement axis was placed by the reader from the center of the otolith to the outer edge of the otolith in a section where banding was the most clear from the center to the edge of the otolith (Penney and Evans 1985). Four types of measurements were recorded for each otolith along the measurement axis: focal radius (radius of otolith at extrusion), total otolith radius, number of daily post-extrusion increments, and widths of each daily post-extrusion increment.

2.3.3 Statistical analyses

Autocorrelation among daily increment widths was calculated in order to determine growth patterns of newly-extruded redfish larvae. Pearson’s r-correlation coefficients were calculated between the first 5 daily increments and the next 5 daily increments using all otoliths analyzed.

Standardized growth was calculated for each increment for each larva along a z-score distribution. To do so, mean increment width for each increment number (proxy for age) was calculated and divided by the standard deviation of the increment widths. A z-score was assigned to each larva for the width of each increment. Positive z-scores represent wider-than-average increment widths, and therefore faster growth than the average, and vice versa. Recent standardized growth was calculated for larvae ≥ 4 days post-extrusion by averaging the standardized growth z-scores for the last 3 days of life before capture. Early life standardized growth was calculated for all larvae by averaging the standardized growth z-scores for the first 3 days post-extrusion.

We relied on non-parametric local density estimation to calculate individual age-dependent scores for SL, BD and carbon consumed (Davison and Hinkley 1997) (Figure. 9A-C). Application of this approach to the description of larval state with age has been detailed by Pepin et al. (1999) and successfully implemented in various studies (Dower et al. 2009; Robert et al. 2014b; Pepin et al. 2015). Briefly, observed measurements for a given variable (e.g. SL, BD or carbon consumed) were used to create a distribution kernel at each larval age (i.e. daily increment). Based on these kernels, we created a cumulative frequency distribution for each variable at each age, ranging from 0 to 1, on which each individual's measured variable was assigned a "score" that reflects the relative rank of that individuals for the appropriate age group. Each analysis was optimized for bandwidth and kernel size. These scores allow for comparison of larval performance amongst individuals of different larval ages. Non-parametric analysis allows for results that are not forced or overfitting the data, as in parametric linear modelling. Local density estimation was calculated in R (V. 3.6.2) using program *ogmap* (Hammill and Evans 2015). All data used for this project can be requested from the corresponding author.

2.4 RESULTS

2.4.1 Larval redfish characteristics

A total of 242 redfish larvae were collected over the two years: 83 larvae from 4 stations in 1999 and 159 larvae from 8 stations in 2000. Only 3 larvae had empty digestive tracts. Larvae averaged 8.21 mm ± 0.74 (SD) in length, 1.07 mm ± 0.19 in body depth, and were aged 6.4 days ± 3.8 post-extrusion (Figure 10A, B). The youngest larva was 1 day post-extrusion, and the oldest larvae were 19 days post-extrusion. Over half (59.7%) of the larvae were 5 days post-extrusion or younger, with the largest percentage of all larvae being 3 post-days post-extrusion (16.9%) (Figure 10B).

Over the two years, redfish larvae consumed an average of 23.5 prey ± 18.0, which corresponded to 5.8 μg ± 4.4 of carbon. Average prey size consumed was 178.2 μm ± 53.1. By prey number, the largest proportion of the larval diet was comprised of eggs from the calanoid copepod, *C. finmarchicus*, which represented 37.6% of the larval diet in both of the years combined (Figure 11). The second largest contributor to the larval diet by prey number was nauplii of the cyclopoid copepod *Oithona* spp. (26.8%), followed by nauplii of *C. finmarchicus* (11.9%) and nauplii of the calanoid copepod *Pseudocalanus* spp. (10.2%). The largest contributor of carbon to the larval diet was *C. finmarchicus* eggs (39.1%), followed by *C. finmarchicus* nauplii (28.1%), *Oithona* spp. nauplii, and *Pseudocalanus* spp. nauplii (7.3%). When combined, *C. finmarchicus* eggs and nauplii contributed the majority of the total carbon (67.2%) to the larval redfish diet. Approximately half of the carbon in the larval redfish diet was contributed by copepod eggs of all sizes (47.8%), and the other half (52.2%) was contributed by mobile prey, defined as the naupliar and copepodite stages of several copepod species.

2.4.2 Otolith microstructure and growth autocorrelation

Average otolith radius at extrusion was 19.05 ± 1.95 μm, but varied widely from 12.92 to 24.38 μm. Amongst all larvae, average daily increment width was 0.66 ± 0.14 μm. There was strong age-dependent autocorrelation between daily increment widths in young larval redfish (Figure 12). Day-to-day growth of recently-extruded (ages 1 to 10 days post-extrusion) was variably influenced by the larva's growth history. Daily growth autocorrelation was strongest (r = 0.5-0.6) during the first 3-4 days post-extrusion, and gradually decreased as larval age and forward lag increased.

2.4.3 Recent growth in relation to standard length and body depth

Standardized recent growth was calculated for all larvae 4 days post-extrusion and older (*n* = 181). Positive significant relationships were found between standardized recent growth and larval body depth-at-age [P(BD|age)] (r = 0.304, $p < 0.001$) (Figure 13A) and standard length-at-age [P(SL|age)] (r = 0.207, $p = 0.005$) (Figure 13B). Correlations strengthened with increasing larval age for P(BD|age) (young larvae: *n* = 108, r = 0.170, $p = 0.079$; old larvae: *n* = 73, r = 0.516, $p < 0.001$) and P(SL|age) (young larvae: r = 0.195, $p = 0.043$; old larvae: r = 0.227, $p = 0.053$ NS). Given that relationships were stronger with P(BD|age) amongst larvae of all ages, we retained P(BD|age) as a proxy for recent growth of newly-extruded redfish larvae.

2.4.4 Recent growth, carbon ingested and prey size in relation to body depth-at-age

All larvae (*n* = 242) were used to calculate relationships between larval morphometrics and diet. There was a significant, positive relationship between P(BD|age) and total carbon consumed [P(C|age)] at age (r = 0.331, $p < 0.001$) (Figure 14). When splitting larvae by age groups, a significant, stronger positive relationship was observed between P(BD|age) and P(C|age) in young larvae < 8 d post extrusion (*n* = 169, r = 0.391, $p < 0.00001$), but no significant relationship persisted in older ≥ 8 d post extrusion larvae (*n* = 73, r = 0.175, $p = 0.139$). A positive, significant relationship was also observed between average prey size ingested-at-age [P(prey size|age)] and P(BD|age) (r = 0.281, $p < 0.00001$) (Figure 15). This relationship was positive and significant for each of the two larval age groups, but stronger in older ≥ 8 d post extrusion larvae (r = 0.504, $p < 0.00001$) than in young < 8 d post extrusion larvae (r = 0.184, $p = 0.017$).

The total carbon consumed for each larva was sorted into carbon source based on prey taxa and developmental stage. Copepod eggs of all sizes were grouped together in an ‘eggs’ group, and naupliar and copepodite stages of copepods were grouped together as a ‘mobile prey’ group. A positive, significant relationship was found between the percentile score of mobile prey carbon consumed-at-age [P(mobile carbon|age)] and that of body depth-at-age P(BD|age) (r = 0.365, $p < 0.00001$) (Figure 16A). This relationship was positive and significant for both larval age groups (larvae < 8 d post extrusion: r = 0.437, $p < 0.00001$; larvae ≥ 8 d post extrusion: r = 0.393, $p = 0.0005$). There was no significant relationship between the percentile score of egg prey carbon consumed-at-age [(P(egg carbon|age)] and P(BD|age) when considering all larvae or larvae < 8 d post extrusion. However, there was a significant, negative relationship between P(egg carbon|age) and P(BD|age) in ≥ 8 d post extrusion larvae (r = -0.238, $p = 0.042$) (Figure 16B).

Early and recent standardized growth z-scores were ranked from 1-73 for all larvae ≥ 8 days post-extrusion to investigate whether diet composition or feeding success of older larvae was the reason for the weakening daily growth autocorrelation around 8 days post-extrusion. There was no relationship between the change in growth ranking and P(C|age) (r = 0.041, $p = 0.731$), P(eggs|age) (r = -0.031, $p = 0.795$), or P(mobile|age) (r = 0.120, $p = 0.312$).

2.5 DISCUSSION

According to the Growth-Mortality hypothesis, if larval fish grow quickly under favorable conditions, then more individuals survive through the critical larval stage and are recruited into the fishery (Anderson 1988). Feeding provides larvae with energy and nutrients that fuel their growth. While it is known that feeding is a limiting factor of larval fish growth (Werner and Gilliam 1984, Fortier and Harris 1989, Leggett and Deblois 1994), the nature of the effects of both the quantity and the quality of food consumed on larval growth has remained elusive given that proxies for feeding success (gut content) and growth (otolith daily increments) correspond to different time scales (Pepin et al., 2015). After 30 years of poor recruitment, deepwater redfish are currently rebounding in the GSL following three successful year classes in 2011-2013. These strong year classes likely correspond to high larval survival fueled by fast growth, but the drivers of growth remain unknown. Previous work by Burns et al. (2020) revealed that larval redfish are relatively generalist feeders, with a diet composed of multiple prey taxa. The most frequently consumed prey taxon by numbers and carbon contribution to the diet was *C. finmarchicus* eggs, a small, immobile, lipid-rich food. In some years, larval redfish demonstrated a feeding preference for *C. finmarchicus* eggs. Based on these results, and those of Runge and de Lafontaine (1996), we hypothesized that larvae that consumed more carbon from *C. finmarchicus* eggs would grow more quickly than larvae that consumed other, non-preferred prey taxa. However, results from the present study showed that individual larvae, especially older individuals that consumed higher amounts of carbon from *C. finmarchicus* eggs, were generally characterized by slower growth during their last 3 days of life relative to those that consumed copepod nauplii. This constitutes a rare observation where the preferred prey taxon, as determined by an electivity index, was not linked with the fastest larval growth rates.

2.5.1 Identification of a critical period using autocorrelation

High autocorrelation in otolith microstructure indicates that larvae that grow quickly continue to grow quickly over time, and larvae that grow slowly continue to grow slowly, whereas low autocorrelation signifies that daily growth rates that are less predictable from past growth history. Growth autocorrelation serves to identify critical periods of growth where individuals become set in a growth trajectory during early larval development (Pepin et al. 2015). In general, fast-growing species such as Atlantic mackerel, bluehead wrasse (*Thalassoma bifasciatum*), and radiated shanny (*Ulvaria subbifurcata*), are characterized by a highly autocorrelated growth trajectory and a strong growth-feeding success relationship. An early, post-hatching critical period was identified for these species, in which larvae must begin to feed successfully or otherwise become entrained in a slow growth trajectory and likely perish (Pepin et al. 2015). Conversely, slower-growing species like Atlantic cod (*Gadus morhua*), Arctic cod (*Arctogadus glacialis*), and yellow perch (*Perca flavescens)* demonstrate low growth autocorrelation, as well as a weak relationship between feeding success and growth (Pepin et al. 2015). Slow-growing species are less likely to have critical feeding periods during the early larval stage as hypothesized by Hjort (1914), because early growth is likely driven primarily by the abiotic environment. Shortbelly rockfish (*Sebastes jordani*), a species from the Pacific Ocean closely related to *S. mentella*, demonstrates different phases in the similarity of daily larval growth rates depending on developmental stage (i.e. fast growth after first-feeding, slow growth during flexion, metamorphosis) (Laidig et al. 1991; Moser and Boehlert 1991). Our autocorrelation analyses revealed that newly-extruded larval redfish demonstrated autocorrelation strengths and patterns most similar to those of Atlantic cod and yellow perch: moderately-strong autocorrelation values (r ~ 0.6) that gradually weakened with increasing larval age and forward lag among daily increments. However, daily autocorrelation values decreased more quickly in redfish larvae than Atlantic cod or yellow perch, indicative of a change in the drivers of growth rates.

The strong autocorrelation values during the first few days post-extrusion are likely driven by residual maternal effects via metabolism of the remaining yolk and/or oil globule. Although larval redfish are extruded well-developed relative to newly-hatched larvae from other marine fish species, many individuals are extruded with remaining endogenous nutrient supplies (Burns et al. 2020). Starved redfish larvae have been shown to survive for 10-14 days after extrusion, suggesting that obligatory exogenous feeding occurs between 1.5 and 2 weeks post-extrusion. (Laurel et al. 2001). Our results suggest that in the field, early larval redfish growth is driven by absorption of the yolk and oil globule until approximately 8 days post-extrusion, when the endogenous supply of nutrients has been depleted and daily growth is no longer strongly influenced by growth immediately following extrusion. Failure to successfully feed exogenously after yolk absorption would result in an increase in mortality due to starvation and predation. A large mortality event following the onset of obligate exogenous feeding after larvae reach 8 days post-extrusion is within the time frame proposed by Anderson (1984) in Flemish Cap redfish, for which an early post-extrusion bottlenecking event explained the massive decrease in larval abundance observed during the first 2 months post-extrusion. These results support our hypothesis of a critical period during the transition from endogenous to exogenous feeding, as suggested by the rapid shift in growth autocorrelation patterns. Future studies should investigate the effects of warming water temperatures on the timing of obligate exogenous feeding, and thus the timing of the critical period, as warmer waters would increase larval metabolic rate and decrease the amount of time larvae are able to survive only on maternally-invested nutrients. While our findings suggest the likelihood of differences in growth drivers before and after the transition to obligatory exogenous feeding, our results show that differences in feeding success and diet composition were not the cause of decreasing growth autocorrelation strength in larval redfish. This suggests that prey capture success at the onset of exogenous feeding was not the main factor driving the decrease in daily growth autocorrelation, or at least that prey capture success has not had sufficient time to impact an individual's rank in terms of growth performance relative to conspecifics.

Otolith increment width autocorrelation was weakest in larvae older than 8 days post-extrusion. Weak autocorrelation values found in the slower-growing species has been interpreted as an element supporting that feeding success is not a strong driver of growth (Pepin et al. 2015). Due to the young ages of larvae in the present study, we were unable to expand the growth autocorrelation analysis to older ages characterized by increased values of forward lag. We can conclude from our analysis that growth in larvae older than 8 days post-extrusion is not related to growth in the first few days following the extrusion event. We cannot conclude, because of limited numbers of older larvae, whether or not individuals become entrained in a growth trajectory following the onset of obligatory exogenous feeding around 8 days post-extrusion. It is possible that autocorrelation values may remain low as larvae age, implying that feeding success does not strongly influence redfish growth at older ages, or, that autocorrelation values may strengthen with increasing age, signifying an importance of successful feeding after yolk absorption. Our results demonstrated a significant relationship between P(mobile prey|age) and P(body depth|age) which suggest that the feeding success of larval redfish on copepod naupliiar stages may play a larger role than the literature would indicate in the growth of older redfish larvae.

2.5.2 The feeding success-growth relationship

In a multi-species meta-analysis, larvae that consumed more carbon were longer in length than conspecifics of the same age (Pepin et al. 2015). While the strength of this relationship was variable among species, these results demonstrated the expected positive link between recent feeding success and growth in fish larvae. According to the Optimal Foraging Theory, is it advantageous for larvae to consume the largest available prey, as prey size is a proxy for carbon content, (Werner and Hall 1974). Our results show that larvae that consumed greater-on-average sizes of prey were deeper bodied, and therefore grew more quickly, than larvae of the same age that consumed smaller prey. This relationship strengthened with larval age, meaning that consuming prey of larger sizes became increasingly more beneficial for faster growth as larvae developed. We also found a positive, significant relationship between the percentile scores of larval body depth-at-age and carbon consumed-at-age when all larvae were pooled, regardless of age. However, this relationship was variable between younger and older age classes, suggesting (1) that young larvae (< 8 days post-extrusion) that consume exogenous carbon, but may not have fully depleted their endogenous nutrient reserves (Burns et al. 2020), show faster growth in terms of body depth relative to larvae of the same age that have not yet initiated exogenous feeding and (2) that the total amount of carbon consumed via the short-term estimates of larval diet may not be a good indicator of larval redfish growth after larvae have exhausted maternally invested nutrients. These results support the conclusions made by Pepin et al. (2015) that growth of relatively slow-growing species is not strongly linked to short-term estimates of feeding success, and that overall, feeding success may not be the best variable to explain differences in larval body depth throughout early development of redfish.

2.5.3 The role of preferred prey in driving growth rate

While relatively few studies have empirically demonstrated a relationship between feeding success and growth in larval fishes (Dower et al. 2009; Robert et al. 2014b; and Pepin et al. 2015), even fewer studies have investigated the relationship between growth and the contribution of preferred prey to feeding success (Robert et al. 2009; Sponaugle et al. 2010; Murphy et al. 2013). The paucity of knowledge of larval prey preferences from highly-resolved taxonomical information, and how this absence of data may be affecting our capacity to predict recruitment, has been increasingly acknowledged in recent years (St. John et al 2001; Robert et al. 2014a). A positive relationship between consumption of a larva's preferred prey and recent growth has been documented for fish species inhabiting various environments (Atlantic mackerel, Robert et al. 2009; Atlantic blue marlin [*Makaira nigricans*], Sponaugle et al. 2010; snapper [*Chrysophrys auratus*], Murphy et al. 2012). In both Atlantic mackerel and blue marlin, consumption of the preferred prey during early larval development, before the onset of piscivory, determined whether an individual would be characterized by fast or slow growth trajectory during the next stages of development (Robert et al. 2009, Sponaugle et al. 2010). In these previous studies, preferred prey taxa have systematically been mobile developmental stages of specific copepods. Based on the few studies that have identified these connections, it can be hypothesized that larvae preferentially consume certain prey taxa, not only based on size, that have the capacity to optimize growth potential and survival probabilities.

Burns et al. (2020) revisited the hypothesis made by Runge and de Lafontaine (1996) that there exists a strong link between the abundance and consumption of *C. finmarchicus* eggs, and the survival of redfish larvae in the GSL. During both 1999 and 2000, the same collection years sampled for this study, *C. finmarchicus* eggs were determined to be selected for by recently-extruded redfish larvae across early larval development (Burns et al. 2020), and we assumed that consumption of *C. finmarchicus* eggs would be linked to faster recent growth in redfish larvae. Redfish larvae examined for this study demonstrated similar diet composition to those larvae analyzed by Burns et al. (2020), with copepod eggs, specifically those from *C. finmarchicus*, contributing the bulk (~ 40-50%) of the carbon in the larval diet. However, the percentile score of carbon contributed from the diet by *C. finmarchicus* eggs was negatively correlated with the score of larval body depth-at-age in larvae older than 8 days post-extrusion, suggesting a growth disadvantage of a diet based on that prey item after the onset of obligatory exogenous feeding. Even though the absence of older individuals in our collections made it impossible to test whether this trend persisted through early ontogeny, our results suggest that the reliance of larval redfish feeding, growth and survival on *C. finmarchicus* eggs may be weaker than initially anticipated. To our knowledge, this is the first study which shows that larval diet based on a prey taxon that is selected for may result in slower growth than the average, and therefore in a lower probability of survival to recruitment. Conversely, there was a positive relationship between the score of carbon contributed to the diet by mobile prey taxa, including the nauplius stages of *C. finmarchicus*, *Pseudocalanus* spp., and *Oithona* spp., and larval body depth-at-age for larvae of all ages. Redfish larvae that consumed mobile prey were deeper bodied, and therefore achieved faster growth than larvae that consumed immobile prey, such as copepod eggs. Mobile prey represented about half of the diet composition (Figure 11), and among those, the naupliar stages of *C. finmarchicus* contributed >50% of the carbon contribution to diet (28.1% of the total carbon ingested). Combined to the positive link found between the percentile score of prey size-at-age and that of body depth-at-age, our results highlight the high importance of *C. finmarchicus* nauplii to condition, growth and potentially survival.

Overall, our results imply that individuals that showed generalist feeding including the consumption of copepod nauplii exhibited faster growth rates than those specialized on *C. finmarchicus* eggs. This finding forces us to ask the question: why would larval redfish demonstrate a preference for eggs if their consumption leads to suboptimal growth? Some potential benefits of consuming eggs were discussed by Burns et al. (2020): eggs are highly concentrated in nutrients such as lipids, redfish have the ability to digest them (e.g. Karamushko and Karamushko 1995), and they are immobile and thus less energetically costly to ingest. In addition, even though the diameter of the eggs is smaller than the average length of a *Oithona* spp. or *Pseudocalanus* spp. nauplius, one *C. finmarchicus* eggs contained, on average, 3× and 1.5× the amount of carbon than *Oithona* spp. nauplii and *Pseudocalanus* spp. nauplii, respectively. However, the efficiency of nutrient assimilation from copepod eggs into the larval redfish body is not known and our results suggest that it may be lower than anticipated. During the season of larval extrusion, copepod eggs are relatively abundant in the environment, comprising approximately 10-40% of the potential larval prey field (Burns et al. 2020). It is possible that larval redfish are both encountering these prey frequently, and capturing them with greater success relative to other prey because of their immobility. Our results support conclusions from Burns et al. (2020) and Runge and de Lafontaine (1996) that *C. finmarchicus* eggs are an important source of carbon, which likely protects larval redfish from starvation mortality. However, our results also demonstrate that consumption of eggs is associated with suboptimal growth, which in turn would lead to suboptimal survival according to the Growth-Survival Paradigm (Anderson 1988). Environmental conditions facilitating the spatiotemporal overlap between larval redfish extrusion and hatching of *C. finmarchicus*, rather than the spawning of *C. finmarchicus*, may be an important driver favoring high larval survival and subsequent recruitment.

2.5.4 Linking redfish recruitment to environmental conditions in the GSL

Redfish produce an average of less than one successful year class per decade, and the sporadic nature of these events makes identifying the drivers of recruitment difficult. It is likely that there are multiple environmental factors, both physical and biological, that must be met in order to generate successful redfish recruitment. The goal of this study was to gain knowledge on larval redfish biology that could be used to better target environmental recruitment drivers of larval redfish in the GSL. Our results suggest that nauplii of *C. finmarchicus* are an important dietary component for recently extruded redfish larvae, pointing to a potential key role of the spatio-temporal overlap between *C. finmarchicus* nauplii peak abundance and the first-feeding stage of redfish. When looking at the time series of *C. finmarchicus* abundance in the GSL, we note that the strong redfish year classes of

2011-2013 occurred during a period of average abundance and after a period of high positive anomaly in 2006-2008 (Blais et al. 2021). Therefore, interannual changes in the phenology of *C. finmarchicus* during early summer months may be more important than variability in abundance for determining the probability of larval redfish survival and subsequent recruitment in the GSL. In the GSL region, the phenology of *C. finmarchicus* is primarily correlated with the timing of spring warming, and to a lesser extent with the timing of the spring bloom (Lehoux et al. 2022).

The two year classes considered in our study (1999 and 2000) were characterized by low recruitment, which prevent us making direct inferences on factors determining the fate of a successful year class. The strong recruitment classes of the early 2010s, as well as the previous strong recruitment event in 1980-1981, were characterized by strong positive anomalies in temperature of the cold intermediate layer (CIL) and the deep layer of the GSL (Galbraith et al. 2021). With its seasonal ice cover and strong Arctic influence through the Labrador current, the GSL likely represents an environment nearing the cold thermal threshold of redfish. While little is known about how interannual variability in temperature affects the timing of redfish extrusion and the schedule of larval development, it is assumed that extrusion occurs within the deep layer of the GSL and larvae must travel through both the deep layer and CIL in order to reach surface waters where they feed and develop during the planktonic larval stage. Warming of these water masses may increase survival of redfish larvae immediately following extrusion. In addition, warming of the deep waters may influence the dynamics and phenology of key zooplankton prey taxa that are later consumed in surface waters. The GSL is rapidly warming due to global climate change and increased intrusion of the Gulf Stream in the deep layer, and this warming trend has accelerated over the past decade (Galbraith et al. 2021). The correspondence of previous strong year classes with particularly warm years suggests that the current warming trend in the surface, intermediate and deep layers of the GSL could lead to increasing recruitment success rate over the next decades. A further analysis of environmental data time series covering multiple climate regimes in the GSL region and spanning the previous strong recruitment events could help us identify the combination of abiotic and biotic variables promoting strong year classes of deepwater redfish in the GSL.

2.6 DATA

The data used for this article can be shared by request to the corresponding author.

2.7 ACKNOWLEDGEMENTS

The authors would like to thank L. Chénard (Université du Québec à Rimouski) for her contributions to the project with laboratory analyses.

2.8 FUNDING

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2.9 FIGURES

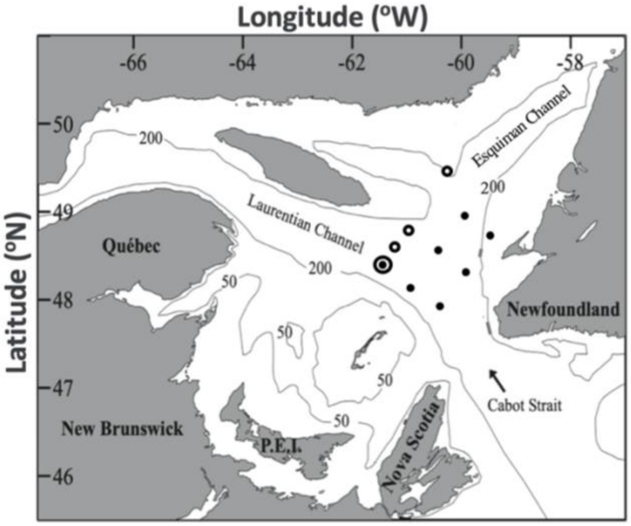

Figure 8. Map of ichthyoplankton and potential prey collection stations in the Gulf of St. Lawrence. Open circles designate collection stations in 1999; solid circles designate collection stations in 2000.

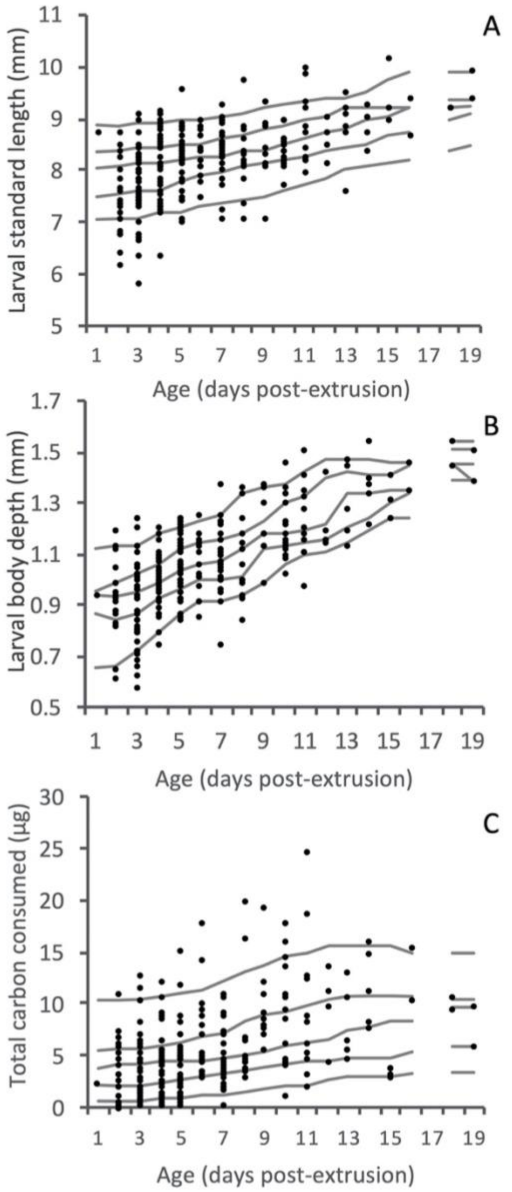

Figure 9. A) Standard length, B) Body depth, and C) Total carbon consumed in recent larval diet by larval age. Lines indicate the 10th, 30th, 50th, 70th, and 90th percentile measurements for each variable at each age as determined by nonparametric local density.

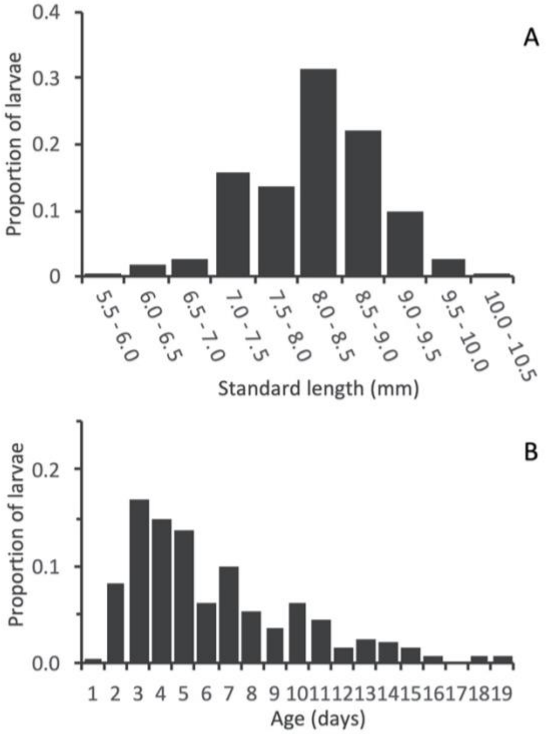

Figure 10. Frequency distribution of larvae used in this study by A.) age in days post-extrusion and B.) standard length.

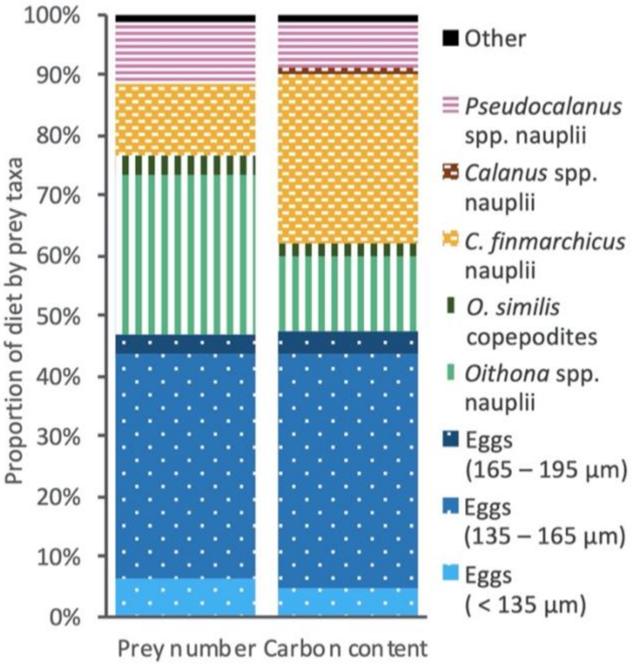

Figure 11. Proportions of commonly consumed prey taxa, by prey number and carbon content, comprising larval redfish diet in each year. Eggs (135-165 µm) represent eggs from the calanoid copepod, *Calanus finmarchicus*.

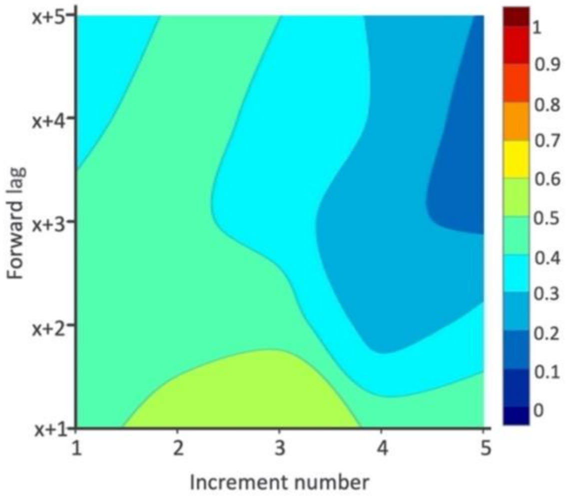

Figure 12. Autocorrelation of otolith increment widths. Increment number, homologous to larval age in days post-extrusion, on the x-axis, and forward lag, the number of increment widths in the future that the original increment number was correlated with, on the y-axis.

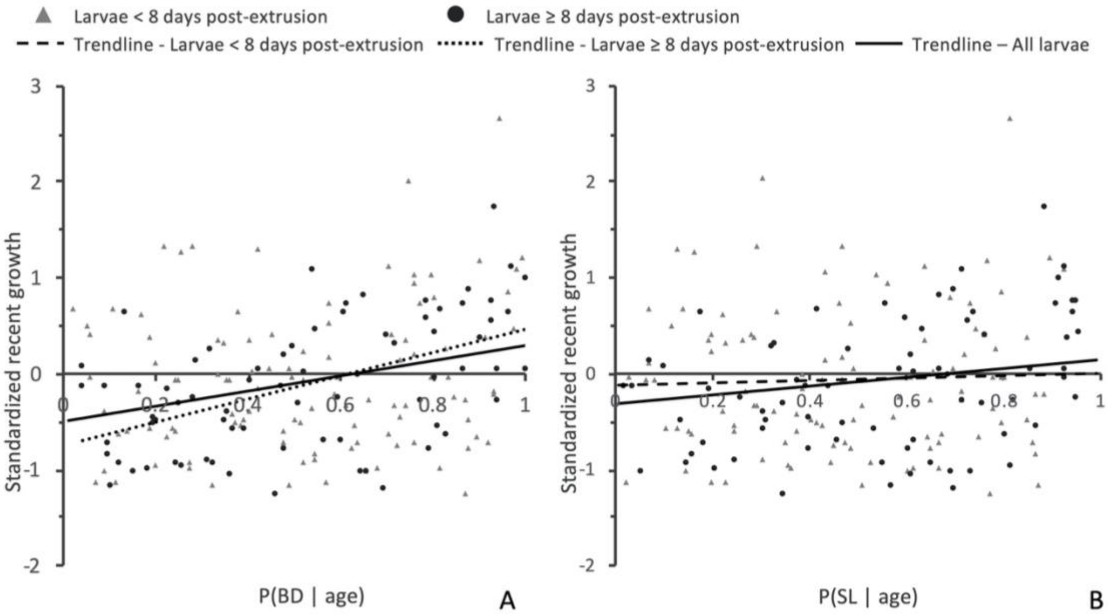

Figure 13.The relationship between standardized recent larval growth and A.) the percentile score of larval body depth-at-age B) the percentile score of larval standard length-at-age. Larval body depth was chosen as our morphological proxy for growth based on the stronger relationship with recent growth. Trendlines represent a significant correlation ($p < 0.05$) between variables.

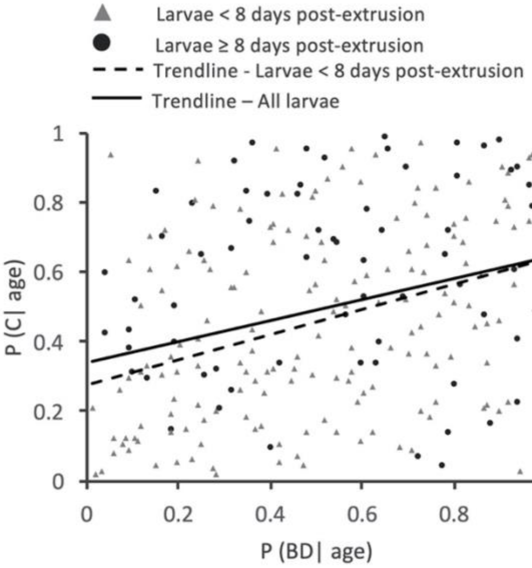

Figure 14. Relationship between total carbon consumed-at-age and larval body depth-at-age. Trendlines represent a significant correlation ($p < 0.05$) between the two variables.

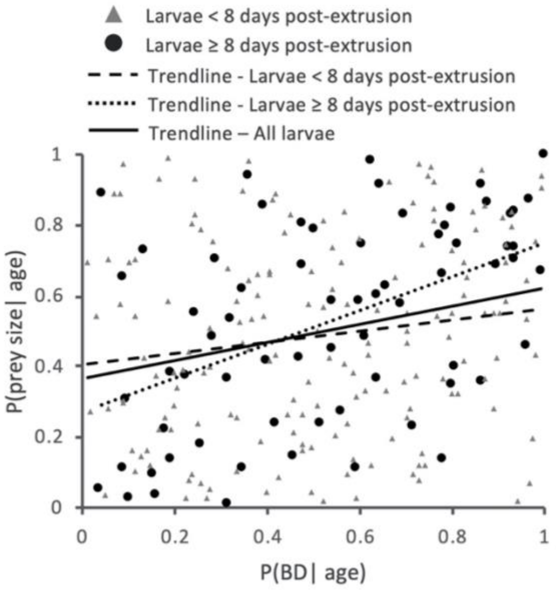

Figure 15. Relationship between average prey size recently consumed-at-age and larval body depth-at-age. Trendlines represent a significant correlation ($p < 0.05$) between the two variables.

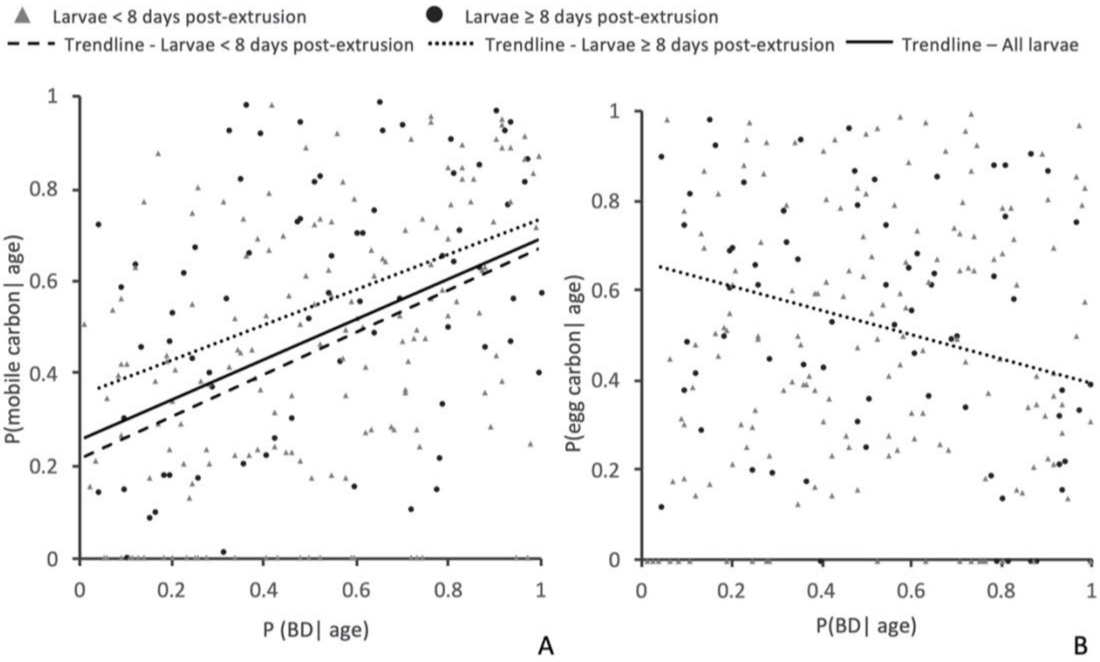

Figure 16. Relationship between larval body depth-at-age and sources of carbon from the larval diet: A.) mobile prey (naupliar and copepodite stages) B.) copepod eggs. Symbols represent the same groups of larvae as in Figure 13. Trendlines represent a significant correlation ($p < 0.05$) between the variables.

CHAPITRE 3

PREDIRE LA FORCE D’UNE CLASSE D’ÂGE CHEZ UN POISSON MARIN CARACTERISE PAR UN RECRUTEMENT SPASMODIQUE

3.1 RESUME EN FRANÇAIS

Depuis les travaux fondateurs de Hjort (1914) sur les processus de recrutement, les halieutes se sont appuyés sur ses hypothèses pour comprendre les moteurs du recrutement chez les espèces pêchées commercialement. L'utilisation de séries chronologiques riches, en données en conjonction avec des données détaillées sur les pêches, a permis aux chercheurs de mieux prédire les événements de recrutement par une meilleure compréhension des mécanismes qui interviennent dans la survie des larves de poissons pour de nombreuses espèces, et en identifiant les paramètres environnementaux importants. Cependant, les facteurs de variabilité du recrutement chez les stocks à recrutement spasmodique (SRS) restent un mystère en raison de la petite taille de l'échantillon d'événements de fort recrutement enregistrés et des conditions environnementales correspondantes, ce qui limite la capacité d'analyse statistique. L'objectif de cet article est d'identifier les moteurs environnementaux potentiels du recrutement dans un SRS, le sébaste (*Sebastes mentella*) du golfe du Saint-Laurent, Canada, en utilisant une approche fondée sur le poids de la preuve. Cette analyse a permis d'identifier 4 moteurs probables du recrutement du sébaste : le volume de la couche intermédiaire froide, l'abondance et la phénologie des proies préférées, et la biomasse du stock reproducteur. L'approche du poids de la preuve peut être utilisée comme méthode initiale pour identifier les moteurs environnementaux potentiels du recrutement dans le SRS. Ces moteurs peuvent être monitorés afin de mieux informer les évaluations des stocks sur les conditions environnementales favorables au recrutement et orienter les efforts de recherche pour mieux prédire les événements de recrutement dans le SRS.

Cet article intitulé « Prédiction de la force des classes d'âge chez un poisson marin caractérisé par un recrutement spasmodique » est en cours de préparation pour soumission au *ICES Journal of Marine Science*. En tant que première autrice, j'ai effectué la majorité de l'organisation des données, des analyses de données, de l'interprétation des résultats et de la rédaction du manuscrit. La troisième autrice, Caroline Lehoux, a été un atout essentiel dans l'extraction et l'organisation des données. Stéphane Plourde et Caroline Lehoux ont été d'importants contributeurs à la compréhension des tendances océanographiques et planctoniques à long terme. Les auteurs Stéphane Plourde, Pascal Sirois et Dominique Robert ont tous contribué aux interprétations biologiques et écologiques de ces résultats. Tous les auteurs participent à la révision de l'article. Cet article a été présenté en personne lors de la l'*American Fisheries Society Annual Meeting* à Spokane, Washington, États-Unis (août 2022) et de la *44th Annual Larval Fish Conference* à San Diego, Californie, États-Unis (août 2022).

3.1.1 Summary in English

Since Hjort’s (1914) seminal work on recruitment processes, fisheries scientists have built upon his hypotheses in order to understand drivers of recruitment in commercially-fished species. Using data-rich time series in conjunction with detailed fisheries data has allowed researchers to better predict recruitment events by understanding mechanisms that mediate larval fish survival for many species and identifying important environmental parameters. However, recruitment drivers in spasmodically-recruiting stocks (SRS) remain a mystery due to the small sample size of recorded strong recruitment events and their corresponding environmental conditions that limit statistical analysis capabilities. The objective of this paper is to identify potential environmental drivers of recruitment in an SRS, the redfish (*Sebastes mentella*) in the Gulf of St. Lawrence, Canada, using a weight-of-evidence approach. This analysis resulted in identification of 4 likely drivers of redfish recruitment: cold intermediate layer volume, preferred prey abundance and phenology, and spawning stock biomass. The weight-of-evidence approach can be used as an initial method to identify potential environmental drivers of recruitment in SRS. These drivers can be monitored to better inform stock assessments about environmental conditions favorable to recruitment and direct research efforts in order to better predict recruitment events in SRS.

This article titled « Prediction of year-class strength in a marine fish characterized by spasmodic recruitment » is being prepared for submission as a « Food for Thought » contribution to the *ICES Journal of Marine Science*. As first author, I performed a majority of the data organization, data analyses, interpretation of results, and writing of the manuscript. Third author, Caroline Lehoux, was a critical asset in data extraction and organization. Stéphane Plourde and Caroline Lehoux were important contributors in understanding of long-term oceanographic and planktonic trends. Authors Stéphane Plourde, Pascal Sirois, and Dominique Robert all contributed to the biological and ecological interpretations of these results. All authors are participating in revision of the article. This article was presented in person at the *American Fisheries Society Annual Meeting* in Spokane, Washington, USA (August 2022) and the *44rd Annual Larval Fish Conference* in San Diego, California, USA (August 2022).

3.2 INTRODUCTION

3.2.1 The ‘recruitment problem’

The scientific conundrum of understanding natural fluctuations in fish populations has plagued fishery scientists since the seminal work of Johan Hjort (1914, 1926), who proposed that year-to-year changes in herring populations were a result of differences in cohort-level mortality during the larval stage. Hjort’s Critical Period hypothesis stated that survival of larval fish and their recruitment to the fisheries was determined during the earliest period of the larval stage, at the onset of exogenous feeding, at which time larvae must find a sufficient amount of suitable prey to avoid starvation (Hjort 1914). The second of Hjort’s hypotheses, the Aberrant Drift hypothesis, stated that larvae must remain in a suitable habitat in order to survive and recruit within a given stock. Years during which environmental conditions are not suitable would result in poor recruitment (Hjort 1914).

Since this early work, many fishery scientists have relied on Hjort’s hypotheses as a framework for their own studies in an attempt to understand the underlying factors determining recruitment strength, and potentially predict its fluctuations in commercially-important fish species. Several of those studies based on Hjort’s original hypotheses have found strong ties among environmental variables, larval fish feeding and growth, and recruitment strength. These findings have evolved into the current Growth-Survival paradigm, which emphasizes the importance of high feeding success and fast growth as *sine qua non* conditions for high larval survival and recruitment (Anderson 1988, Cushing 1990). Fast-growing larvae are larger-at-age and show better condition-at-size than slower-growing conspecifics, and are thus less likely to be preyed upon by predators (Houde 1987, 2008, Takasuka et al. 2003, 2007). Fast-growers also reach a competent size for metamorphosis at an earlier age, which decreases the amount of time spent during the highly vulnerable pelagic larval stage (Chambers and Leggett 1987). The synthesis of results acquired to date demonstrates how both physical (e.g. temperature mediating metabolism [Portner et al. 2001; Sponaugle et al. 2006], water stratification [Jenkins et al. 2010]) and biological (e.g. prey abundance [Burrow et al. 2011; Brochier et al. 2013], prey quality [Robert et al. 2009, Sponaugle et al. 2010, Murphy et al. 2013]) environmental conditions can influence growth of larval fish and ultimately regulate year-class strength.

In addition to the influence of environmental effects, a relationship often exists between recruitment and spawning stock biomass (SSB) for the vast majority of stocks (Pepin 2016). In a recent meta-analysis based on data from the Ransom Myers Legacy Fishery Assessment Database (Ricard et al. 2012) comprising > 200 stocks, Pepin (2016) has demonstrated that mean recruitment is positively correlated to SSB, and that stocks characterized by higher variability in SSB tend to display higher variability in annual recruitment. In many cases, there is very limited data regarding recruitment success of stocks with very low SSB, which makes predicting future recruitment success using models very inaccurate and unreliable (Pepin 2016). In addition to SSB, the utilization of environmental variables in stock assessment models has the potential to improve the accuracy of these models.

Overall, even though predicting recruitment remains a formidable challenge (Houde 2008), our forecasting capacity has improved in recent decades with a better understanding of mechanisms regulating year-class strength. Detailed species-specific information on early life stage requirements has allowed assessing the role of environmental variability on recruitment. One of the key factors is the availability of preferred prey during the larval stage, which depends on the combination of prey production and its spatio-temporal overlap with the larvae (Anderson 1994, Robert et al. 2008, Voss et al. 2009, Murphy et al. 2012, Llopiz and Cowen 2014). The production and phenology of the different copepod prey are in turn strongly driven by temperature regimes, which also affect larval fish directly through changes in energy demand. The species-specific consideration of environmental variability, combined with state-of-the-art statistical models (e.g. Generalized Additive Models), explain a large portion of recruitment variability for an increasing number of stocks, including groundfish (e.g. Beaugrand et al. 2003; Brodziak and O'Brien 2005; Huebert et al. 2018) and forage fish (Plourde et al. 2015, Brosset et al. 2019, Brosset et al. 2020, Yu et al. 2020; Quattrocchi and Garofalo 2022).

3.2.2 The case of species characterized by spasmodic recruitment

Despite the progress made in understanding recruitment dynamics for various fish stocks, the identification of recruitment drivers in spasmodically-recruiting stocks (SRS) remains elusive. These species are characterized by exceptionally strong year classes, often preceded and followed by long periods (on the scale of decades) of weak recruitment (Caddy and Gulland 1983; Spencer and Collie 1997; Caddy and Agnew 2004; Licandeo et al. 2021). Recruitment indices resulting in these strong year classes can be three orders of magnitude higher than those associated with more frequent weak year classes. In these species, a stock-recruit relationship is typically non-existent. In addition, the low number of high recruitment events over multidecadal time series of stock dynamics and environmental variables generally prevents statistical models from identifying the environmental drivers of year-class strength.

3.2.3 Redfish in the Gulf of St. Lawrence

Redfish (*Sebastes* spp.), like all species within the genus *Sebastes*, is a classic example of a spasmodically-recruiting species in the Gulf of St. Lawrence (GSL), Canada. Multiple *Sebastes* species occur in the GSL (e.g. *S. mentella, S. fasciatus, S. marinus*), however the term "redfish" will be used to refer only to *S. mentella* throughout this chapter. An increase in fishing pressure on redfish following the collapse of the cod fishery in the early 1990s quickly depleted redfish biomass within the region, resulting in a moratorium in

1995. Even with the release of fishing pressure, the lack of a strong recruitment event since the early 1980s prevented stock biomass from replenishing through the early 2000s. After 30 years of weak recruitment, three times the average length of time between strong year classes, an unprecedentedly strong recruitment event was observed in 2011, quickly followed by a relatively strong recruitment event in 2013 (Licandeo et al. 2020). Individuals from these strong year classes are currently reaching the minimum size of exploitation, being recruited into the fishery, and the fishery is poised to reopen soon. Redfish presently comprise > 90% of the demersal biomass in the GSL (Senay et al. 2021). However, fishery managers now must deal with the challenge of implementing management plans to sustainably harvest a resource for which supply dynamics remains unknown.

For decades, fishery managers and scientists have cited knowledge gaps on recruitment dynamics as one of the most critical sources of uncertainty hampering our capacity to implement a sustainable redfish fishery in the long term (Lilly 1987, DFO 2010, DFO 2020, Licandeo et al. 2020, Senay et al. 2021, Cadigan et al. 2022). The occurrence of the historically-strong recruitment events of 2011 and 2013 provides an opportunity to delve into the environmental conditions in the GSL that potentially promoted high survival in the early life stages of these year classes. Prior to the 2010s, strong recruitment events occurred in the early 1970s and 1980s, with the latter supporting the fishery until its collapse in the early 1990s. While some environmental data were collected from the GSL during these periods, the capacity for environmental monitoring was low and gaps in the data are numerous. The rareness of strong year classes combined with a lack of reliable environment variables make it impossible to develop robust modeling approaches (e.g. Generalized Additive Model) for a quantitative statistical analysis with the goal of identifying drivers of recruitment for this species.

In the summer, the GSL is characterized by 3 water layers of distinct origins: the warm surface waters formed locally, the cold intermediate layer (CIL) partly originating from the Labrador current, and the relatively warm deep waters from the Atlantic Ocean. The temperature of each of these water layers is driven by separate processes: the surface layer is directly influenced by atmospheric temperature, the CIL by winter surface water temperature and the degree of water mixing in the spring, and the deep layer by the temperature of waters originating from the Gulf Stream entering the Laurentian Channel through Cabot Strait (Galbraith et al. 2021). Adult redfish are demersal and live in the deep-water layer. In the GSL, redfish are believed to copulate in the deep-water layer during the autumn-winter months (September-December) (Gascon 2003). All *Sebastes* species are ovoviviparous, and newly-hatched larvae continue to develop within the females. Larvae are extruded into the deep-water layer during late-spring/early summer (May- mid-June) (Sévigny et al. 2000), and migrate vertically through the water column, passing through the CIL to reach warm surface waters where they begin to feed on planktonic prey. They remain in surface waters until they become juveniles (15-20 cm) and begin to descend the water column towards the deep-water layer (Gascon 2003). Therefore, young redfish encounter multiple environments and environmental conditions during the first few months of life and it is likely that one or more of these environmental conditions is driving the strength of annual cohorts.

The objective of this paper is to identify key environmental characteristics associated to strong year classes of the spasmodically-recruiting GSL redfish using a weight-of-evidence approach. In order to accomplish this, we compiled potential drivers of recruitment that may occur throughout early life development (e.g. adult condition, development inside females, extrusion event, early larval stage). Existing environmental data time-series specific to each hypothesis were compared against recruitment indices in order to identify the most likely drivers of the rare and exceptional recruitment events in our SRS species. The overarching goal of this project is to present a means of identifying key environmental parameters that are important drivers of SRS recruitment that can be monitored to better predict natural population fluctuations and sustainably manage commercial SRS species.

3.3 METHODS

3.3.1 Recruitment and spawning stock biomass indices

Currently, there is no annual survey in the region that aims specifically to collect larval or early juvenile redfish in order to estimate year-class strength. We therefore relied on redfish recruitment indices estimated by the Department of Fisheries and Oceans Canada (DFO) for the Redfish Management Strategy Evaluation using an empirical Bayes approach to model deviation of recruitment strength and SSB (McAllister et al. 2021). The recruitment index is a unitless estimation of year-class strength, relative to other years of redfish cohorts. Likewise, SSB values were estimated using the same Redfish Management Strategy Evaluation using data from annual research surveys (McAllister et al. 2021). Estimated recruitment indices during the period 1967 – 2016 averaged 13.9 with a standard deviation of 83.4 (Figure 17). The highest recruitment value was obtained for the 2011 year class (589.9), and the lowest for both the 1991 and 1992 year classes (0.2). If the recruitment value for 2011 is not included in the dataset, the average recruitment index of the time series is 2.1. We considered the year classes of 1972 (6.3), 1980 (4.8), 1981 (12.1), 2011 (589.9), and 2013 (46.5) as strong recruitment years as these were years in which recruitment indices were greater than the historical mean excluding the 2011 year-class. Recruitment data were log-transformed when creating the figures for optimal visualization. During the same time period, mean estimated SSB was 272.4 ± 244.7 kt. The highest estimated SSB occurred at the beginning of the time series in 1967 (994.5 kt) and the lowest estimated SSB occurred in 2016 (47.8 kt).

3.3.2 Environmental indices

Physical and biological environmental indices that corresponded to variables within the recruitment hypotheses were respectively extracted from Galbraith et al. (2021) and Blais et al. (2021) (Table 5). These data are generated annually by the DFO to monitor and describe trends in oceanic and ecosystem conditions. Physical oceanographic indices were recorded from 1967 until present, however some years of data for some indices are missing due to various circumstances. Biological indices, such as zooplankton abundance and phenology, were recorded since 1999 with the creation of the Atlantic Zone Monitoring Program (AZMP) (Blais et al. 2021). To test for covariance among recruitment predictors, Pearson correlation coefficients were calculated among all environmental indices considered in our analyses.

3.3.3 Spatial scale

Larval redfish extrusion is known to occur in the central GSL and southern NE Gulf regions within a narrow temporal window (Sévigny et al. 2000). There is no information in the literature regarding the extent and timing of larval drift within the GSL throughout early larval development in the summer months. The physical and biological indices used for this project were weighted and averaged based on regional area data collections in the central and NE Gulf regions following the methods of Lehoux et al. (2021) using regions outlined in Figure 18.

3.3.4 Determining relationships and effect strength

Long-term trends in environmental conditions were plotted for each environmental index throughout the entirety of the time series data available (Figure 19). Z-scores for each annual environmental index were calculated using historical means and standard deviations in order to determine how conditions compared to the historical mean for each year (Table 2). Scatterplots of each environmental index z-score versus the recruitment index were plotted in order to determine if there were trends between environmental conditions and recruitment strength (Figure 20). Each variable was classified as “likely” or “unlikely” having an effect on recruitment. Variables in which strong recruitment occurred only when z-scores were grouped on one side of the historical mean (all positive or all negative) were categorized as “likely” having an effect on redfish recruitment. Variables in which strong recruitment occurred when z-scores were on either side of the historical mean were categorized as “unlikely” having an effect on redfish recruitment. For SRS fishes, it is likely that a combination of environmental conditions must be met in order to produce a strong year class (Sysoeva 2000; Gascon 2003).

3.4 HYPOTHESES

Drivers of recruitment were categorized into two groups: physical variables and biological variables. We list a series of hypotheses on how each variable might act as recruitment driver based on published literature (Table 5). Then, we present results supporting or not supporting each hypothesis. Hypotheses are listed following the sequential order of events experienced through ontogeny, from development within the female throughout the early juvenile stage.

3.4.1 Spawning stock biomass (SSB)

A larger spawning stock biomass would increase the number of larvae released into the environment during the extrusion season (Beverton and Holt 1957). If the proportion of larvae that survive to recruitment is relatively constant across years, then the production of more larvae by a larger adult biomass will result in more individuals surviving the larval stage and increased recruitment success. Pepin (2016) found that, in most marine fish stocks, there is a positive relationship between SSB and recruitment strength.

However, the spasmodic recruitment success of redfish does not follow classic stock-recruitment dynamics (DFO 2020) and redfish stock-recruitment models have systematically failed in predicting recruitment success of redfish in the GSL (Licandeo 2020). This was the only variable included in this chapter that has not been supported by redfish-specific literature. Furthermore, the unprecedentedly strong recruitment event in 2011 arose from an estimated historically low SSB in the region, and based on scientific surveys, there were no estimated changes in SSB prior to 2011 that would have allowed predicting multiple strong recruitment events in the early 2010s (McAllister et al. 2021).

We proposed two contrasting hypotheses to explain the influence of SSB on redfish recruitment in the GSL: (1) there is a positive relationship between recruitment strength and redfish SSB and (2) there is a negative relationship between recruitment strength and redfish SSB, due to density-dependent effects. Strong recruitment events in the early 1980s, as well as the early 2010s, were produced during periods of low SSB (Figure 19A; Figure 20A). It is possible that young juvenile of potentially strong year classes are heavily cannibalized during periods of high SSB (Cadigan et al. 2022). Young redfish make up a substantial proportion of the diet of redfish > 20 cm (Senay et al. 2021, Brown-Vuillemin et al. 2022). Therefore, since it is likely that there is some density-dependent effect of SSB on redfish recruitment, we hypothesize that this effect is likely mild and negative.

3.4.2 Deep layer water temperature

Temperature is the primary driver of metabolism in fishes (Wells 1935). Metabolic rate mediates how much energy is available to be allocated to physiological processes after being used to maintain basal life functions. One of these processes is reproduction. Little is known about redfish reproduction, but it is considered that copulation occurs in the GSL in autumn, embryos develop and hatch inside the females during the early spring, and larvae are extruded during early summer into deep waters where adults reside (Sévigny et al. 2000). Changes in bottom water temperature may modify the amount of energy that is allocated by females to egg production, yolk volume, and/or the developmental rate of hatched larvae inside the female. Fecundity of multiple important commercial groundfish species such as haddock (*Melanogrammus aeglefinus*), winter flounder (*Pseudopleuronectes americanus*), and yellowtail flounder (*Limanda ferruginea*) have been shown to be negatively affected by increasing bottom water temperatures (Klein et al. 2017). Latitudinal differences in cod (*Gadus morhua*) fecundity have been shown to be driven by differences in metabolism due to temperature (Pörtner et al. 2001). In addition to energy devoted to fecundity, *Sebastes* sp. have been shown to transfer nutrients to the larvae while larvae still reside inside the female due to their ovoviviparous reproduction strategy (Boehlert and Yoklavich 1984). Changes in water temperature may mediate how much energy from the maternal diet is available to be allocated to offspring during their development after hatching while inside the female. Bottom water temperatures (recorded at 300 m) in the GSL are rising, and are predicted to continue to rise, as a result of climate change, with each of the years 2015-2020 exceeding 6.0 ^{o}C relative to the 10-year historical mean of 5.72 ^{o}C (Galbraith et al. 2021).

Preliminary work investigating the effect of temperature on the metabolism of adult *S. fasciatus*, a closely related *Sebastes* species in the GSL, shows that metabolic scope of *S. fasciatus* increases with increasing water temperatures until at least 10^{o}C (Guitard et al. *in prep*). Metabolic scope is the difference between standard metabolic rate and active metabolic rate and is used to identify environmental conditions that lead to changes in energy budgeting (Lefrançois and Claireaux 2003). A small metabolic scope means there is limited excess energy that can be allocated to other physiological processes. Therefore, it is possible that *Sebastes* sp. in the GSL are not yet occupying their optimal thermal environment, and may continue to thrive physiologically in warming GSL waters, given there is sufficient food available for adults.

We hypothesized that warm bottom temperature waters may provide a more ideal environment for adult redfish, which would result in high offspring quality and therefore strong recruitment events. We used bottom water temperatures (depth of 300 m) during August and September to test this hypothesis.

We did not find a trend between temperature of deep water at 300 m and recruitment strength (Figure 20B). The strong recruitment event of 1972, and the strongest recruitment event of 2011, occurred when bottom water temperatures were 4.85 ^{o}C and 5.42 ^{o}C, respectively, which fall at or below the historical average (1971-2016) of 5.43 °C. Strong recruitment events were recorded at 1.90 SD below the historical mean (1972) as well as 1.73 SD above the historical mean (1980). Therefore, bottom water temperature is an unlikely driver of strong redfish recruitment in the GSL.

3.4.3 Cold intermediate layer (CIL) volume

Boundaries of the CIL are defined by water that is colder than 1 °C, much colder than the neighboring surface and bottom water masses. Larval redfish are extruded from females in the deep-water layer and must pass vertically through the CIL in order to reach surface waters (defined as the upper 50m) where they reside until metamorphosis. Mortality of redfish (*S. fasciatus*) larvae has been shown to increase as temperatures decrease below 6 °C, with approximately 30% of newly-extruding larvae exposed to temperatures of 0 °C dying within 96 hours (Gascon 2003). Therefore, it is likely that encountering waters colder than 1 °C could represent a physiological challenge for newly-extruded larvae that may result in poor condition, slow growth, and high mortality rate. In years when the CIL volume is high, its temperature is generally lower so larvae must pass through a colder, thicker water mass in order to reach warmer surface waters, which may result in higher mortality from a longer exposure to stressful conditions, relative to years when the CIL is thinner.

We hypothesized that there is a negative relationship between CIL volume in the year of extrusion and redfish recruitment strength because of a decreased physiological stress on newly-extruded larvae that must vertically pass through very cold temperatures as they migrate towards the surface (Gascon 2003). Time series data represent the CIL volume during August and September of each year.

There was a negative trend between the log-transformed recruitment index and summer CIL volume (August-September) in the GSL. Strong recruitment only occurred when CIL volume was less than 3000 × 10^3 km^3 (range: 1803.5 – 2904.8) (Table 7). The largest CIL volume associated with a strong recruitment event was in 1972 when the CIL was 2904.8 × 10^3 km^3. Recent strong recruitment events (2011, 2013) occurred when the CIL volume was 2036.6 and 1803.5 respectively. These recent CIL volumes are 1.4 and 1.7 SD below the long-term average, respectively (Figure 20C). Although recorded data for CIL volume in this time series is absent for the early 1980s recruitment events, the CIL was described as being anomalously warm and thin during the beginning of that decade (Plourde et al. 2014, Galbraith et al. 2021). Based on this relationship, CIL volume is categorized as a “likely” driver of recruitment as recent successful recruitment events appear to only occur beyond a CIL volume at or below 2000 × 10^3 km^3 and below the long-term average.

3.4.4 Sea surface temperature (SST)

Like adult fish, larval fish growth is often tightly correlated with SST (Houde and Zastrow 1993). Fast larval fish growth is a favored trait to increase chances of survival, and therefore recruitment into the fishery (Houde 1987; Anderson 1988; Takasuka et al. 2003, 2004). Due to differences in morphology and physiology, thermal preferences and range of tolerance often differ between adult and larval life stages. Therefore, suitable environmental conditions must also consider suitable temperatures across all life stages. Recruitment in many fish species has been shown to be related to sea surface temperatures during early life stages (Atlantic cod [Pörtner et al. 2000]; Caribbean reef fish [Sponaugle et al. 2006]; multiple North Atlantic species and stocks [Øttersen et al. 2013]).

Gascon (2003) found that mortality of newly-extruded *S. fasciatus* larvae was lowest when water temperatures were between 6-9 ^{o}C, with mortality increasing at temperatures > 9 ^{o}C. Sysoeva (2000) found that SST was positively correlated with post-flexion larval redfish (9-16 mm) condition, which was often reached during the 2nd month post-extrusion. Larval condition is often a proxy for likelihood of survival in larval fish. In GSL redfish, this developmental stage of 9-16 mm would be reached during late June and early July for the majority of larvae.

Relying on a limited redfish larval growth dataset from a published study that investigated drivers of growth in larval redfish (Burns et al. 2021), we found a positive trend, although not statistically significant, between larval redfish growth and SST (upper 5 m of water column) in individuals older than 8 days post-extrusion (r = 0.33; p = 0.12), a developmental stage during which larvae have exhausted endogenous yolk and oil globule reserves for nutrition and must thus feed exogenously (Figure 21A). The fact that the relationship is not statistically significant is likely due to the low number of observations.

Based on the large literature outlining the relationship between SST and recruitment of multiple fish species, and previously collected, unpublished data on the effect of SST on larval redfish growth, we hypothesize that there is a positive relationship between redfish recruitment and SST in the first 3 months post-extrusion (June, July, August).

We found no clear trend between recruitment strength and the SST in the GSL during June (month of extrusion), July, or August. To date, mean SST exceeded 9 ^{o}C in June during only 1 year (2005), a temperature at which increased mortality of larval redfish has been documented (Gascon 2003). Successful recruitment events in 2011 and 2013 occurred when SST in the first 3 months of life were similar to the long-term historical mean for each month (7.1 ^{o}C, 12.6 ^{o}C, and 15.0 ^{o}C, respectively). Data from the successful recruitment event in 1981 were available for August only, and recruitment occurred when August SST was relatively cool at 13.1 ^{o}C, or -1.8 SD below the historical mean (Figure 20D-F). We conclude that SST in the first three months post-extrusion is unlikely to drive recruitment success of larval redfish.

3.4.5 Water column stratification

Strong water column stratification has been shown to increase larval fish feeding success by concentrating prey at boundary layers and therefore increasing the encounter rate between larval fish and prey (Lasker 1981; MacKenzie 2000). Stratification is thus likely increasing the amount of prey consumed by larvae, increasing growth, and strengthening recruitment success for many species (Northern anchovy [Lasker 1975]; haddock [Buckley and Lough 1987]; walleye pollock [Bailey et al. 1995]; anchovy [Clemmesen et al. 1997]).

Growth of redfish has been shown to be significantly influenced by a larva's ability to feed successfully, but the physical environmental factors that facilitate successful feeding for larval redfish are unknown (Burns et al. 2021). *Sebastes* sp. recruitment success has been linked to storm frequency in Barents Sea populations: increased storm activity during the larval stage resulted in decreased recruitment success (Sysoeva 2000). These authors hypothesized that wind and rain from the storms disrupted water stratification resulting in increased water mixing, decreased SST, decreased localized prey densities, and decreased feeding success that resulted in smaller, slower-growing larvae that were more vulnerable to mortality by starvation and predation.

Using larval redfish growth data generated in Chapter 2 (Burns et al. 2021), we found a significant positive trend between growth of exogenously-feeding redfish (> 8 days post-extrusion) and the strength of water stratification (Figure 21B). Growth of redfish larvae was measured using methods described in Burns et al. (2021). In the aforementioned study, water stratification was measured as the difference between SST and the temperature of the water at the top of the thermocline, both of which were measured at the time of larval collection. Therefore, larvae that had recently grown more quickly were found in areas where water column stratification was strong.

We hypothesized that there is a positive relationship between redfish recruitment and the strength of water column stratification, which may lead to increased feeding success, growth, and survival of larval redfish.

In the present study, the strength of water column stratification was measured as the difference in water density in the upper 5m of the water column and the water density at 50m. This index was calculated by DFO for only the months of June and August. These months coincide with the timing of larval extrusion and the onset of first-feeding, and approximately

2 months post-extrusion when all larvae are obligate exogenous feeders, respectively. Strong recruitment events of 2011 and 2013 occurred at stratification strengths that were similar to the historical mean in both June and August (1.6 and 3.5, respectively) (Figure 20G,H). There does not appear to be a trend or a threshold of stratification strength that is driving larval redfish recruitment during the early (June) or late (August) larval stage, and we classified stratification as an unlikely driver of recruitment success of larval redfish in the GSL.

3.4.6 Preferred prey abundance

Hjort's (1914) Critical Period hypothesis was rooted in both larvae's ability to feed successfully, but also in the interannual variability of potential prey available for larvae to feed on. Potential prey taxa usually refer to species and developmental stages of prey that fall within a suitable size range and behavioral patterns that are able to be consumed by larvae based on their mouth gape width and foraging ability. Recent studies have shown that the vast majority of larval fish species demonstrate a preference for highly specific prey taxa, and that larval growth and survival is directly linked to successful feeding on preferred prey taxa (Robert et al. 2009, Sponaugle et al. 2010, Murphy et al. 2013). Failure to acknowledge species-specific prey preference has potential to result in a negative or lack of a relationship between prey abundance and larval fish survival, because abundance of other suitable prey species creates noise around the important relationship (Robert et al. 2014).

Throughout early larval development, redfish in the GSL commonly consume various life stages (egg, nauplius, copepodite) of the large calanoid copepod *Calanus finmarchicus* (Anderson 1994, Runge and de Lafontaine 1996, Burns et al. 2020), which was determined to be the preferred prey taxon of larval redfish (Burns et al. 2020). Anderson (1994) found that redfish larvae on the Flemish Cap were in better condition during years in which *C. finmarchicus* comprised a majority of the larval diet, versus another common prey taxa, the small cyclopoid copepod, *Oithona similis*. However, Burns et al. (2021) did not observe the expected positive relationship between local densities of *C. finmarchicus* eggs or nauplii and larval redfish condition or growth in the GSL. This may be a result of a lag between prey in the environment that is available to be consumed by larvae and the incorporation of nutrients from the larval diet into the body for growth and development as growth and condition indices can represent past days or weeks of an individual's feeding success (Robert et al. 2014).

We hypothesized that there is a positive relationship between redfish recruitment strength and the abundance of early *C. finmarchicus* life stages (egg and nauplius) during the early summer months when larval redfish begin to feed exogenously. Higher preferred prey densities would increase encounter rates between larval redfish and their prey and likely increase feeding success, growth, and the likelihood of survival to recruitment. Time series data available represent the abundance of *C. finmarchicus* during early summer months

We found no relationship between redfish recruitment index and *C. finmarchicus* abundance in the early summer in the GSL. Recent strong redfish year classes (2011, 2013) emerged when *C. finmarchicus* abundances were in the middle of the historical range and 0.19 (2013) and 0.72 (2011) SD above the historical mean (Figure 20I). It is however important to note that no strong recruitment events occurred when *C. finmarchicus* densities were below $15 \times 10^3 \bullet \mathrm{m}^{-2}$ individuals, which was the historical mean density. These patterns are similar to the relationship described between recruitment and CIL volume, in that successful recruitment events only occurred when environmental z-scores were all negative, or in the case of prey abundance, all z-scores were positive relative to the historical mean. *C. finmarchicus* abundance is considered a "likely" driver of recruitment of redfish in the GSL because there is potentially an environmental abundance threshold above the current historical mean that must be met in order to produce a strong recruitment event.

3.4.7 Preferred prey phenology

David Cushing (1975, 1990) built upon Hjort’s (1914) Critical Period hypothesis by proposing his Match-Mismatch hypothesis, in which fish recruitment depends both on the spatial and temporal overlap between larval fish and their suitable prey. A large overlap in the timing and local abundance of larval fish and their suitable prey is considered an environmental “match” and will result in strong recruitment, whereas environments in which larval fish do not occur at the same time or space as suitable prey will result in poor recruitment due to poor nutrition and starvation. Cushing (1975) also hypothesized that this “match” or “mismatch” between larval fish and their prey is ultimately driven by climatic physical oceanographic variables that determine the developmental rates of both larval fish and their planktonic prey. Brosset et al. (2020) found that the best predictor of annual recruitment strength in Northwest Atlantic mackerel (*Scomber scombrus*) was the timing of its preferred prey species, and not solely its abundance. Likewise, the phenology of *C. finmarchicus and C. hyperboreus*, and not overall abundance, was an important driver of juvenile and adult capelin (*Mallotus villosus*) condition, a proxy for survival throughout its first two years of life (Lehoux et al. 2022).

While larval redfish diets in the GSL are largely comprised of *C. finmarchicus*, Burns et al. (2021) found that there was a positive correlation between recent growth and consumption of *C. finmarchicus* nauplii by larval redfish, whereas there was a negative correlation between recent growth and consumption of *C. finmarchicus* eggs. This result suggests that the developmental stage of the preferred *C. finmarchicus* that is available in the environment is potentially an important driver of recruitment, rather than the overall abundance of species. The relationship between larval redfish condition, survival, and recruitment and the phenology of *C. finmarchicus* was hypothesized by Runge and de Lafontaine (1996) in conclusion of their 1-year study on the *C. finmarchicus*-redfish connection in the GSL. Multi-year datasets examining larval diet and condition of redfish also proposed an important relationship between the timing of *C. finmarchicus* reproductive events and redfish recruitment in Flemish Cap (Anderson 1994) and Barents Sea (Sysoeva

2000) populations. Sysoseva (2000) hypothesized that late-season *C. finmarchicus* reproductive events resulted in higher larval condition, survival, and ultimately stronger recruitment events.

We described *C. finmarchicus* phenology by calculating the ratio of early *C. finmarchicus* copepodite stages (CI-IV) to the total abundance of *C. finmarchicus* copepodites within the samples. Ratios closer to 1 signify a younger, less developed *C. finmarchicus* spring (G_1) generation at the time of sampling compared to lower ratios in which later-stage *C. finmarchicus* individuals are more abundant. A less developed G1 implies a greater abundance of late naupliar stages. We hypothesize that there is a positive relationship between redfish recruitment and *C. finmarchicus* development during the early summer months. However, we also hypothesize that the range of developmental rates over which strong recruitment events can occur will be narrow, signifying a specific seasonal timing of *C. finmarchicus* which maximizes the environmental “match” between larval redfish and their preferred prey taxa and developmental stage. Time series data represent the phenology of *C. finmarchicus* during early summer months.

Strong recruitment events of 2011 and 2013 occurred during years when *C. finmarchicus* phenology was late during the early summer months (0.89, 0.67 respectively). *C. finmarchicus* development in 2011 was the second latest since the AZMP began monitoring biological variables in 2001. These phenologies were 1.33 and 0.22 SD above the historical mean of *C. finmarchicus* development in the same season (Figure 20J). There was no strong redfish recruitment during years in which *C. finmarchicus* development was faster or earlier than the historical mean. Recruitment indices did not exceed 1.0 in any year in which *C. finmarchicus* phenology was earlier than the historical mean. We considered *C. finmarchicus* phenology is categorized as a “likely” driver of redfish recruitment in the GSL based on the apparent necessity of late *C. finmarchicus* development during strong recruitment years.

3.4.8 Correlation among variables

The joy and frustration of working with ecological phenomena is that each measurable variable within the environment is potentially intertwined with many others, therefore it is important to test the level of co-variance in potential recruitment drivers that have been identified. Ideally, we aimed to identify multiple potential drivers of redfish recruitment that were weakly correlated with one another in order to explain the greatest amount of variability in recruitment success. At minimum, there were 16 data points for each variable, therefore a Pearson correlation coefficient > |0.50| between any of the variables was statistically significant ($p < 0.05$) and we considered the variables to be strongly correlated. We did not include SSB in these calculations because it is a density-dependent variable (Figure. 22).

CIL volume was not strongly correlated with any of the other potential drivers of redfish recruitment, nor was it strongly correlated with any of the non-likely drivers of recruitment considered in this study. Therefore it is likely explaining a unique proportion of redfish recruitment variability.

C. finmarchicus abundance and phenology in the early summer were strongly, positively correlated ($r = 0.57$), meaning that they are likely explaining the same portion of variability in redfish recruitment. *C. finmarchicus* abundance was not strongly correlated with any other potential variable. *C. finmarchicus* phenology was strongly, negatively correlated with SST in June ($r = -0.53$). It is likely that when SST in June is cooler, there will be a later occurrence of *C. finmarchicus*, which would be conducive for strong redfish recruitment.

3.5 DISCUSSION

Understanding the mechanisms driving recruitment of fish stocks is difficult, and has plagued scientists for the last century. With the advancement of data-collection technology and statistical analyses, there has been significant progress in our understanding of the environment-recruitment relationships, and increased accuracy in predicting year-class strength in many commercially-important species (Plourde et al. 2015; Huebert et al. 2018; Brosset et al. 2019; Brosset et al. 2020; Lehoux et al. 2022). However, SRS often lack a sufficient number of strong recruitment class replicates, and the corresponding environmental data, that are necessary for the quantitative assessment of recruitment drivers. Therefore, alternative methods of identifying drivers of recruitment should be explored in order to gain an understanding of the mechanisms behind the spasmodic recruitment events.

We applied a weight-of-evidence approach to identify physical and biological drivers of GSL redfish, with the objective of revealing the combination of environmental conditions that facilitated the largest recruitment event for this stock in 2011, and advancing our capacity to predict successful year classes before they are recruited in to the fishery around age 7-9 years (Gascon 2003). Based on this approach, we have identified CIL volume, *C. finmarchicus* phenology and abundance during the early summer months, and SSB as likely drivers of redfish recruitment (Table 7). Based on our findings, we hypothesize that a suite of environmental conditions must simultaneously occur to result in the emergence of strong recruitment events in redfish (Figure 23).

3.5.1 Identifying the drivers of redfish recruitment towards an ecosystem approach

Our results suggest that there are multiple critical periods mediating interannual variability in mortality, which in turn drive recruitment success (Figure 23). Once larvae are extruded from females in the bottom water mass, they must vertically pass through the CIL in order to reach surface waters where they will grow and develop. Passage through the CIL likely induces high mortality, with the magnitude of mortality likely directly linked to CIL volume. Years in which the CIL volume is low are likely conducive to higher survival of newly-extruded redfish larvae. Once larvae reach the surface waters, they must begin to feed successfully around the age of 8 days-post extrusion (Burns et al. 2021). At this time, both the high abundance and late cohort development of the preferred prey *C. finmarchicus* would play a critical role in determining larval survival. Burns et al. (2021) determined that consumption of the naupliar stage of *C. finmarchicus* was conducive for fast larval growth, whereas consumption of *C. finmarchicus* eggs was suboptimal to redfish growth. Results from the present analysis support the importance of a correspondence between larval redfish and specific developmental stages of key prey species. These results also support the Match-Mismatch hypothesis proposed by Cushing (1975, 1990). Finally, as larvae grow into juveniles, they move downward to occupy habitats located nearby that of pre-adult and adult redfish. Large redfish pre-adult and adult biomass may result in a high mortality event as a result of cannibalism on early juvenile redfish as they move through the water column.

The concept of a « perfect storm » of conditions implies that multiple independent recruitment drivers need to aling for the production of a strong year class. SSB is a density-dependent variable, and fluctuations have historically been driven by spasmodic strong recruitment events and fishing pressure. CIL volume is driven by winter air temperatures and mixing strength, and althought *C. finmarchicus* abundance and phenology are strongly correlated, they appear to be driven partially by sea surface temperatures in the early summer. Therefore, this strongly suggest that a suite of environmental conditions that are not connected must be met in space and time for the production of a strong redfish recruitment event.

Because of the complexity of ecosystem processes, there is a high probability that some important recruitment drivers were not included in the present analysis. For example, any assumptions of larval redfish growing and recruiting outside of the central and NW GSL were not considered, but should not be discounted in future works if larval transport studies conclude in wider dispersion than currently conceptualized. Additionally, environmental conditions considered in the present study are those that are encountered within the first few weeks/months post-extrusion. Strong mortality events may occur later in redfish development, which would be outside the scope of our study. This gap in ontogenetic research may explain average recruitment strength for the 2012 cohort even though all key environmental conditions were met for the production of a strong year class. Alternatively, it is possible that the modeled recruitment index used in the present study has underestimated the strength of the 2012 year class by assigning a part of the 2012 recruits to one of the two adjacent year classes. Large mortality events during the juvenile stage have also been proposed by Gascon (2003) to explain sudden decreases in estimated biomass of year classes initially considered strong.

Results from this study lay the groundwork for future studies to test our hypotheses on drivers of redfish recruitment, as well as outline a potential new way of identifying drivers of recruitment in SRS. We have identified CIL volume, SSB, and *C. finmarchicus* abundance and phenology as a suite of important drivers to monitor for predicting potential strong year-classes of redfish 6-7 years before they are recruited into the fishery. Our results have the potential to support the development of an ecosystem-based or ecosystem-approach to fisheries management by providing key environmental conditions determining the fate of a critical life stage. Identification of recruitment drivers allows for fishery managers to proactively prepare for future population fluctuations, rather than react to these changes with dramatic shifts in fishing regulations, which is especially important in SRS fisheries that are generally sustained by individuals from one successful year class for up to 10 years. Additionally, in the face of global climate change, an understanding of physical and biological conditions that facilitate early-life survival is critical for predicting how populations will react to unprecedented environmental variability. During the last decade, CIL volumes have continued to decrease and *C. finmarchicus* phenology has trended towards later development (Figure 19C,J). While both of these conditions are trending in the right directions for continued successful recruitment events of redfish in the GSL, we must continue to monitor the ecosystem for any indication of additional key drivers of recruitment.

3.5.2 A revival of the recruitment problem

Rice and Browman (2014) described a decline in the number of recruitment-focused studies published in relevant journals since the 1990s. One of their proposed reasons for this decline was the "repackaging" of recruitment studies into more "trendy" research topics such as climate change and ecosystem-based fisheries management (EBFM). The study of recruitment may have been deemed "too difficult" because of the complex, interactive nature among environmental processes that drive survival of the early life stages of fish. Along with the increased modelling capabilities (e.g. Generalized Additive Models) that allow identifying key drivers of recruitment and forecast population dynamics in many commercially-important species (e.g. CITE REFERENCES), we demonstrate how a weight-of-evidence approach can also be implemented to identify recruitment drivers in SRS with only 5 replicates of strong recruitment events and a few decades of environmental data. While Rice and Browman (2014) state that incorporating recruitment-focused research into other fields such as fisheries management may result in a politicization of the science or a loss of "old" recruitment science concepts, it can also be argued that not using results from recruitment studies for the progression of fisheries science is withholding application of information in an otherwise applied field of science as "research into the drivers of recruitment variability is directly relevant to ecosystem-based fisheries police and management". A shift towards EBFM requires knowledge of complex ecosystem processes in order to monitor and predict present and future stock dynamics. The results from this study, and others that identify recruitment processes, are able to describe the mechanism of many ecosystem processes that contribute to variability of year-class strengths of commercially-fished species, now including SRS.

3.6 FUNDING

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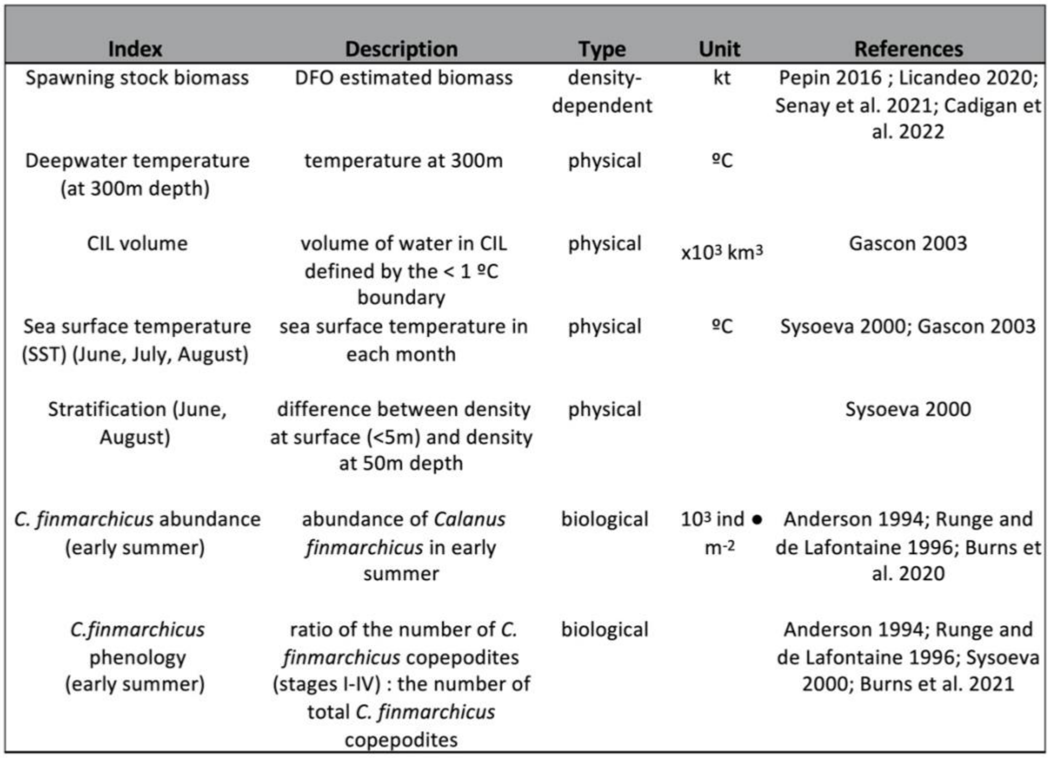
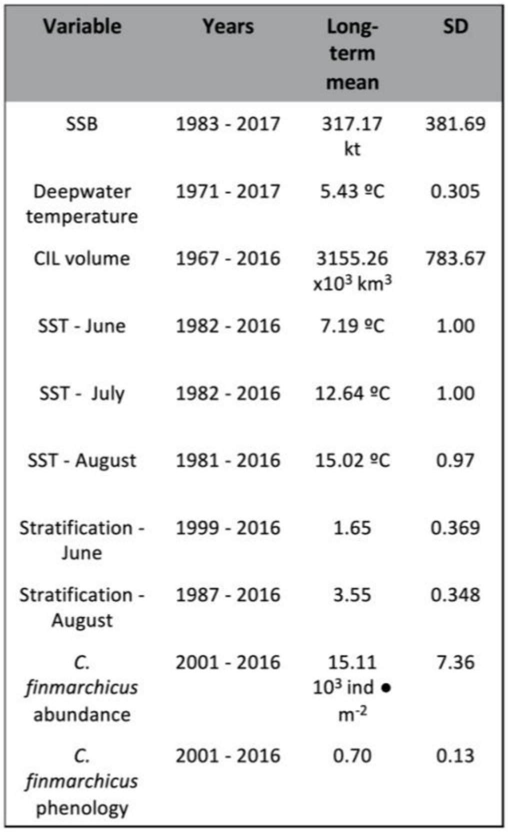
3.8 TABLES



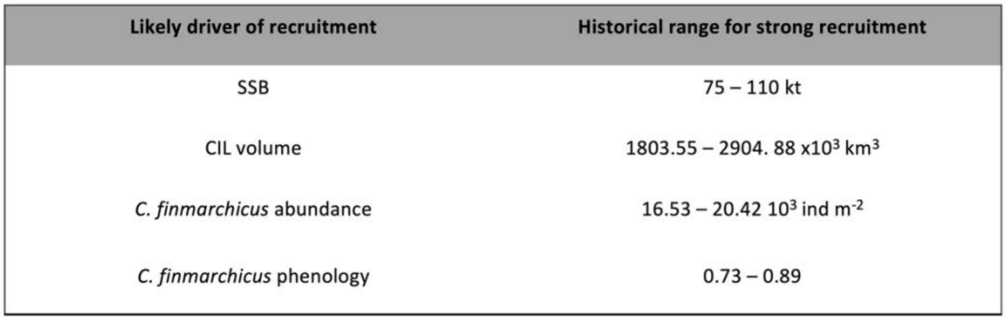
Index	Description	Type	Unit	References
Spawning stock biomass	DFO estimated biomass	density-dependent	kt	Pepin 2016 ; Licandeo 2020; Senay et al. 2021; Cadigan et al. 2022
Deepwater temperature (at 300m depth)	temperature at 300m	physical	ºC	
CIL volume	volume of water in CIL defined by the < 1 ºC boundary	physical	x10^3 km^3	Gascon 2003
Sea surface temperature (SST) (June, July, August)	sea surface temperature in each month	physical	ºC	Sysoeva 2000; Gascon 2003
Stratification (June, August)	difference between density at surface (<5m) and density at 50m depth	physical		Sysoeva 2000
C. finmarchicus abundance (early summer)	abundance of *Calanus finmarchicus* in early summer	biological	10^3 ind • m^{-2}	Anderson 1994; Runge and de Lafontaine 1996; Burns et al. 2020
C.finmarchicus phenology (early summer)	ratio of the number of *C. finmarchicus* copepodites (stages I-IV) : the number of total *C. finmarchicus* copepodites	biological		Anderson 1994; Runge and de Lafontaine 1996; Sysoeva 2000; Burns et al. 2021

Tableau 5. List of potential drivers of recruitment used in the weight-of-evidence approach. Data were compiled by DFO (Galbraith et al. 2021; Blais et al. 2021).



Variable	Years	Long-term mean	SD
SSB	1983 - 2017	317.17 kt	381.69
Deepwater temperature	1971 - 2017	5.43 ºC	0.305
CIL volume	1967 - 2016	3155.26 $x10^3$ km^3	783.67
SST - June	1982 - 2016	7.19 ºC	1.00
SST - July	1982 - 2016	12.64 ºC	1.00
SST - August	1981 - 2016	15.02 ºC	0.97
Stratification - June	1999 - 2016	1.65	0.369
Stratification - August	1987 - 2016	3.55	0.348
C. finmarchicus abundance	2001 - 2016	15.11 10^3 ind • m^{-2}	7.36
C. finmarchicus phenology	2001 - 2016	0.70	0.13

Tableau 6. Years of data available, long-term means, and standard deviations (SD) for all tested environmental indices. Means and SD were used to calculate z-scores.



Likely driver of recruitment	Historical range for strong recruitment
SSB	75 – 110 kt
CIL volume	1803.55 – 2904. 88 x10^3 km^3
C. finmarchicus abundance	16.53 – 20.42 10^3 ind m^{-2}
C. finmarchicus phenology	0.73 – 0.89

Tableau 7. Identified likely drivers of redfish recruitment and historical range of environmental conditions that resulted in strong redfish recruitment in the GSL.

3.9 FIGURES

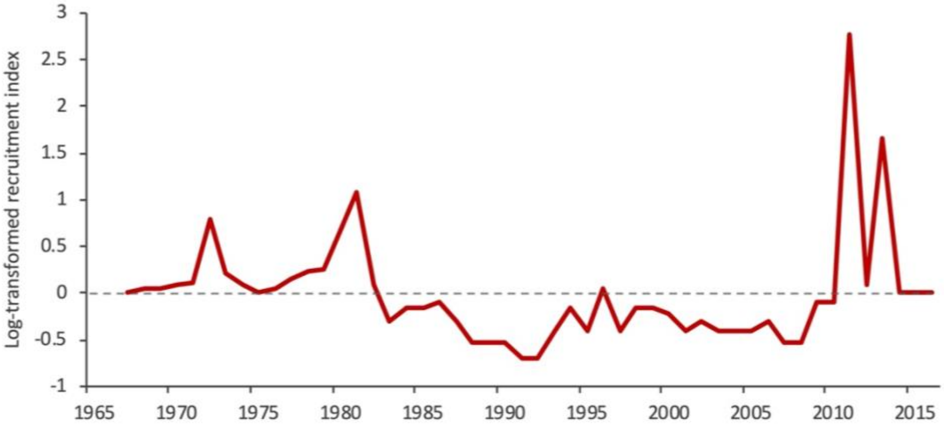


Figure 17. Time series of log-transformed recruitment indices by year from 1967 – 2016 estimated by a DFO MSE model from Duplisea et al. (2016).

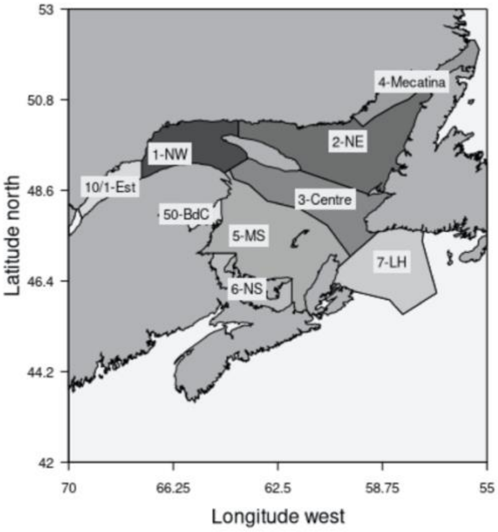
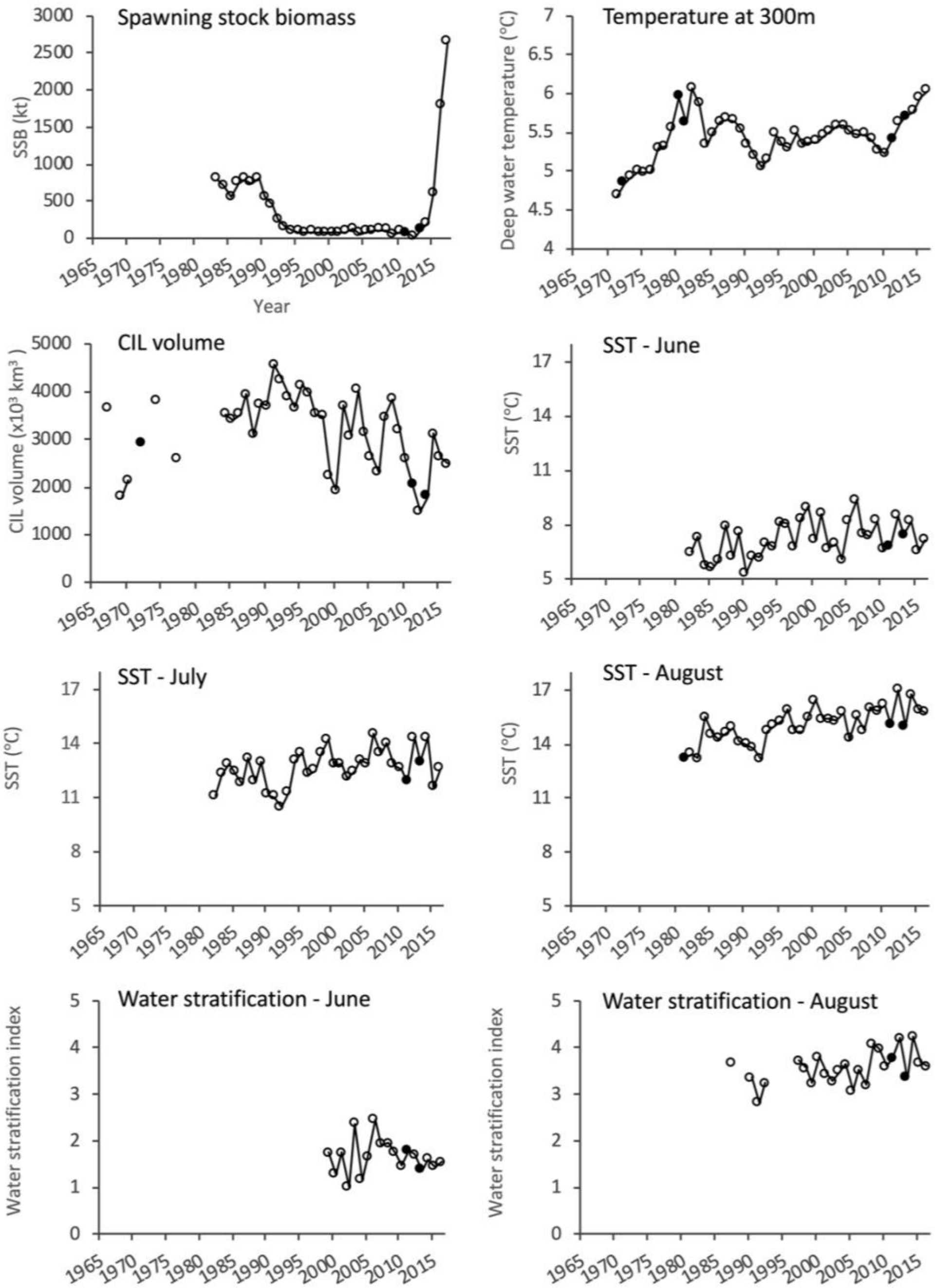


Figure 18. Oceanographic regions of the GSL as defined by the DFO. Modified from Duplisea et al. 2020.


Spawning stock biomass
SSB (kt)
3000
2500
2000
1500
1000
500
0
Year
Temperature at 300m
Deep water temperature (°C)
7
6.5
6
5.5
5
4.5
4
CIL volume
CIL volume (x10³ km³)
5000
4000
3000
2000
1000
0
SST - June
SST (°C)
17
14
11
8
5
SST - July
SST (°C)
SST - August
SST (°C)
Water stratification - June
Water stratification index
Water stratification - August
Water stratification index
5
4
3
2
1
0
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015

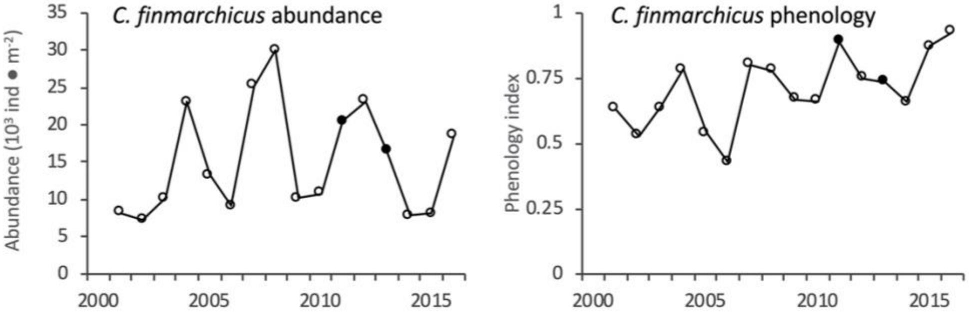


Figure 19. Time series of potential environmental indices that may drive redfish recruitment. Filled circles represent years of strong redfish recruitment.

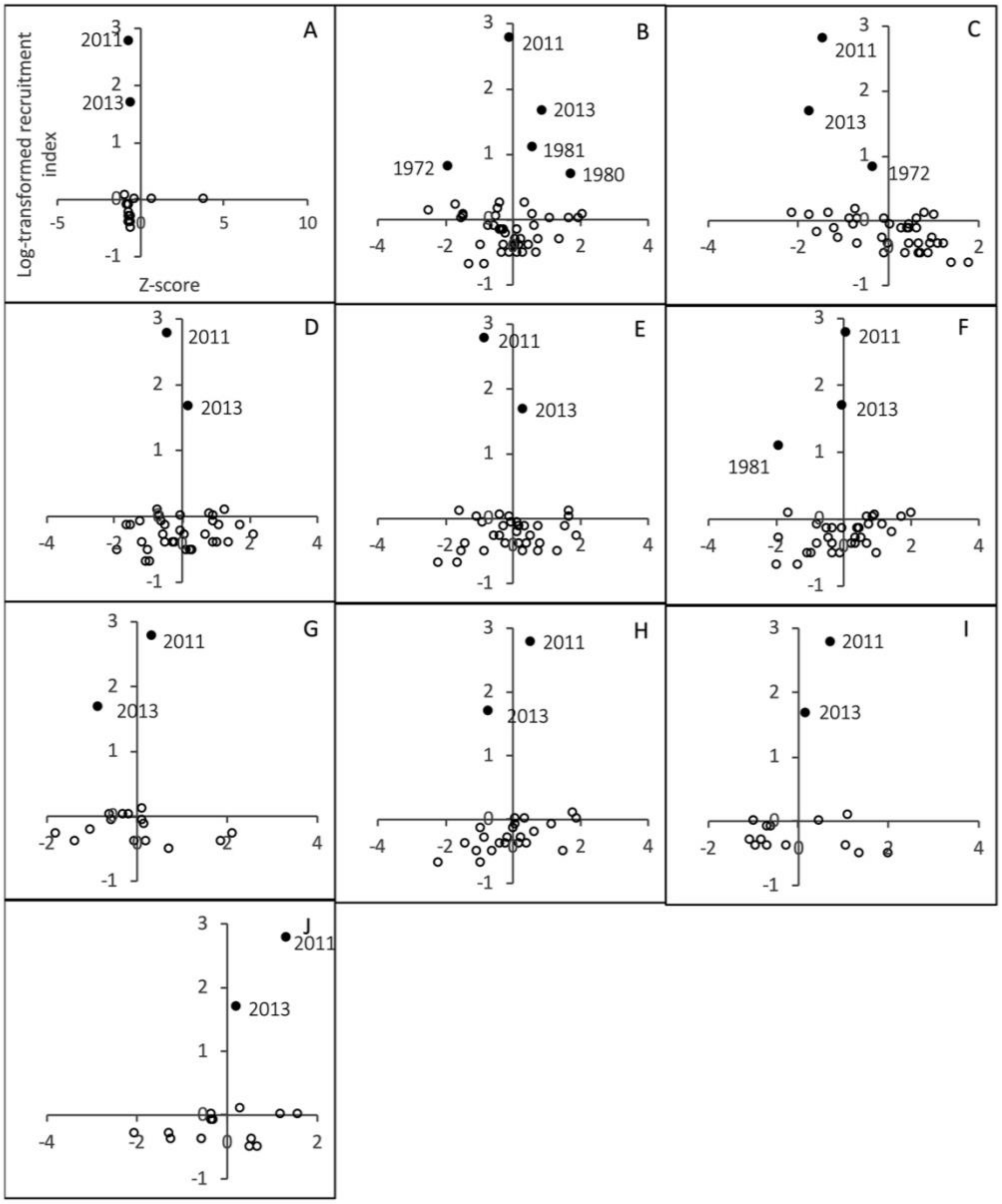


Figure 20. Z-scores of each environmental index versus log-transformed recruitment indices: (A) SSB; (B) deep water temperature; (C) CIL volume; (D) SST – June; (E) SST – July; (F) SST – August; (G) Water stratification – June; (H) Water stratification – August; (I) *C. finmarchicus* abundance; (J) *C. finmarchicus* phenology. Filled circles represent years of strong redfish recruitment.

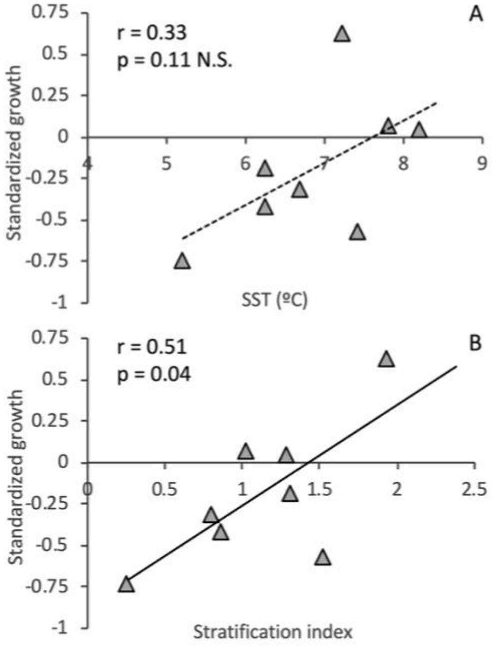
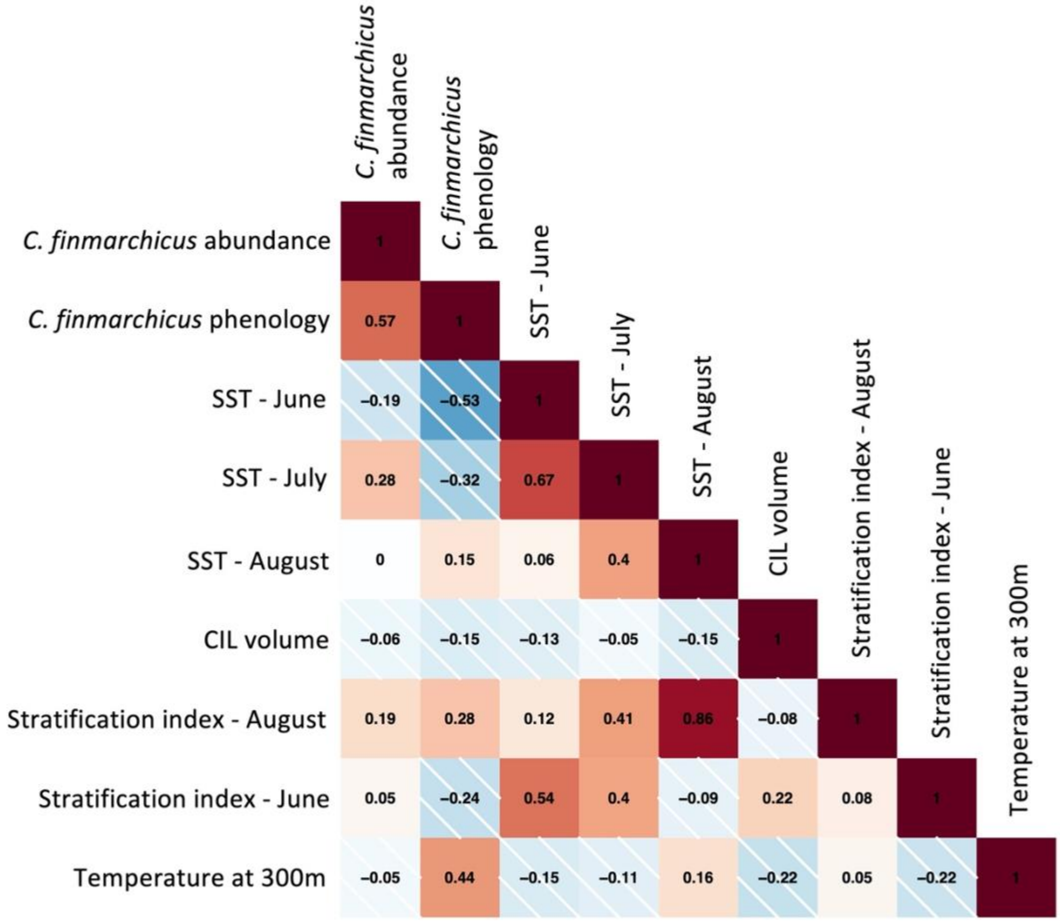


Figure 21. Relationship between (A) SST and (B) Water stratification at the time of larval collection, and standardized recent larval redfish growth in redfish larvae 8 days post-extrusion and older. Data originates from Chapter 2 of this thesis investigating drivers of larval redfish growth. Each data point represents mean standardized growth from multiple larvae collected from the same sampling event. Solid trendline represents a significant relationship ($p < 0.05$).



	C. finmarchicus abundance	*C. finmarchicus* phenology	SST - June	SST - July	SST - August	CIL volume	Stratification index - August	Stratification index - June	Temperature at 300m
C. finmarchicus abundance	1								
C. finmarchicus phenology	0.57	1							
SST - June	−0.19	−0.53	1						
SST - July	0.28	−0.32	0.67	1					
SST - August	0	0.15	0.06	0.4	1				
CIL volume	−0.06	−0.15	−0.13	−0.05	−0.15	1			
Stratification index - August	0.19	0.28	0.12	0.41	0.86	−0.08	1		
Stratification index - June	0.05	−0.24	0.54	0.4	−0.09	0.22	0.08	1	
Temperature at 300m	−0.05	0.44	−0.15	−0.11	0.16	−0.22	0.05	−0.22	1

Figure 22. Pearson correlation coefficients between potential environmental variables that may drive redfish recruitment.

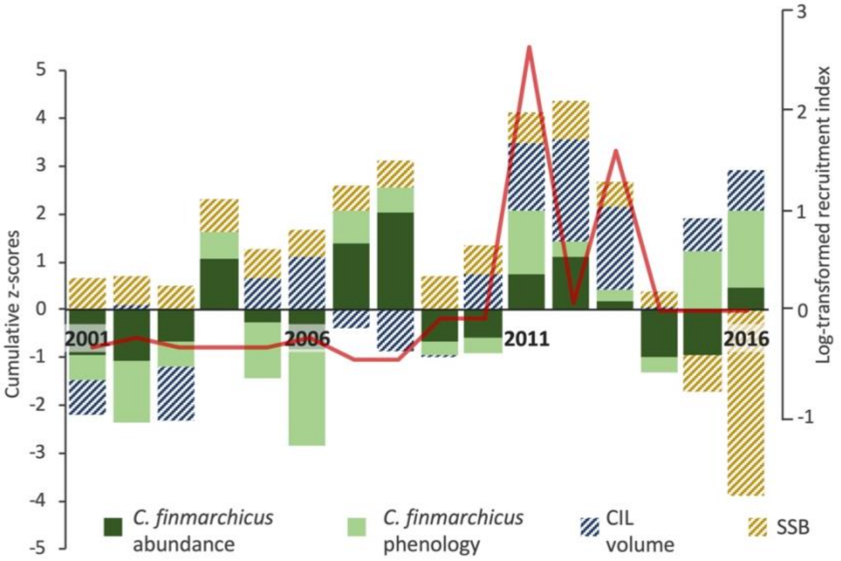


Figure 23. Cumulative z-scores of all likely environmental drivers of redfish recruitment compared to log-transformed redfish recruitment index for each year. Z-scores for CIL volume and SSB were multiplied by [-1] to account for their negative effect on redfish recruitment.

CONCLUSION GÉNÉRALE

Recruitment success of marine fish is strongly dependent on the number of individuals that survive through the larval stage (Houde 1987). In order to understand variability in recruitment, it is critical to understand sources of larval fish mortality. There are 3 primary pillars of larval fish mortality: starvation, predation, and advection out of a suitable habitat. These 3 pillars are connected by the concept of growth, in which the rate at which a larva grows impacts its susceptibility to each of the pillars of mortality. A collection of hypotheses discussed throughout these studies comprise the framework of the Growth-Survival paradigm, which emphasizes the importance of fast growth for increasing chances of survival through the larval stage and recruitment into the fishery (Anderson 1988). Larval growth is fueled by the amount of energy and nutrients consumed by a larva to carry out metabolic processes. Therefore, growth, and ultimately survival and recruitment, of a larva is strongly linked to its feeding success, the amount of carbon consumed. While quantifying a larva's feeding success can help explain its growth performance, it is also important to identify how food quality, inferred by the types of prey being consumed, also affect growth of an individual. Cushing's Match-Mismatch Hypothesis (1975, 1990) stated that recruitment events would be strong in years when larval emergence overlapped temporally and spatially with suitable, abundant prey. However, many experiments have failed to support this hypothesis. One of the major reasons why there has been a failure to find a relationship between prey abundance and larval growth lies in the term "suitable prey" (Robert et al. 2014). While larval fish may have the morphology to consume various potential types of prey, many marine fish species demonstrate preference for one or few prey taxa during the larval stage, and consumption of these prey by larvae has resulted in faster growth and increased chances of survival (Robert et al. 2009; Sponaugle et al. 2010; Murphy et al. 2013). Therefore, if we build on Cushing's work, it is likely that in years when the abundance of the preferred prey taxon overlaps with larval fish in space and time, there will be fast larval growth, higher chances of survival, and stronger recruitment events.

While larval growth is fueled by energy and nutrients obtained through the diet, the amount of energy necessary for growth is mediated by temperature. Likewise, the growth and development of planktonic prey taxa is also mediated by physical oceanographic conditions. Therefore, recruitment success and its dependence on the spatial and temporal overlap of larval fish and their prey, is ultimately rooted in physical oceanographic and climatic conditions through a series of bottom-up processes (Cushing 1975). In order to assess recruitment variability, it is necessary to understand direct relationships between physical oceanographic variables and the growth of the species of interest, as well as indirect relationships among oceanographic variables and the dynamics of preferred prey species that larvae rely on for growth and survival. It is important to address recruitment variability as a process that is highly dependent on a suite of ecosystem processes and conditions, and piecing together the puzzle of recruitment drivers requires an understanding of the entire ecosystem.

As a result of the strong recruitment events of 2011 and 2013, redfish currently comprise more than 90% of the demersal biomass in the GSL. Redfish from these cohorts continue to grow, have mostly all reached minimum commercial size, and the reopening of the commercial fishery is on the horizon. The return of the redfish posed two primary ecological questions for researchers to address: 1) What were the conditions that facilitated the unprecedentedly large recruitment event of 2011 and the strong cohort of 2013?; and 2) What impacts will redfish impose on the rest of the GSL ecosystem as they re-establish themselves as a common fish species? Research presented in this thesis focused on the former of these questions.

In order to identify drivers of recruitment of larval redfish in the GSL, I first identified important prey taxa in the diet that supply larvae with carbon and other nutrients. I used previously collected larval redfish from the years 1997-2000 to identify commonly consumed prey species, and developmental stages, and how diet composition varied with larval growth on an annual basis. I also compared diet composition to environmental prey fields in order to calculate preferential feeding on certain prey taxa. Next I described the nature of the relationship between the quality and quantity of the diet and larval redfish growth. I extracted otoliths and identified diets from larvae collected in 1999 and 2000 in order to compare feeding success and diet composition to larval condition and daily growth increment widths, with a special emphasis on identifying whether consumption of the preferred prey taxa had an effect on recent larval redfish growth, as seen in other species. Lastly, using a weight-of-evidence approach, I compiled a list of oceanographic variables, both biotic and abiotic, that play a role in larval redfish metabolism/growth or in prey abundance/development, and described the nature of the relationships between these variables and historic redfish recruitment indices. Long-term environmental series collected by DFO were used for this project. Examination of these relationships led to identification of likely drivers of redfish recruitment that must occur in order to produce strong year-class events by using a weight-of-evidence approach.

I found that redfish larval frequently consume 8 different types of prey throughout the early larval stage. Within the size ranges examined in our study (4.6 mm – 10.2 mm), there was no change in diet composition or mean prey size with increasing larval size. *Calanus finmarchicus* contributed the largest proportion of carbon to the larval redfish diet across all years, with eggs contributing at least 25% of all carbon to the diet and nauplii contributing at least 15% in each year. In some years and environments, larval redfish showed a preference for *C. finmarchicus* egg consumption. As a result of its large contribution of carbon to the larval diet, and a demonstrated preference for egg consumption, *C. finmarchicus* was identified as an important prey species for the survival of larval redfish in the GSL. Results from Burns et al. (2020) were the first to utilize taxon-specific identification to identify components of the larval redfish diet in the GSL, as well as identify a prey preference in GSL redfish larvae. My results supported and expanded upon the earlier work of Runge and de Lafontaine (1996) who had hypothesized a critical connection between *Calanus* sp. and redfish in the GSL, a hypothesis that I was able to investigate throughout the entirety of my dissertation work.

When I analyzed redfish otolith microstructure to describe redfish growth, I found a change in growth autocorrelation patterns around 8 days post-extrusion where daily otolith increment widths were strongly correlated during the first 8 days post-extrusion, and were weakly correlated thereafter. I identified this as a likely critical period in which larvae must obligately feed exogenously. Prior to 8 days post-extrusion, larval redfish are likely utilizing maternally-invested nutrients from remaining yolk, a consistent source of nutrition leading to strong daily growth autocorrelation. At the onset of exogenous feeding, nutrients consumption is less stable because larvae must forage for prey and daily growth was weakly correlated to growth patterns that immediately followed extrusion. Therefore, I grouped larvae for our project based on age: larvae less than 8 days post-extrusion that are likely still utilizing maternally-invested nutrients, and larvae 8 days post-extrusion and older that are likely obligate exogenous feeders. I also found that recent daily growth was most closely correlated with larval body depth, which we used as a proxy for growth throughout the project. I found a positive relationship between the amount of carbon consumed and larval body depth at age in larvae younger than 8 days post-extrusion, but no relationship between the two variables in larvae 8 days post-extrusion or older. Larval body depth at age was best explained in older larvae when sources of carbon were split between mobile (naupliar, copepodite stages of prey) and immobile (egg stage) carbon. There was a positive relationship between the amount of carbon consumed from mobile prey and larval body depth at age, suggesting that the developmental stage of prey was important in driving larval condition and fast growth in redfish larvae that were obligate exogenous feeders. Since *C. finmarchicus* is the most important contributor of carbon to the larval diet, I concluded that an overlap in space and time between redfish larvae and *C. finmarchicus* nauplii was important for facilitating fast growth of larval redfish and likely, strong recruitment events. Results from Burns et al. (2021) highlighted the importance of the type of prey, and not just the quantity of prey ingested, for larval redfish condition and growth. This project also utilized an uncommon statistical analysis, non-parametric local density estimation (Davison and Hinkley, 1997). This approach was necessary in order to accurately compare redfish larvae across different developmental stages, in which morphology, swimming capabilities, and sensory capabilities vary considerably.

I compiled a list of oceanographic variables that were hypothesized to drive recruitment of redfish populations around the world, from nearby regions such as the Flemish Cap to farther populations found in the Barents Sea. In addition, I included *C. finmarchicus* abundance and phenology as potential drivers of recruitment based on results from the first two thesis chapters. I identified 4 likely drivers of recruitment: CIL volume, *C. finmarchicus* phenology, *C. finmarchicus* abundance, and SSB. There was a positive relationship between *C. finmarchicus* phenology, abundance, and redfish recruitment strength. Strong redfish recruitment only occurred when *C. finmarchicus* phenology was later than the historical mean, and more abundant than the historical mean. This supports Cushing's (1975) Match-Mismatch Hypothesis, as larval redfish are more likely to survive and be recruited during years in which prey are abundant and occurring in the environment at the same time as larval redfish. There was a negative relationship between CIL volume and redfish recruitment strength. Strong redfish recruitment only occurred when CIL volume was lower than the historical mean. When CIL volume is low, the water mass is likely warmer and thinner, presenting a more permissive environment for newly-extruded redfish to pass through on their vertical migration towards surface waters. There was also a negative relationship between SSB and redfish recruitment strength, with the strongest recruitment events occurring when SSB was at its historical minimum. Adult redfish are cannibalistic, and SSB is likely a density-dependent driver of recruitment. Strong recruitment only occurred during years in which all of these conditions were met. While using a weight-of-evidence approach to execute our objective was not our initial plan, this pivot in experimental planning allowed us to really delve into our mechanistic understanding of bottom-up processes that could potentially drive redfish recruitment. Results from this study generated testable hypotheses for statistical modelling in the future when more environmental data corresponding to strong recruitment years are available. For the present, these results provide redfish stock assessment biologists with potential drivers of recruitment that can be monitored annually to help predict natural population fluctuations. Our list of potential drivers to be monitored for redfish recruitment can be added to drivers of recruitment for other GSL species, such as Atlantic mackerel and capelin, that have been previously investigated using other statistical analyses (Plourde et al. 2015 ; Lehoux et al. 2022).

One of the overarching goals of this project was to provide DFO with results that would aid in the creation of an ecosystem-based approach to fishery management (EBFM) for the future commercial redfish fishery. EBFM uses a holistic approach to manage fisheries by acknowledging that fish stocks and their dynamics do not act independently from other species within the ecosystem and are ultimately rooted in physical oceanographic processes. Identification of recruitment drivers of other commercially fished species in the GSL has already been performed and published for the same goal of moving towards an EBFM approach for many commercial fisheries in the region (Plourde et al. 2015; Brosset et al. 2019; Brosset et al. 2020). All of the identified drivers of redfish recruitment are measured throughout the GSL by DFO and can be used as potential predictors of successful redfish recruitment events in the future. Redfish are a spasmodically-recruiting fish species, and successful recruitment events can occur on the timeframe of decades. One successful recruitment event can supply the fishery with enough fishable biomass until the next strong year-class occurs. In addition, redfish are a slow-growing species and are not recruited into the fishery until they are approximately 7-9 years of age. Therefore, identification of drivers of redfish recruitment that could alert fisheries managers of a strong recruitment event up to 7 years before individuals are recruited into the fishery could allow management to prepare and adjust fishing strategies to maximize profit as well as maintain sustainability of the stock.

While the conclusions I have made during my studies have advanced knowledge of the early life history of redfish in the GSL, there is still plenty of research that can be performed in the future to further our understanding of this species. Expanding on the conclusions from Chapter 1, future research should assess the diet of larval redfish during recent years in order to compare results to our redfish collection from poor recruitment years in the late 1990s, early 2000s. I hypothesize that larval redfish diet composition and feeding preferences will be similar to those presented in Chapter 1, but future research should investigate whether changes in decadal temperature regimes (warmer waters in the 2010s) have changed larval diet composition or preference. In addition, analyses of larval redfish diet should be performed during the later larval stage/late summer months in order to better describe ontogenetic shifts in diet composition that occur within the first few months post-extrusion. A shift in diet composition outside of the scope of larval sizes investigated in Chapter 1 may reflect a critical period during the larval stage in which specific prey taxon become more or less important for the larval diet. Larval redfish collection during the late summer months would also help us expand on research performed in Chapter 2 on larval redfish growth. Future research should investigate patterns of larval redfish growth using similar otolith microstructure analyses and autocorrelation in order to identify ages during which there is a shift in growth patterns and likely a critical period for larval survival. Additional laboratory research should also compare and contrast the nutritional composition of *C. finmarchicus* eggs and nauplii, as well as foraging behaviors of young larval redfish, in order to better understand why is it advantageous for larval redfish to consume nauplii instead of eggs, and whether this advantage is due to differences in nutritional composition of nutrients such as fatty acids or if this advantage has a behavioral and sensory basis. Finally, I presented likely potential drivers of redfish recruitment in Chapter 3. This chapter sets up multiple hypotheses for fisheries scientists to investigate and test in the future in order to see whether the likely drivers of recruitment described are present during future strong recruitment events, and/or whether these relationships between likely drivers and recruitment success breakdown over time with dramatic shifts in climatic regimes.

Throughout my doctoral studies, I’ve had the bittersweet realization that recruitment studies are underappreciated and only quietly communicated within a small field. Rice and Browman (2014) described a dramatic decrease in the number of recruitment-based publications post-1990. One of their hypotheses for this decrease is that many researchers might believe that understanding recruitment variability is “too difficult” and choose to focus their studies elsewhere. However, an understanding of recruitment is critical in proper management of commercial fisheries, and will become increasingly important to monitor the status of fisheries in the face of global climate change. It has become my personal goal throughout this academic journey to effectively communicate the methodologies used in these studies, and the applicability of the results of these publications in order to demonstrate to fisheries science community that understanding recruitment processes is possible and incredibly important for understanding stock dynamics of our world's fisheries. I hope that my dissertation work is a step in the right direction towards rejuvenating recruitment science studies and communicating the importance of this critical process for the future.

RÉFÉRENCES BIBLIOGRAPHIQUES

Agostini, V.N., Bakun, A., Francis, R.C. (2007). Larval stage controls on Pacific sardine recruitment variability: high zooplankton abundance linked to poor reproductive success. *Marine Ecology Progress Series*, 345:237-244.

Anderson, J.T. (1984). Early life history of redfish (*Sebastes* spp.) on Flemish Cap. *Canadian Journal of Fisheries and Aquatic Science*, 41:1106-1116.

Anderson, J.T. (1988). A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwestern Atlantic Fisheries Science*, 8:55-66.

Anderson, J.T. (1994). Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp. *Marine Ecology Progress Series*, 104:211-226.

Bainbridge, V. (1965). A preliminary study of *Sebastes* larvae in relation to the planktonic environment of the Irminger Sea. *Special Publication International Commission for the Northwest Atlantic Fisheries*, 6:303-308.

Bainbridge, V., McKay, B.J. (1968). The feeding of cod and redfish larvae. *Special Publication International Commission for the Northwest Atlantic Fisheries,* 7:187-218.

Bailey, K.M., Houde, E.D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25:1-83.

Bailey, K.M., Canino, M.F., Napp, J.M., Spring, S.M., Brown, A.L. (1995). Contrasting years of prey levels, feeding conditions and mortality of larval walleye *Theragra chalcogramma* in the western Gulf of Alaska. *Marine Ecology Progress Series*, 119: 11-23.

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661-664.

Bergvik, M., Leiknes, O., Altin, D., Rennan, R., Olsen, Y. (2012). Dynamics of the lipid content and biomass of *Calanus finmarchicus* (copepodite V) in a Norwegian Fjord. *Lipids*, 47:881-895.

Beverton, R.J., Holt, S.J. (1957). On the dynamics of exploited fish populations. Fishery Investigations Series II Volume XIX, Ministry of Agriculture, Fisheries and Food.

Blais, M., Galbraith, P.S., Plourde, S., Scarratt, M., Devine, L., Lehoux, C. (2019). Chemical and biological oceanographic conditions in the estuary and Gulf of St. Lawrence during 2017. *DFO Canadian Science Advisory Secretariat Research Document*, 2019/009. iv + 56 pp.

Blais, M., Galbraith, P.S., Plourde, S., Devine, L., Lehoux, C. (2021). Chemical and biological oceanographic conditions in the estuary and Gulf of St. Lawrence during 2019. *DFO Canadian Science Advisory Secretariat Research Document,* 2021/002, iv + 66 pp.

Blaxter, J.H.S. (1986). Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*, 115:98-114.

Brander, K.M. (1992). A re-examination of the relationship between cod recruitment and *Calanus finmarchicus* in the North Sea. *ICES Journal of Marine Science Symposia*, 195:393-401.

Brochier, T., Echevin, V., Tam, J., Chaigneau, A., Goubanova, K., Bertrand, A. (2013). Climate change scenarios experiments predict a future reduction in small pelagic fish recruitment in the Humboldt Current system. *Global Change Biology*, 19:1841-1853.

Brodziak, J. and O'Brien, L. (2005). Do environmental factors affect recruits per spawner anamolies of New England groundfish? *ICES Journal of Marine Science*, 62:1394-1407.

Brosset, P., Bourdages, H., Blais, M., Scarratt, M., & Plourde, S. (2019) Local environment affecting northern shrimp recruitment: a comparative study of Gulf of St. Lawrence stocks. *ICES Journal of Marine Science,* 76:974-986.

Brosset, P., Smith, A.D., Plourde, S., Castonguay, M., Lehoux, C., Van Beveren, E. (2020). A fine-scale multi-step approach to understand fish recruitment variability. *Scientific Reports*, 10: 16064.

Brown-Vuillemin, S., Chabot, D., Nozères, C., Tremblay, R., Sirois, P., Robert, D. (2022) Diet composition of redfish (*Sebastes* sp.) during periods of population collapse and massive resurgence in the Gulf of St. Lawrence. *Frontiers in Marine Science*, 9: 963039.

Buckley, L.J., and Lough, R.G. (1987). Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. *Canadian Journal of Fisheries and Aquatic Science*, 44:14-25.

Burns, C.M., Lauzon, F., Plourde, S., Sirois, P., Robert, D. (2020). Interannual variability of diet composition and prey preference of larval redfish (*Sebastes* spp.) in the Gulf of St. Lawrence. *Journal of Plankton Research*, 42:581-594.

Burns, C.M., Pepin, P., Plourde, S., Veillet, G., Sirois, P., Robert, D. (2021). Revealing the relationship between feeding and growth of larval redfish (*Sebastes* sp.) in the Gulf of St. Lawrence. *ICES Journal of Marine Science*, 78:3757-3766.

Burrow, J.E., Horwood, J.W., Pitchford, J.W. (2011). The importance of variable timing and abundance of prey for fish larval recruitment. *Journal of Plankton Research*, 33:1153-1162.

Caddy, J.F., and Gulland, J.A. (1983). Historical patterns of fish stocks. *Marine Policy*, 7:267-278.

Caddy, J.F., and Agnew, D.J. (2004). An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. *Reviews in Fish Biology and Fisheries*, 14: 43-112.

Castellani, C., Irigoien, X., Harris, R.P., Lampitt, R.S. (2005). Feeding and egg production of *Oithona similis* in the North Atlantic. *Marine Ecology Progres Series*, 288:173-182.

Chambers, R.C., Leggett, W.C. (1987). Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. *Canadian Journal of Fisheries and Aquatic Sciences*, 44:1936-1947.

Chesson, J. (1978). Measuring preference in selective predation. *Ecology*, 59:211-215.

Clemmesen, C., Sanchez, R., Wongtschowski, C. (1997). A regional comparison of the nutritional condition of SW Atlantic anchovy larvae, *Engraulis anchoita*, based on RNA/DNA ratios. *Archive of Fishery and Marine Research*, 45:17-43.

Cushing, D.H. (1975). Marine ecology and fisheries. Cambridge University Press, Cambridge, England.

Cushing, D.H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26:249-294.

Davison, A.C., Hinkley, D.B. (1997). Bootstrap methods and their application. *Cambridge University Press*, New York.

Demontigny, F., Ouellet, P., Sirois, P., Plourde, S. (2012). Zooplankton prey selection among three dominant ichthyoplankton species in the northwest Gulf of St. Lawrence. *Journal of Plankton Research*, 34:221-235.

DFO. (2010). Assessment of redfish stocks (*Sebastes fasciatus* and *S. mentella*) in units 1 and 2 in 2009. *DFO Canadian Science Advisory Secretariate Science Advisory Report*, 2010/037.

DFO. (2018). Assessment of redfish stocks (*Sebastes mentella* and *S. fasciatus*) in units 1 and 2 in 2017. *DFO Canadian Science Advisory Secretariate Science Advisory Report*, 2018/032.

DFO. (2020). Redfish (*Sebastes mentella* and *S. fasciatus*) stock assessment in units 1 and 2 in 2019. *DFO Canadian Science Advisory Secretariat Science Advisory Report* 2020/019.

Dower, J.R., Pepin, P., Kim, G. (2009). Covariation in feeding success, size-at-age and growth in larval radiated shanny (*Ulvaria subbifurcata*): insights based on individuals. *Journal of Plankton Research*, 31:235-247.

Duplisea, D.E., Bourdages, H., Brassard, C., Gauthier, J., Lambert, Y., Nitschke, P.C., Valentin, A. (2016). Fitting a statistical catch at length model (NFT-SCALE) to unit 1+2 redfish (*Sebastes mentella* and *Sebastes fasciatus*). *Canadian Science Advisory Secretariat Research Document*, 2016/095.

Duplisea, D.E. (2018). Fisherman's historical knowledge leads to a re-evaluation of redfish catch. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 10:3-11.

Duplisea, D.E., Merette, D., Roux, M-J., Benoît, H., Blais, M., Galbraith, P., Plourde, S. (2020). gslea: the Gulf of St. Lawrence ecosystem approach data matric R-package. R pacakage version 0.1 https://github.com/duplisea/gslea.

Economou, A.N. (1991) Food and feeding ecology of five gadoid larvae in the northern North Sea. *ICES Journal of Marine Science*, 47:339-351.

Einarsson, H. (1960). The fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskideildar*, 2:1-67.

Ferron, A., Legget, W.C. (1994) An appraisal of condition measures for marine fish larvae. *Advances in Marine Biology*, 30: 217-303.

Field, J.C., Ralston, S. (2005). Spatial variability in rockfish (*Sebastes* spp.) recruitment events in the California Current System. *Canadian Journal of Fisheries and Aquatic Science*, 62: 2199-2210.

Fortier, L., and Harris, R.P. (1989). Optimal foraging and density-dependent competition in marine fish larvae. *Marine Ecology Progress Series*, 51:19-33.

Fuiman, L.A., Connelly, T.L., Lowerre-Barbieri, S.K., McClelland, J.W. (2015). Egg boons: central components of marine fatty acid food webs. *Ecology*, 96:362-372.

Galbraith, P.S., Chassé, J., Caverhill, C., Nicot, P., Gilbert, D., Lefaivre, D., Lafleur, C. (2019). Physical oceanographic conditions in the Gulf of St. Lawrence during 2018. *DFO Canadian Science Advisory Secretariat Research Document* 2019/046. iv + 79 p.

Galbraith, P.S., Chassé, J., Shaw, J.-L., Dumas, J., Caverhill, C., Lefaivre, D., Lafleur, C. (2021). Physical oceanographic conditions in the Gulf of St. Lawrence during 2020. *DFO Canadian Science Advisory Secretariat Research Document*, 2021/045, iv + 81 pp.

Gascon, D. (ed.) (2003). Redfish multidisciplinary research zonal program (1995-1998): final report. *Canadian Technical Report of Fisheries and Aquatic Sciences* 2452: xiii + 139 p.

Govoni, J.J., Ortner, P.B., Al-Yamani, F., Hill, L.C. (1986). Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croacker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. *Marine Ecology Progress Series*, 28:175-183.

Hammill, C., Evans, G. (2015). Probability distribution estimation dependent on covariates. https://github.com/cfhammill/ogmap/

Heath, M.R., and Lough, R.G. (2007). A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fisheries Oceanography*, 16:169-185.

Hirch, H.J., Kattner, G. (1993). Egg production and lipid content of *Calanus glacialis* in spring: indication of a food-dependent and food-independent reproductive mode. *Marine Biology*, 117:615-622.

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 20:1-228.

Houde, E.D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, 2:17-29.

Houde, E.D. and Zastrow, C.E. (1993). Ecosystem- and taxon-specific dynamic and energetics properities of larval fish assemblages. *Bulletin of Marine Science*, 53:290-335.

Houde, E.D., (2008). Emerging from Hjort's shadow. *Journal of Northwestern Atlantic Fisheries Science*, 41:53-70.

Huebert, K.B., Patsch, J., Hufnagl, M., Kreus, M., Peck, M.A. (2018). Modeled larval fish prey fields and growth rates help predict recruitment success of cod and anchovy in the North Sea. *Marine Ecology Progress Series*, 600:111-126.

Hunter, J.R. (1981). Feeding ecology and predation of marine fish larvae. *In:* Marine fish larvae. Morphology, ecology and relation to fisheries. R. Laster (ed.) University of Washington Press, Seattle, p. 34-77.

Jenkins, G.P., Conron, S.D., Morison, A.K. (2010). Highly variable recruitment in an estuarine fish is determined by salinity stratification and freshwater flow: implications of a changing climate. *Marine Ecology Progress Series*, 417:249-261.

Kane, J. (1984). The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Marine Ecology Progress Series*, 16:9-20.

Karamushko, O., Karamushko., L. (1995) Feeding and bioenergetics of the main commercial fish in the Barents Sea on different stages of ontogenesis. *Apatity*, 220 pp. (in Russian)

Klein, E.S., Smith, S.L., Kritzer, J.P. (2017). Effects of climate change on four New England groundfish species. *Reviews in Fish Biology and Fisheries*, 27:317-338.

Laidig, T.E., Ralston, S., Bence, J.R. (1991) Dynamics of growth in the early life history of shortbelly rockfish *Sebastes jordani*. *Fisheries Bulletin*, 89:611-621.

Lasker, R. (1975). Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bulletin*, 73: 453-462.

Lasker, R. (1981). The role of a stable ocean in larval fish survival and subsequent recruitment. In: Lasker, R. (Ed.), Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries. Univ. Washington Press, Seattle, pp. 80-87 (131pp).

Laurel, B.J., Brown, J.A., Anderson, R. (2001) Behaviour, growth and survival of redfish larvae in relation to prey availability. *Journal of Fish Biology*, 59:884-901.

Lefrançois, C., and Claireaux, G. (2003). Influence of ambient oxygenation and temperature on metabolic scope and scope for heart rate in the common sole *Solea solea*. *Marine Ecology Progress Series*, 259:273-284.

Leggett, W.C., Deblois, E. (1994). Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research*, 32:119-134.

Lehoux, C., Plourde, S., Chamberland, J.-M., Benoît, H. (2022). Linking interannual variation in capelin abundance indices in the Gulf of St. Lawrence to environmental proxies of bottom-up regulation of survival and cohort strength. *DFO Canadian Science Advisory Secretariat Research Document*, .2021/nnn. vi + xx p.

Licandeo, R., Duplisea, D.E., Senay, C., Marentette, J.R., McAllister, M.K. (2020). Management strategies for spasmodic stocks: a Canadian Atlantic redfish fishery case study. *Canadian Journal of Fisheries and Aquatic Sciences*, 77:684-702.

Llopiz, J.K., Cowen, R.K. (2008) Precocious, selective and successful feeding of larval billfishes in the oceanic Straits of Florida. *Marine Ecology Progress Series*, 358:231-244.

Llopiz, J.K. (2013) Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: A literature synthesis. *Journal of Marine Systems*, 109-110:69-77.

Longhurst, A. (2002). Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fisheries Research,* 56:125-131.

MacKenzie, B.R. (2000). Turbulence, larval fish ecology and fisheries recruitment: a review of field studies. *Oceanologica Acta*, 23:357-375.

Markel, R.W., Lotterhos, K.E., Robinson, C.L.K. (2017). Temporal variability in the environmental and geographic predictors of spatial-recruitment in nearshore rockfishes. *Marine Ecology Progress Series*, 574:94-111.

McLaren, L.A., Sevigny, J.M., Corkett, C.J. (1988). Body sizes, development rates, and genome sizes among *Calanus* species. *Hydrobiologia*, 167:275-284.

Miller, T.J., Crowder, L.B., Rice, J.A., Marschall, E.A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*, 45:1657-1670.

Mitsuzawa, A., Miyamoto, H., Ueda, H. (2017). Feeding selectivity of early-stage fish larvae on the nauplii and eggs of different copepod species. *Plankton Benthos Research*, 12:115-122.

Montagnes, D.J.S., Dower, J.F., Figueiredo, G.M. (2010). The protozooplankton - ichthyoplankton trophic link: an overloked aspect of aquatic food webs. *Journal of Eukaryotic Microbiology*, 57:223-228.

Moser, H.G., Boehlert, G.W. (1991). Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *Environmental Biology of Fishes*, 30:203-224.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2012). Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. *Canadian Journal of Fisheries and Aquatic Science*, 69:1340-1351.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2013). Interannual variation in larval abundance and growth in snapper *Chrysophrys auratus* (Sparidae) is related to prey availability and temperature. *Marine Ecology Progress Series*, 487:151-162.

Paradis, V., Sirois, P., Castonguay, M., Plourde, S. (2012). Spatial variability in zooplankton and feeding of larval Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. *Journal of Plankton Research*, 34:1064-1077.

Pearre, S., Jr. (1982). Estimating prey preference by predators: uses of various indices, and a proposal of another based on X^2. *Canadian Journal of Fisheries and Aquatic Sciences*, 39:914-923.

Pearre, S. (1986). Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Marine Ecology Progress Series*, 27:299-314.

Penney, R.W., Evans, G.T. (1985). Growth histories of larval redfish (*Sebastes* spp.) on an offshore atlantic fishing bank determined by otolith increment analysis. *Canadian Journal of Fisheries and Aquatic Science*, 42: 1452-1464.

Pepin, P., Penney, R.W. (1997). Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? *Journal of Fisheries Biology*, 51:84-100.

Pepin, P., Evans, G.T., Shears, T.H. (1999). Patterns of RNA/DNA ratios in larval fish and their relationship to survival in the field. *ICES Journal of Marine Science*, 56, 697-706.

Pepin, P. Dower, J.F., Benoît, H.P. (2001). The role of measurement error on the interpretation of otolith increment width in the study of growth in larval fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 58:503-518.

Pepin, P., Robert, D., Bouchard, C., Dower, J.F., Falardeau, M., Fortier, L., Jenkins, G.P., Leclerc, V., Levesque, K., Llopiz, J.K., Meekan, M.G., Murphy, H.M., Ringuette, M., Sirois, P., Sponaugle, S. (2015). Once upon a larva: revisiting the relationship between feeding success and growth in fish larvae. *ICES Journal of Marine Science*, 72:359-373.

Pepin, P. (2016). Reconsidering the impossible – linking environmental drivers to growth, mortality, and recruitment of fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 73:205-215.

Pershing, A.J., Greene, C.H., Jossi, J.W., O'Brien, L., Brodziak, J.K.T., Bailey, B.A. (2005). Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. *ICES Journal of Marine Science*, 62:1511-1523.

Plourde, S., and Joly, P. (2008). Comparison of in situ egg production rate in *Calanus finmarchicus* and *Metridia longa*: discriminating between methodological and species-specific effects. *Marine Ecology Progress Series*, 353**:**165-175.

Plourde, S., Starr, M., Devine, L., St-Pierre, J.-F., St-Amand, L., Joly, P., Galbraith, P.S. (2014). Chemical and biological oceanographic conditions in the estuary and Gulf of St. Lawrence during 2011 and 2012. *DFO Canadian Science Advisory Secretariat Research Document.* 2014/049. v + 46 pp.

Plourde, S., Grégoire, F., Lehoux, C., Galbraith, P.S., Castonguay, M., Ringuette, M. (2015). Effect of environmental variability on body condition and recruitment success of Atlantic Mackerel (*Scomber scombrus* L.) in the Gulf of St. Lawrence. *Fisheries Oceanography*, 24:347-363.

Pörtner, H.O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Guiliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F.J., Serendero, I., Sirabella, P., Thorkildsen, S., Zakhartsev, M. (2001). Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research*, 21:1975-1997.

Quattrocchi, F., and Garofalo, G. (2022). Revealing environmental synchronicity that enhances anchovy recruitment in the Mediterranean Sea. *Scientific Reports*, 12:5600.

Reiss, C., McLaren, I., Avendaño, P., Taggart, C. (2005). Feeding ecology of silver hake larvae on the Western Bank, Scotian Shelf, and comparison with Atlantic Cod. *Journal of Fish Biology*, 66 :703-720.

Rice, J., and Browman, H.I. (2014). Where has all the recruitment research gone, long time passing? *ICES Journal of Marine Science*, 71:2293-2299.

Ringuette, M., Castonguay, M., Runge, J.A. et al. (2002). Atlantic mackerel (*Scomber scombrus*) recruitment fluctuations in relation to copepod production and juvenile growth. *Canadian Journal of Fisheries and Aquatic Sciences*, 59:646-656.

Robert, D., Castonguay, M., Fortier, L. (2008). Effects of intra- and inter-annual variability in prey field on the feeding selectivity of larval Atlantic mackerel (*Scomber scombrus*). *Journal of Plankton Research*, 30:673-688.

Robert, D., Castonguay, M., Fortier, L. (2009). Effects of preferred prey density and temperature on feeding success and recent growth in larval mackerel of the southern Gulf of St. Lawrence. *Marine Ecology Progress Series*, 377:227-237.

Robert, D., Levesque, K., Gagné, J.A., Fortier, L. (2011). Change in prey selectivity during the larval life of Atlantic cod in the southern Gulf of St. Lawrence. *Journal of Plankton Research*, 33:195-200.

Robert, D., Murphy, H.M., Jenkins, G.P., Fortier, L. (2014a). Poor taxonomical knowledge of larval fish prey preference in impeding our ability to assess the existence of a “critical period” driving year-class strength. *ICES Journal of Marine Science*, 71:2042-2052.

Robert, D., Pepin, P., Dower, J.F., Fortier, L. (2014b). Individual growth history of larval Atlantic mackerel is reflected in daily condition indices. *ICES Journal of Marine Science*, 71:1001-1009.

Robichaud-LeBlanc, K.A., Courtenay, S.C., Hanson, J.M. (1997). Ontogenetic diet shifts in age-0 striped bass, *Morone saxatilis*, from the Miramichi River estuary, Gulf of St. Lawrence. *Canadian Journal of Zoology*, 75:1300-1309.

Rønnestad, I., Thorsen, A., Finn, R.N. (1999). Fish larval nutrition: a review of recent advances in the roles of amino acids. *Aquaculture*, 177:201-216.

Runge, J.A., de Lafontaine, Y. (1996). Characterization of the pelagic ecosystem in surface waters of the northern Gulf of St. Lawrence in early summer: the larval redfish-*Calanus*-microplankton interaction. *Fisheries Oceanography*, 5:21-37.

Sargent, J.R., McEvoy, L.A., Bell, J.G. (1997). Requirements, presentation and sources of polyunsaturated fatty acids in marine fish larval feeds. *Aquaculture*, 155:117-127.

Sargent, J., Bell, G., McEvoy, L., Tocher, D., Estevez, A. (1999). Recent developments in the essential fatty acid nutrition of fish. *Aquaculture*, 177:191-199.

Schoener, T.W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2:369-404.

Senay, C., Ouellette-Plante, J., Bourdages, H., Bermingham, T., Gauthier, J., Parent, G., Chabot, D., and Duplisea, D. (2021). Unit 1 Redfish (*Sebastes mentella* and *S. fasciatus*) stock status in 2019 and updated information on population structure, biology, ecology, and current fishery closures. *DFO Canadian Science Advisory Secretariat Research Document* 2021/015. Xi + 119 p.

Sévigny, J-M., Gagné, P., de Lafontaine, Y., Dodson, J.J. (2000). Identification and distribution of larvae of redfish (*Sebastes fasciatus* and *S. mentella*: Scorpaenidae) in the Gulf of St. Lawrence. *Fishery Bulletin*, 98:375-388.

Sorochan, K. A., Plourde, S., Morse, R., Pepin, P., Runge, J., Thompson, C., & Johnson, C.L. (2019). North Atlantic right whale (*Eubalaena glacialis*) and its food:(II) interannual variations in biomass of *Calanus* spp. on western North Atlantic shelves. *Journal of Plankton Research*, 41:687-708.

Spencer, P.D., and Collie, J.S. (1997). Patterns of population variability in marine fish stocks. *Fisheries Oceanography* 6:188–204.

Sponaugle, S., Grorud-Colvert, K., Pinkard, D. (2006). Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Marine Ecology Progress Series*, 308:1-15.

Sponaugle, S., Walter, K.D., Denit, K.L., Llopiz, J.K., Cowen, R.K. (2010). Variation in pelagic larval growth of Atlantic billfishes: the role of prey composition and selective mortality. *Marine Biology*, 157:839-849.

Starr, M., Runge, J.A., Therriault, J-C. (1999). Effects of diatom diets on the reproduction of the planktonic copepod *Calanus finmarchicus*. *Sarsia*, 84:379-389.

St. John, M.A., Clemmesen, C., Lund, T., Köster, T. (2001) Diatom production in the marine environment: implications for larval fish growth and condition. *ICES Journal of Marine Science*, 58:1106-1113.

St-Pierre, J.F., de Lafontaine, Y. (1995). Fecundity and reproduction characteristics of beaked redfish (*Sebastes fasciatus* and *S. mentella*) in the Gulf of St. Lawrence. *Canadian Technical Report of Fisheries and Aquatic Sciences*, No. 2059, pp. 32.

Sysoeva T.K. (2000). Diet and survival of larvae and juveniles of redfish from genus *Sebastes* in the Norwegian Sea. In the Marine hydrobiological research. Moscow, *VNIRO Press. P.* 157-170. (in Russian)

Takasuka, A., Aoki, I., Mitani, I. (2003). Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicas* in Sagami Bay. *Marine Ecology Progress Series*, 252:223- 238.

Takasuka, A., Oozeki, Y., Kimura, R., Kubota, H., Aoki, I. (2004). Growth-selective predation hypothesis revisited for larval anchovy in offshore waters: cannibalism by juveniles versus predation by skipjack tunas. *Marine Ecology Progress Series*, 278:297-302.

Taning, A.V. (1961) Larval and postlarval stages of *Sebastes* species and *Helicolenus dactylopterus*. Rapports et Procès-Verbeaux des Réunions du Conseil International pour l'Exploration de la Mer, 150:234-240.

Voss, R., Dickmann, M., Schmidt, J.O. (2009). Feeding ecology of sprat (*Spratus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the German Bight, North Sea. *Oceanologia*, 51:117-138.

Ware, D.M. (1975). relation between egg size, growth, and natural mortality of larval fish. *Journal of the Fisheries Research Board of Canada*, 32:2503-2512.

Watanabe, T., Kiron, V. (1994). Prospects in larval fish dietetics. *Aquaculture*, 124:223-251.

Wells, N.A. (1935). Change in rate of respiratory metabolism in a teleost fish induced by acclimatization to high and low temperature. *Biological Bulletin*, 69:361-367.

Werner, E.E., Hall, D.J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, 55:1042-1052.

Werner, E.E., Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology, Evolution, and Systematics*, 15:393-425.

Wheeler, S.G. (2015). Biological and oceanographic drivers of larval growth, settlement, and recruitment of rockfishes (*Sebastes* spp.). Ph.D. Dissertation, University of California, Davis.

Wilson, J.R., Broitman, B.R., Caselle, J.E., Wendt, D.E. (2008). Recruitment of coastal fishes and oceanographic variability in central California. *Estuarine, Coastal and Shelf Science*, 79:483-490.

Yu, H., Yu, H., Ito, S., Tian, Y., Wang, H., Liu, Y., Xing, Q., Bakun, A., Kelly, R.M. (2020). Potential environmental drivers of Japanese anchovy (*Engraulis japonicus*) recruitment in the Yellow Sea. *Journal of Marine Systems*, 212: 103431.