AN ANALYSIS OF LARVAL FISH COMMUNITY STRUCTURE AND CAPELIN (*MALLOTUS VILLOSUS*) EARLY LIFE DYNAMICS ON THE NORTHEAST COAST OF NEWFOUNDLAND

By

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ABSTRACT

Coastal embayments of Newfoundland are key spawning and nursery areas for numerous socioeconomically and ecologically important fish species. Survival during the vulnerable larval stage regulates recruitment and adult population dynamics. Larval fish community structure and larval capelin population dynamics were examined over two years in two relatively unstudied northern coastal embayments of Newfoundland (White Bay and Notre Dame Bay) and compared to that of Trinity Bay. Differences in community structure were driven primarily by sampling month, with no significant differences observed between years and among bays. However, larval capelin otolith microstructure analyses revealed that growth was significantly higher in the northern bays in 2015, but lower in 2016, relative to Trinity Bay. This research suggests that seasonally driven larval fish community structure is consistent along much of the Northeast coast of Newfoundland, while larval capelin dynamics vary spatially, and these spatial differences in growth and abundance may vary substantially on an interannual basis.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Newfoundland Fisheries

A Brief History

Fish in Newfoundland have been of great socioeconomic importance for centuries. From the early 16th century to the late 20th century, the Atlantic cod (*Gadus morhua*) fishery was a primary economic activity in Newfoundland and Labrador (Cushing, 1988; Harris, 1990; Hutchings and Myers, 1995). The northern cod stock supported the largest and most productive cod fishery in the world (McGrath, 1911; Thompson, 1943), which grew dramatically in the mid-1900s (Hutchings and Myers, 1995) as a result of new technologies and the arrival of European trawlers. Fisheries for redfish (*Sebastes* spp.), haddock (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus*), and flatfishes also increased during the same period (Rose, 2003). The cod fishery removed approximately 50 million tonnes in the 20th century, with annual catches of over 1 million tonnes in the 1960s, resulting in an unsustainable fishery (Rose, 2003). During the late 1980s and early 1990s, changing environmental conditions compounded the impacts of overfishing. The early 1990s were the coldest years in record (Colbourne et al., 1997; Drinkwater, 2002), with low zooplankton and forage fish productivity (Carscadden and Nakashima, 1997; Carscadden et al., 2001). The combined effects of the fishery and environmental conditions led to drastic declines in stock abundances in 1991 (Myers et al., 1996; Hutchings, 2000; Drinkwater, 2002; Lilly et al., 2013), resulting in a moratorium being placed on the northern cod fishery in 1992 (Rose et al., 2000). Coincidental to the collapse of the cod stocks were declines in the population biomass of numerous other ecologically and economically important groundfish and pelagic species, with a moratorium being placed on the majority of Newfoundland groundfish fisheries by 1993 (Rose et al., 2000; Rice, 2002; Rose, 2003). Although the cause remains uncertain, these declines are generally attributed to biotic and abiotic changes to the environment rather than overfishing, as species such as American plaice (*Hippoglossoides platessoides*) and capelin dropped to less than 10% and 1%, respectively, of their historical values, under low to moderate levels of exploitation (Gomes et al., 1995; Bowering et al., 1997; Carscadden and Nakashima, 1997; Rose, 2003; DFO, 2005; DFO, 2015). Subsequently, the change in environmental conditions along with the decline of many mid-level predators led to a regime shift in the early to mid-1990s (DFO, 2012; Buren et al., 2014; Pedersen et al., 2017).

Current fisheries

Commercial fishing remains the most important industry supporting numerous small communities throughout Newfoundland (Fisheries and Oceans Canada, 2011). Since the mid-1990s, the Newfoundland ecosystem shifted towards an invertebrate-dominated community, with the fisheries primarily targeting northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*) (Orr and Sullivan, 2013; DFO, 2017; Mullowney et al., 2018). These two species rose in abundance following the collapse of the groundfish stocks (Frank et al., 2005; Scheffer et al., 2005) and have since supported lucrative fisheries, with a combined landed value of nearly $650 million in 2015 (DFO, 2017). However, despite the current low abundance of Atlantic cod, capelin, and many other fishes relative to their historical levels, marine finfish remain a valuable resource for the Newfoundland economy. Marine fish in NL had an overall landed value of $125 million in 2015 (DFO, 2017). Of that, Greenland halibut (*Reinhardtius hippoglossoides*) was the most valuable, with a landed value of $67 million, while Atlantic cod comprised approximately $14 million of the total landed value. Capelin is of both direct and indirect economic importance. There has been a productive inshore fishery for capelin since the late 1970s (DFO, 2015), targeting females and their roe, which are exported to markets mainly in Asia and the United States (DFA, 2016). In 2015, capelin landings of 36,500 metric tonnes in NL were valued at over $10 million (DFO, 2017). In addition to its direct economic value, capelin is an important prey item for numerous piscivorous fish including cod and Greenland halibut (Carscadden and Vilhjálmsson, 2002; Rose and O'Driscoll, 2002; Dwyer et al., 2010), thus supporting other lucrative fisheries.

1.2 Early life stages

Importance

The question of recruitment variability has been a major focus of fisheries science since the early 20th century (Hjort, 1914). Understanding the factors that influence interannual variability in recruitment and subsequent year-class strength can allow for forecasting of recruitment and thus effective management of fish stocks. It has been shown in numerous species that recruitment strength is largely driven by survival during the larval stage (Campana, 1996; Dalley et al., 2002; Jenkins and King, 2006; Fontes et al., 2011). It is thus crucial to understand the factors that impact interannual variability in survival of the early life stages of fishes.

The larval stage of fishes is often the shortest of all life stages, yet it is also the most vulnerable, as it has the highest mortality of any life stage (Cushing, 1975; McGurk, 1986). Consequently, even slight changes in larval survival can result in important fluctuations of recruitment and thus of adult fish populations (Hjort, 1914; Houde, 1987; Anderson, 1988; Cushing and Horwood, 1994; Horwood et al., 2000), making it vital to understand the factors that can affect larval mortality, and how they interact within a given ecosystem. There are numerous hypotheses regarding processes regulating larval mortality, which is likely governed by multiple, interacting, biotic and abiotic factors.

Critical period & match-mismatch

Hjort (1914) first theorized that the early larval stage is most important in determining year-class strength, and that larval mortality is likely most affected by the abundance of prey during the period when newly-hatched larvae first begin feeding, a so-called "critical period." Building on Hjort's theory, the match-mismatch hypothesis (Cushing, 1975; 1990) proposed that the timing of larval fish emergence is key to recruitment variability. It was theorized that relatively high survival and subsequent recruitment will occur when larvae hatch at a time that corresponds to peak prey abundance, termed a "match" year. Correspondingly, a "mismatch" year characterized by poor larval survival and weak recruitment may occur when there is a notable offset between larval emergence and zooplankton abundance. This hypothesis has gained support over the years (Gotceitas et al., 1996; Kristiansen et al., 2011; Toupoint et al., 2012), although it has since been proposed that there is a more extended critical period during which high food availability is necessary for larval survival, and that the duration of this critical period varies among species (Theilacker et al., 1996; Chambers et al., 2001; Houde, 2008; Pepin et al., 2015).

Growth rate

One of the most important factors impacting larval survival and subsequent recruitment is larval growth. Variability in larval growth rates has often been linked to fluctuations in survival and recruitment (Meekan and Fortier, 1996; Hare and Cowen, 1997; Sirois and Dodson, 2000; Takasuka et al., 2003; Fontes et al., 2011; Payne et al., 2013), a link that can reflect the influence of several different mechanisms (Anderson, 1988). First, the bigger-is-better mechanism, whereby faster-growing larvae are larger at a given age and thus typically experience lower mortality as mortality rates generally decrease with increasing size of marine organisms (Peterson and Wroblewski, 1984; Folkvord and Hunter, 1986; Miller et al., 1988). Building on this is the stage-duration hypothesis, wherein higher growth rates equate to a shorter period of time spent in the smallest, most vulnerable life stage, thereby reducing the period of time during which larval mortality is highest (Chambers and Leggett, 1987; Houde, 1987; Anderson, 1988). Finally, larval growth rates measured at a given time can reflect growth-selective losses through predation. Growth-selective predation is a process wherein predators are more likely to consume slower-growing individuals at a given size (Takasuka et al., 2003, 2004). In instances of growth-selective predation, increased predation mortality is independent of size and stage duration, and is thought to occur due to suboptimal condition and thus anti-predator response in slow-growing larvae (Takasuka et al., 2003, 2004). The impact of factors regulating larval growth is species-specific. Faster-growing species such as Atlantic mackerel (*Scomber scombrus*) require greater nutrition and demonstrate strong otolith growth autocorrelation (i.e. that growth of a larva on a given day is correlated with its growth in subsequent days). These two factors indicate that feeding success is directly linked to growth and that growth in the early larval stage has a substantial impact on subsequent feeding and growth (Pepin et al., 2015), making the early larval stage critical period potentially more important in such species (Pepin et al., 2015).

Aberrant drift & member-vagrant hypotheses

Another factor potentially impacting recruitment, larval dispersal, is related to physical characteristics and flow regimes where eggs are spawned (Hjort, 1914; Iles and Sinclair, 1982; Sinclair, 1988; Bradbury et al., 2000). Hjort (1914) proposed the aberrant drift hypothesis, which first theorized that fluctuations in larval dispersal away from nursery areas contributed to variability in year-class strength. The member-vagrant hypothesis (Iles and Sinclair, 1982; Sinclair, 1988) built on the aberrant drift theory and proposed that discrete retention areas caused by local flow regimes allow for a high level of larval retention within a spawning area, and that fluctuations in larval abundance may be linked to interannual variability in retention potential, and thus in the relative proportion of individuals that are retained (members) over those that are dispersed out of the system (vagrants). This hypothesis was first introduced in relation to herring (*Clupea harengus*) in the NE Atlantic, where there exist several biologically and genetically distinct stocks (Iles and Sinclair, 1982), and was further expanded for application to numerous marine species (Sinclair, 1988).

1.3 Capelin

Biology

Capelin is a key species in the waters surrounding Newfoundland and Labrador, as it is the primary forage fish in the NW Atlantic ecosystem (Lavigne, 1996). A small, circumpolar, pelagic species that feeds predominantly on meso- and macro-zooplankton, capelin is an important prey item for groundfish, seabirds, and marine mammals, thus transferring energy to higher trophic levels (Lilly, 1987; Lilly, 1991; Carscadden and Vilhjálmsson, 2002; Rose and O'Driscoll, 2002; Davoren and Montevecchi, 2003; Montevecchi, 2007; Dwyer et al., 2010; Buren et al., 2012; Stenson, 2012). However, in the early 1990s, the capelin population off the coast of Newfoundland and Labrador suffered a drastic decline in abundance, from an estimated 6 million tonnes to ~150,000 tonnes, with a subsequent shift in life-history strategy, including a reduction in the age of maturity from three to two years of age and a seasonal delay in spawning of approximately three weeks, as well as a shift in distribution (Lilly and Davis, 1993; Frank et al. 1996; Carscadden and Nakashima, 1997). While the population appears to be slowly recovering, it remains far below pre-collapse abundance estimates (DFO, 2015), and the fishery removes a significant proportion of the estimated stock biomass annually (DFO, 2015, 2017).

Early life history and recruitment variability

Because of the short life span and variable recruitment of capelin, its stock size can change rapidly (DFO, 2015), making it crucial to understand the factors that influence recruitment variability. It has been shown that in capelin, year-class strength is determined during the larval stage (Frank and Leggett, 1981; Leggett et al., 1984; Anderson et al., 1999; Dalley et al., 2002; Murphy et al., 2018). Prior to the stock collapse in the early 1990s, larval survival was highly correlated with the frequency of onshore winds, which allow for increased larval emergence and condition (Frank and Leggett, 1981; Leggett et al., 1984). However, because of the change in phenology of capelin spawning in the 1990s, there is now a temporal mismatch between onshore winds and larval capelin emergence, which has likely led to reduced larval survival (Murphy et al., 2018). Availability of preferred prey (*Pseudocalanus* spp.), which has increased in the last decade, has been linked to increased larval survival, and may thus partially offset the detrimental effect of reduced onshore winds (Murphy et al., 2018). Larval growth rates have also been linked to recruitment, based on a subsample of three years, with high growth occurring in the year with the highest recruitment (Murphy et al., 2018).

Stock assessment

Given the importance of capelin, both commercially and ecologically, Fisheries and Oceans Canada (DFO) conducts annual surveys of the stock via spring acoustic surveys. Additionally, inshore larval surveys were conducted annually in Trinity Bay, NL by DFO in summer-fall of 1982-1986 (Dalley, 2002), and a similar larval survey was re-introduced in 2002, although covering fewer stations (DFO, 2015). These larval surveys aim to estimate the abundance of larval capelin population in Trinity Bay, and thus provide an index of potential recruitment to the capelin stock as a whole. While inshore emergent larval densities correlated with recruitment, no clear link has been reported so far between year-class strength and late larval dynamics (DFO, 2015; Murphy et al., 2018). Larval survival in capelin is likely driven by environmental conditions (Frank and Leggett, 1981; Leggett et al., 1984; Carscadden et. al., 2000), and as such may differ among coastal areas of Newfoundland. Where the current larval assessment only surveys one coastal embayment, its limited spatial coverage may not fully capture interannual fluctuations in larval capelin population dynamics within the stock, thus limiting its ability to predict recruitment.

1.4 Study area

Coastal embayments are important habitat for early life stages of many marine fishes. They provide spawning grounds and larval retention areas where temperatures are higher, promoting fast development and a shorter embryonic period, where eggs/larvae are somewhat protected from widespread dispersal, and where prey are often more abundant (Frank and Leggett, 1982; Taggart and Leggett, 1987; Laprise and Pepin, 1995; Pepin et al., 1995; Bradbury et al., 2008). The Northeast coast of Newfoundland is largely comprised of such embayments. These bays are key spawning sites for many species, including Atlantic cod (Rose et al., 2008) and capelin (Frank and Leggett, 1982), as well as nursery areas for newly hatched larvae, and are thus important habitat for fish stocks.

As coastal habitat is crucial for reproduction and early life success in many fishes, the oceanography, ecology, and ichthyoplankton community of several of the bays in southern Newfoundland, such as Placentia Bay, Conception Bay, and Trinity Bay, have been extensively studied over the past few decades (Bradbury et al., 2001; Tittensor et al., 2002; Templeman and Davis, 2006; Carter-Lynn, 2009). However, two coastal embayments along the Northeast coast of Newfoundland, White Bay and Notre Dame Bay, remain largely unstudied. Because of the successful inshore capelin fishery in this area (Nakashima and Slaney, 1998), it is presumed that these two bays may be important spawning grounds for capelin. Furthermore, the ichthyoplankton community has not yet been described, but is likely diverse if these two northern bays provide important egg and larval retention areas like the more studied coastal habitat of Newfoundland.

1.5 Thesis objectives

The aim of this thesis is to improve the state of knowledge of key inshore ecosystems of Northeastern Newfoundland by providing a comparison between the northern bays (White Bay and Notre Dame Bay) and Trinity Bay, both in terms of larval fish communities and, more specifically, in regard to capelin early life dynamics. First, seasonal and interannual trends in larval fish community structure will be examined in order to provide a baseline of the ichthyoplankton community in these areas for future studies. Next, the spatial distribution and density of larval capelin will be examined, and, using otolith microstructure analysis, larval capelin growth dynamics between the northern bays and Trinity Bay will be explored. This will allow testing of the assumption that larval capelin population dynamics in Trinity Bay are representative of the entire stock by assessing the potential spatial and interannual variability in larval capelin population dynamics between two important spawning areas. It will also allow exploration of the validity of otolith microstructure analysis for age and growth analyses in larval capelin.

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CO-AUTHORSHIP STATEMENT

The work presented in this thesis was primarily conducted by Violaine Shikon, under the guidance of her supervisory committee: Dominique Robert, David Schneider, Pierre Pepin, and Martin Castonguay. This thesis is presented in manuscript format, in which there are two data chapters (i.e. manuscripts) preceded by a general thesis introduction and followed by a thesis summary and general discussion. Both data chapters present a comparison of the northern bays (White Bay and Notre Dame Bay) and Trinity Bay. Violaine Shikon assisted in two of the five inshore surveys conducted in the northern bays, and conducted the majority of ichthyoplankton analysis and larval identification for samples from this survey, with assistance from Carissa Wilson. Fieldwork, ichthyoplankton analysis, and larval identification for Trinity Bay were completed by Fisheries and Oceans Canada (DFO). Violaine Shikon conducted all otolith extraction, imaging, and analysis for the second data chapter, with preliminary guidance from Hannah Murphy and Heather Penney, and all statistical analyses and manuscript preparation, with editorial feedback from Dominique Robert, Pierre Pepin, and David Schneider.

CHAPTER 2: LARVAL FISH COMMUNITY STRUCTURE ALONG THE NORTHEAST COAST OF NEWFOUNDLAND: SPATIO-TEMPORAL PATTERNS IN SPECIES DIVERSITY AND COMPOSITION

2.1 Introduction

Coastal embayments are key to the success of many marine species, as they comprise important spawning and nursery habitat, providing an environment that is more favourable to embryonic, larval, and juvenile success than the surrounding coastal waters. The abiotic and biotic conditions that create such a favourable environment include typically warmer water temperatures, increased egg and larval retention, higher prey abundance, and potentially fewer predators (Frank and Leggett, 1982; Taggart and Leggett, 1987; Laprise and Pepin, 1995; Pepin et al., 1995; Bradbury et al., 2008).

Along the Northeast coast of Newfoundland, such coastal embayments are critical to the success of numerous commercially important fish stocks, providing key spawning sites and nursery grounds for species such as Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*), and Atlantic herring (*Clupea harengus*) (Frank and Leggett, 1982; Anderson and Dalley, 1997; Rose et al., 2008; Stanley et al., 2013; DFO, 2015b). In 2015, the Newfoundland and Labrador (NL) cod, capelin, and herring fisheries were valued at approximately \$14 million, \$10 million, and \$6.5 million, respectively (DFO, 2017). Despite the socioeconomic and ecological importance of these species, knowledge of their reproductive ecology and larval life dynamics in these waters is limited by a lack of information on processes occurring in the northern portion of the stock distribution. Research into the trends in spatiotemporal variability of larval fish population dynamics and the factors that affect these trends is crucial, because mortality during the larval stage is higher than during any other life stage in fish (Cushing, 1975; McGurk, 1986).

Consequently, even slight changes in larval survival can result in drastic fluctuations of recruitment, and subsequently, of adult fish population abundance (Hjort, 1914; Houde, 1987; Anderson, 1988; Horwood et al., 2000).

Given the importance of the larval stage, there has been extensive research into the factors affecting dispersal, distribution, growth, and survival of eggs and larvae of cod (Bradbury et al., 2000; Zhao, 2001; Knickle and Rose, 2010; Stanley et al., 2013) and, to a lesser degree, of capelin (Frank and Leggett, 1981; Leggett et al., 1984; Carscadden et al., 2000; Murphy et al., 2018) in coastal Newfoundland. However, there exist few studies of ichthyoplankton communities in Newfoundland (Templeman and Davis, 2006; Templeman, 2007; Carter-Lynn, 2009). Knowledge of larval fish community structure can shed light on larval transport, interspecific competition during the early life stages, and adult spawning locations (Parker and Franzin, 1991; Donald, 1997; Quist et al., 2004; Pritt et al., 2015; Ribeiro et al., 2015), all of which can impact recruitment and thus the abundance and dynamics of adult fish stocks (Iles and Sinclair, 1982; Bradbury et al., 2000; Bolle et al., 2009). Furthermore, changes in community structure can signal disturbances and impending regime shifts earlier than such changes may be seen in a single species, potentially allowing for earlier detection of such disturbances (Villagarcía et al., 1999; Sá-Oliveira et al., 2015).

Past efforts in characterizing larval community structure in the coastal embayments of Newfoundland have focused on southerly coastal embayments, such as Trinity Bay, Conception Bay, and Placentia Bay (Templeman and Davis, 2006; Templeman, 2007; Carter-Lynn, 2009), despite the more northern bays, such as White Bay and Notre Dame Bay, being presumed to also be important spawning sites. Even within the geographically close southerly bays, Carter-Lynn (2009) found a higher abundance of the larvae of cold-water species in Trinity Bay and Conception Bay relative to Placentia Bay, indicating the presence of among-bay differences in larval fish community structure in coastal embayments of Newfoundland.

The main objective of this study is to describe the community structure, namely the seasonal and spatial diversity, distribution, and abundance of fish larvae, in coastal embayments of Northeast Newfoundland. In order to achieve this, ichthyoplankton surveys were conducted in two northern bays, White Bay and Notre Dame Bay, over the summer months in 2015 and 2016. Relative abundances and distribution, richness, evenness, and diversity were assessed seasonally and annually, comparing these results to those found in Trinity Bay. Specific objectives were to (1) provide baseline knowledge of larval fish communities in coastal embayments of NE Newfoundland, and (2) determine seasonal, interannual, and spatial (among bay) trends in the diversity, distribution, and abundance of these communities. As larval fish assemblages typically display strong seasonality (McGowen, 1993; Sassa et al., 2007; Carter-Lynn, 2009), it was hypothesized that temporal variability in larval fish community structure would be greater than spatial variability.

2.2 Materials and Methods

Study Area

White Bay and Notre-Dame Bay are two bays along the northeast coast of Newfoundland, Canada. White Bay is long and narrow, topographically similar to the more southerly Trinity Bay and Conception Bay (Fig. 2.1). It is approximately 90 km long and 30 km wide at its northern mouth, and has a maximum depth of ~500 m. Notre

Dame Bay is a more open embayment, approximately 50 km long and 85 km wide at its mouth, and has a maximum depth of ~360 m. Trinity Bay is long and narrow in shape, similar to White Bay, and is approximately 100 km long and 40 km wide at its northeastern mouth (Fig. 2.1), with a maximum bottom depth of ~600 m (Tittensor et al., 2002).

Field Sampling

Samples were collected from Notre Dame Bay and White Bay during three consecutive surveys in 2015 (June 30-July 1, July 25-28 and August 24-26) and two consecutive surveys in 2016 (July 20-22 and August 24-25) that covered a grid of 26 stations (Figure 2.2). In 2015, all surveys were carried out aboard the *FV Fisherman's Dream*, while in 2016, the July survey was carried out on the *CCGS Vladykov*, and the August survey was completed aboard the *FV Twisted Sisters*. For all surveys, 61 cm diameter bongo nets equipped with 333 μm mesh were deployed in a double-oblique fashion and towed at 2.5 knots for ca. 10 minutes at a 45° angle. The bongo was lowered to a maximum depth of 50 m, with target descent and ascent rates of 0.5 $m\ s^{-1}$. Upon retrieval, nets were washed with seawater to minimize the potential loss of plankton, and the samples were rinsed from the cod ends onto 150 μm sieves and then immediately preserved in 2% buffered formaldehyde. Mechanical flowmeters with a one-way clutch and standard rotor-threshold were placed at the mouth of each net to estimate the volume of water sampled (Dalley et al., 2002).

Samples from Trinity Bay were collected during the annual DFO ichthyoplankton surveys targeted at capelin. These assessments cover a grid of 19 stations (Figure 2.3) that were sampled during each of two consecutive surveys in 2015 (August 14-21 and

September 16-23) and two consecutive surveys in 2016 (August 17-20 and September 17-21). These surveys were conducted on the *CCGS Vladykov* using the same bongo sampler. The bongo was deployed to a maximum depth of 200 m, with a target descent rate of 0.33 m s^{-1} and a target ascent rate of 0.17 m s^{-1}. Mechanical flowmeters were once again used to determine the volume of water filtered by the nets (Nakashima and Mowbray, 2014). Plankton samples were immediately preserved in 2% buffered formaldehyde.

Laboratory analyses

Larval fish were extracted from the preserved plankton samples using a stereomicroscope (15X magnification), and then identified to species using Fahay's (2007) detailed descriptions and drawings of the larval stage of fishes of the Northwest Atlantic Ocean.

Larval densities were then calculated using the formula:

(1) $\rho = C * \frac{Z}{V}$

where larval density per square meter (ρ) is the product of the number of larvae in the sample (C) and the depth of the tow in meters (Z), divided by the volume of water filtered in cubic meters (V), which provides a measure of abundance integrated over the water column (Nakashima and Mowbray, 2014). Previous work in coastal embayments of NL has shown that ichthyoplankton are limited to the top 50 m of the water column (P. Pepin, pers. comm.). Thus, by incorporating both depth and volume sampled into the calculation of larval density, the difference in sampling depth between the northern bays and Trinity Bay was controlled for.

Data analyses

Differences in species composition and relative abundance of the larval fish community in the northern bays (Notre Dame Bay and White Bay) and in Trinity Bay were explored using various indices of community structure and non-metric multidimensional scaling (NMDS). For each sampling site in the two survey locations from June-September in 2015 and 2016, I determined the overall larval fish density (sum of all species), the species richness (number of species), and the Gini-Simpson index of species diversity as defined by:

(2) $D' = 1 - D$

(3) $D = \sum p_i^2$

where p is the proportional abundance of species i. I then determined Pielou's index of species evenness as defined by:

(4) $H' = -\sum_i p_i ln\, p_i$

(5) $J = H' / \ln(S)$

where *H'* is the Shannon Wiener diversity index, *p* is the proportional abundance of species i, and *S* is the total number of species. Measures of central tendency for these four indices of community structure were then assessed. Simpson's index of species diversity was selected over the Shannon Wiener index as the larval fish communities in this study have numerous rare species, and Simpson's index is a dominance index and is thus unaffected by the presence of rare species (Lande, 1996; Clarke and Warwick, 2001). Pielou's evenness index was included to allow comparison between richness, evenness, and diversity, the latter of which incorporates both of the former (Jost, 2010).

NMDS was used to analyze differences in species composition among sampling sites and months, and between survey locations and years. NMDS is well-suited for such analysis, as it assumes little about the form of the data, allows great flexibility in the measure of dissimilarity, and preserves relationships well in low-dimensional space (Clarke and Warwick, 2001). As a result of the high number of rare species in this study, only species occurring in at least 3% of sites were included in the NMDS analysis to allow for an increased goodness-of-fit when placing multidimensional data on a 2D plane. An NMDS ordination plot was constructed from a dissimilarity matrix generated using Bray-Curtis distances. A sequential agglomerative hierarchical non-overlapping cluster analysis (Sneath and Sokal, 1973) using average linkage clustering was then conducted on the NMDS dissimilarity matrix, and the resulting dendogram was cut at a height of 0.86 (i.e. 86% dissimilarity). The resulting clusters were then overlaid onto the NMDS ordination plot, and a similarity of percentages (SIMPER) analysis was conducted to determine the relative contribution of each species to the overall dissimilarity among clusters.

An analysis of similarity (ANOSIM) was then applied to the species data matrix for each predictor variable to determine if differences in species composition and abundance were significantly different (having a global R statistic greater than 0.25) between survey locations, among months, or between years. Variables with global R values lower than 0.25 may yield significant p-values, as the R statistic may be significantly different from zero, yet its value can be so low as to be biologically insignificant (Clarke and Warwick, 2001). For factors found to significantly affect community structure, similarity of percentages (SIMPER) analysis was conducted to determine the relative contribution of each species to the overall dissimilarity. All analyses were performed in R 3.4.0 with the car, ggplot2, and vegan packages.

2.3 Results

Species composition of the larval fish assemblage was qualitatively similar between the northern bays and Trinity Bay in August of both 2015 and 2016, and in September in Trinity Bay (Fig. 2.4, Appendix A). In the northern bays, larval fish species composition and distribution was similar in June 2015 and July 2016, where numerous species (eight and five, respectively) each contributed at least 5% of the total abundance. Of these dominant species, four were common between surveys: Atlantic cod, Arctic shanny (*Stichaeus punctatus*), snailfish (*Liparis* spp.), and redfish (*Sebastes* spp.). July of 2015, however, resembled the August/September community. This late summer/early fall ichthyoplankton community was strongly dominated by capelin, which constituted 74-94% of the total larval fish abundance during these months. However, in 2015, Atlantic cod was the second most abundant species (4-5%) while 2016 saw a markedly higher proportion of cunner (*Tautogolabrus adspersus*) larvae in both survey locations, from 0.6-2% of the total larval population in 2015 to 12-15% of the larval fish population in 2016. Additionally, 2016 showed an increased relative abundance of Atlantic herring in August in the northern bays, from 1% of the total larval population in 2015 to 9% in 2016, and in September in Trinity Bay, where herring larvae doubled in relative abundance from 2015 to 2016, although capelin was still the dominant species.

Larval distribution was also similar among bays and between years (Figures 2.5 and 2.6). In the northern bays, larvae were diverse and evenly distributed in June 2015 and July 2016. However, capelin larvae were most abundant towards the mouth of the bays in August of both years and both survey locations. Additionally, a relatively high abundance of herring larvae was found near the mouth of the northern bays (White Bay predominantly) in August 2016 and at the mouth of Trinity Bay in September 2016, while the increased abundance of cunner was found inshore in Notre Dame Bay and in Trinity Bay in August 2016. Atlantic cod was evenly distributed in all surveys in the northern bays and in both surveys in Trinity Bay in 2015, but was rare in Trinity Bay in 2016. Witch flounder was found in low densities in Notre Dame Bay in June 2015 and August 2016, and in Trinity bay in September 2015 and August 2016. Numerous species, such as American plaice (*Hippoglossoides platessoides*) and rockling, occurred at a single sampling site within a survey.

Variation in total larval density between survey locations differed greatly between years, while species diversity was consistently higher in the northern bays (Figure 2.7). Although larval density was similar between bays in 2015, it was substantially higher in Trinity bay in August 2016 (Figure 2.7A). Total species richness across all stations of a given survey was 2-5 times higher than the median species richness per sampling site, indicating a large proportion of rare species. Indeed, 58% of species (14 of the 24 species found in this study) occurred at fewer than 3% of all sampling sites (Figure 2.7B, C). Diversity, richness, and evenness were highest in the northern bays in June 2015 and July 2016, while diversity and evenness were markedly low in Trinity Bay in August of both years, and September 2016 (Figure 2.7B-E).

Sampling month (ANOSIM; R = 0.45) meaningfully contributed to differences in larval fish community between sites, while sampling year and survey location (northern bays vs. Trinity Bay) did not (Table 2.1). SIMPER analysis showed that eight species contributed to the overall dissimilarity in larval community between June and July, with individual species contribution ranging from 20% (sandlance, *Ammodytes* spp.) to 5% (redfish), while differences in capelin abundance contributed 69-79% of the overall dissimilarity in all other month comparisons. However, August was additionally set apart by cunner, which contributed 7-10% of the dissimilarity between August and other sampling months (Appendix B).

The hierarchical cluster analysis yielded five distinct clusters at 86% dissimilarity and the NMDS showed that these clusters are segregated primarily due to sampling month, where June, July, and an amalgamation of August and September comprised distinct groupings (Figure 2.8). Cluster 1 was comprised of the majority of stations sampled in June, cluster 2 contained most of the stations sampled in July, and cluster 4 contained a subset of stations sampled in August. SIMPER analysis showed that the same eight species contributed to the dissimilarity between June and July and the dissimilarity between clusters 1 and 2, while cluster 4 had very low capelin density (<0.1 m^{-2}) and was set apart predominantly due to a relatively high abundance of cunner (Appendix C). The large distance among these clusters indicates very different species composition and relative abundance. However, clusters 3 and 5 overlapped almost entirely, and contained a large number of August and nearly all the September sites. SIMPER showed that they occupied the same space in the ordination plot as they were dominated by capelin, but that they were distinct clusters due to a large difference in mean capelin density (0.08 ind. m^{-2} vs. 23 ind. m^{-2}) (Appendix C).

2.4 Discussion

This study aimed to describe the larval fish community along the Northeast coast of Newfoundland, thus providing a baseline for future research, and to determine seasonal, interannual, and among-bay trends in the abundance, diversity, and distribution of the larval fish communities in coastal embayments of Northeastern Newfoundland.

While there exist few studies on ichthyoplankton communities of Newfoundland coastal systems, Carter-Lynn (2009) explored larval fish community structure in Placentia Bay, Conception Bay, and Trinity Bay, and found that seasonal variability predominated over spatial variability. In Placentia Bay, there were two distinct communities, a spring community (April/May) and a late summer community (August/September). The community in June fell between the distinct spring and late summer communities (July was not studied) (Carter-Lynn, 2009). The five most abundant species in Placentia Bay in spring were sandlance, Arctic shanny, shorthorn sculpin (*Myoxocephalus Scorpius*), radiated shanny (*Ulvaria subbifurcata*), and snailfish. The late summer community, however, was dominated by capelin, Atlantic cod, and cunner, as well as redfish and fourbeard rockling (*Enchelyopus cimbrius*) (Carter-Lynn, 2009). While capelin and cunner were fairly abundant throughout the sampling period, their densities fluctuated drastically on an interannual basis (Carter-Lynn, 2009).

The present study showed similar results to those found by Carter-Lynn (2009). Sampling month meaningfully impacted community structure, and the larval fish community in Notre Dame Bay, White Bay, and Trinity Bay displayed distinct clusters for June, July, and August/September. Furthermore, four of the five species that predominated Placentia Bay in spring (sandlance, Arctic shanny, radiated shanny, and snailfish) were also abundant in Notre Dame Bay and White Bay in early summer, while three of the species that predominated in the late summer community in Placentia Bay (capelin, cunner, and Atlantic cod) were also among the most abundant in the late summer community of Trinity Bay and the northern bays. Of these three late summer species, capelin dominated the larval fish assemblage in August and September, which was expected as capelin is a predominant forage fish in the waters surrounding Newfoundland and Labrador that spawns inshore during July and August (DFO, 2015a).

However, while July 2015 in the northern bays resembled the later summer/fall community and was dominated by capelin, July 2016 more closely resembled the community present in June 2015, with low larval density, high diversity, and a similar species composition. Mean sea surface temperature along the NE coast of Newfoundland was colder in June 2016 than in June 2015 (Colbourne et al., 2017), and the average size of mature capelin decreased by 5.5 mm from 2015 to 2016 (H. Murphy, pers. comm.). As lower temperatures and smaller fish size have been linked to delayed spawning in capelin in the NW Atlantic (Carscadden and Nakashima, 1997; Carscadden et al., 1997), the lag in community structure seen in 2016 is likely due to such a delay. The high abundance of cunner and Atlantic herring in 2016 relative to 2015 further highlights the interannual differences in community structure. Furthermore, these interannual differences can vary spatially, as shown by the drastically lower total larval abundance in the northern bays in 2016, while total larval abundance in Trinity Bay was higher in 2016 than in 2015.

The agreement of our findings with those of Carter-Lynn (2009) suggests that larval fish communities of Newfoundland coastal embayments are determined predominantly by season/month, and that seasonal patterns of community structure are consistent among years and along much of the Newfoundland coast, from the southerly Placentia Bay to the northeastern White Bay. However, while seasonal trends in the species composition, distribution, and relative abundance of larval fish may be present in different bays, and remain stable over time, there is evidence from our results, as well as those of Carter-Lynn (2009), that the relative abundance of species as well as overall larval density may still fluctuate among bays and years.

It should be noted that in this study, only the northern bays were sampled in June and July, while only Trinity Bay was sampled in September. However, given the similarity in community structure between sampling areas in August of both years, and between August and September in Trinity Bay, we expect that the northern bays in September have a similar larval fish community to that found in Trinity Bay.

This study expands our knowledge of larval fish communities and early life history northward to the northeastern bays of Newfoundland, which are productive spawning grounds for many important species including capelin and Atlantic cod. It was evident from the results presented in this study that larval fish communities in these waters are highly seasonal, which supports previous findings in the region (Carter-Lynn, 2009) and in the nearby Gulf of St. Lawrence (Bui et al., 2010). However, the lag in community structure present in 2016, coinciding with lower water temperatures and smaller adult capelin, suggests that interannual variability in environmental conditions can greatly impact the phenology of ichthyoplankton communities. While this dataset is limited to only two years, the baseline knowledge provided by this study could be used to detect and assess impacts of changing oceanographic conditions or ecosystem shifts (Villagarcía et al., 1999; Das and Chakrabarty, 2007; Mapes et al., 2015). In the northwest Gulf of St. Lawrence, decadal changes in the ichthyoplankton community showed a shift from large groundfish predators to smaller, non-commercial demersal fishes. The shift in ichthyoplankton community reflected known changes in the abundance of commercial fish stocks, thus allowing inference as to the decadal change in adult population abundance of non-commercial species from their larval densities (Bui et al., 2010). Given the ease and utility of ichthyoplankton studies, continued monitoring of the ichthyoplankton community of Newfoundland is important. However, the consistency of the seasonally-driven community structure along the NE coast of Newfoundland indicates that efforts would be best focused on increasing the temporal scope of the annual survey run by DFO in Trinity Bay.

2.5 Literature cited

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2.6 Tables

Table 2.1: Analysis of similarity (ANOSIM), where sample global R is the test statistic that ranges from 0 to 1, indicating the level of variability between factor levels relative to the variability within factor levels. Data were permutated 999 times.

Factor	**ANOSIM statistic R**	**Significance**
Year	0.03814	0.003
Month	0.4533	0.001
Bay	0.07383	0.001

2.7 Figures

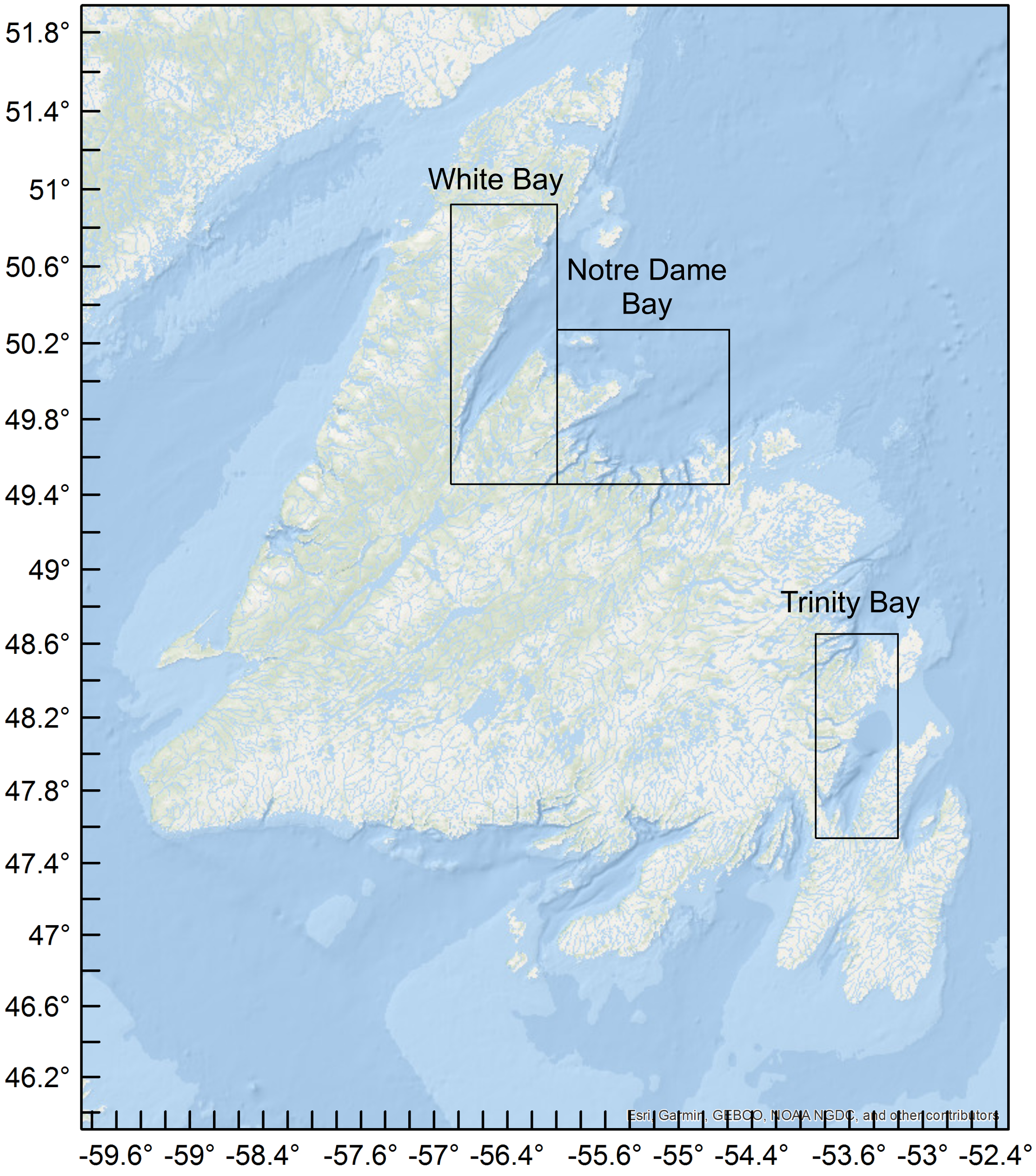


Figure 2.1: Location of northern bays (White Bay and Notre Dame Bay) and Trinity Bay within the Newfoundland coastline.

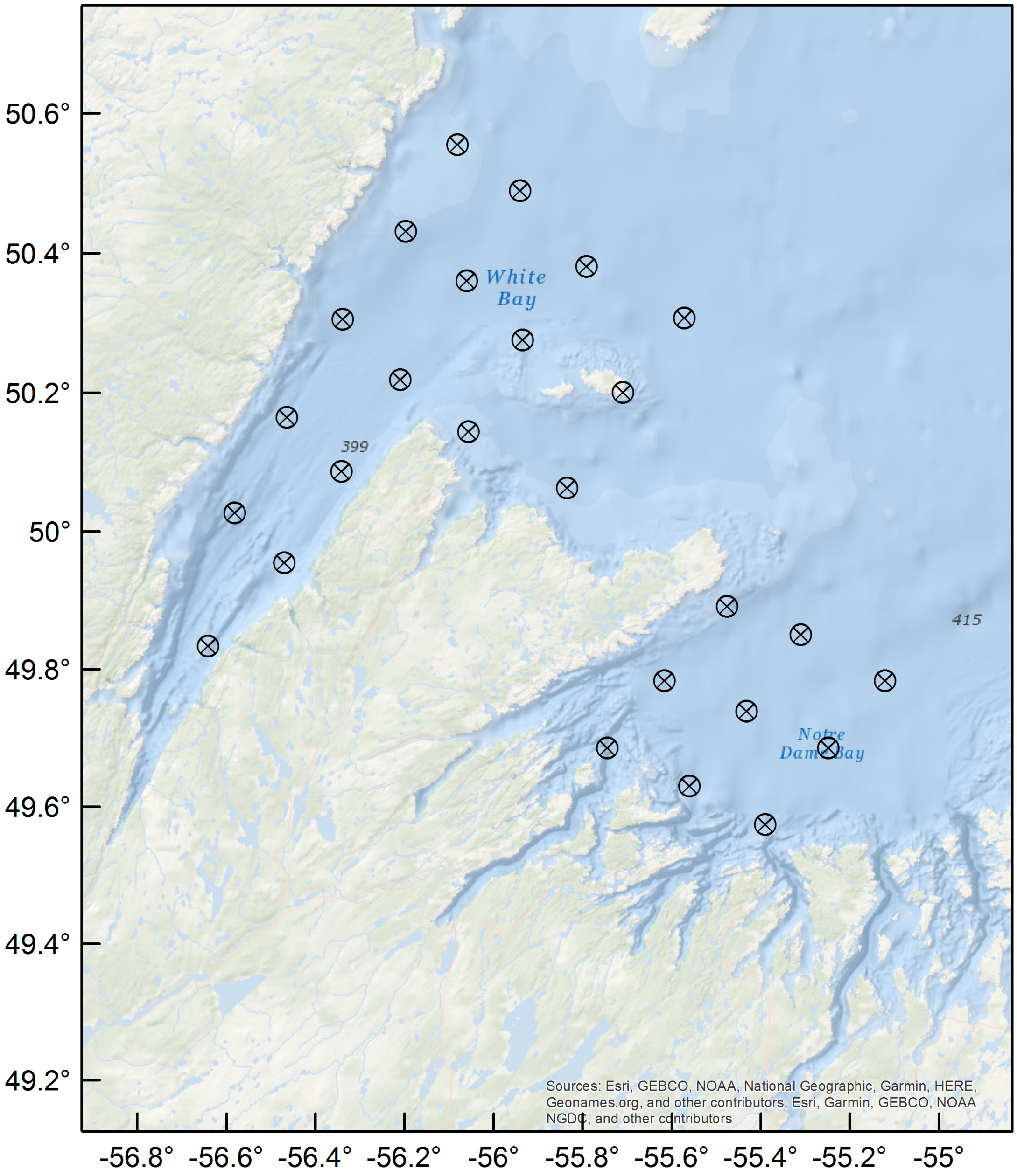


Figure 2.2: Sampling grid for stations sampled in the northern bays in 2015 and 2016.

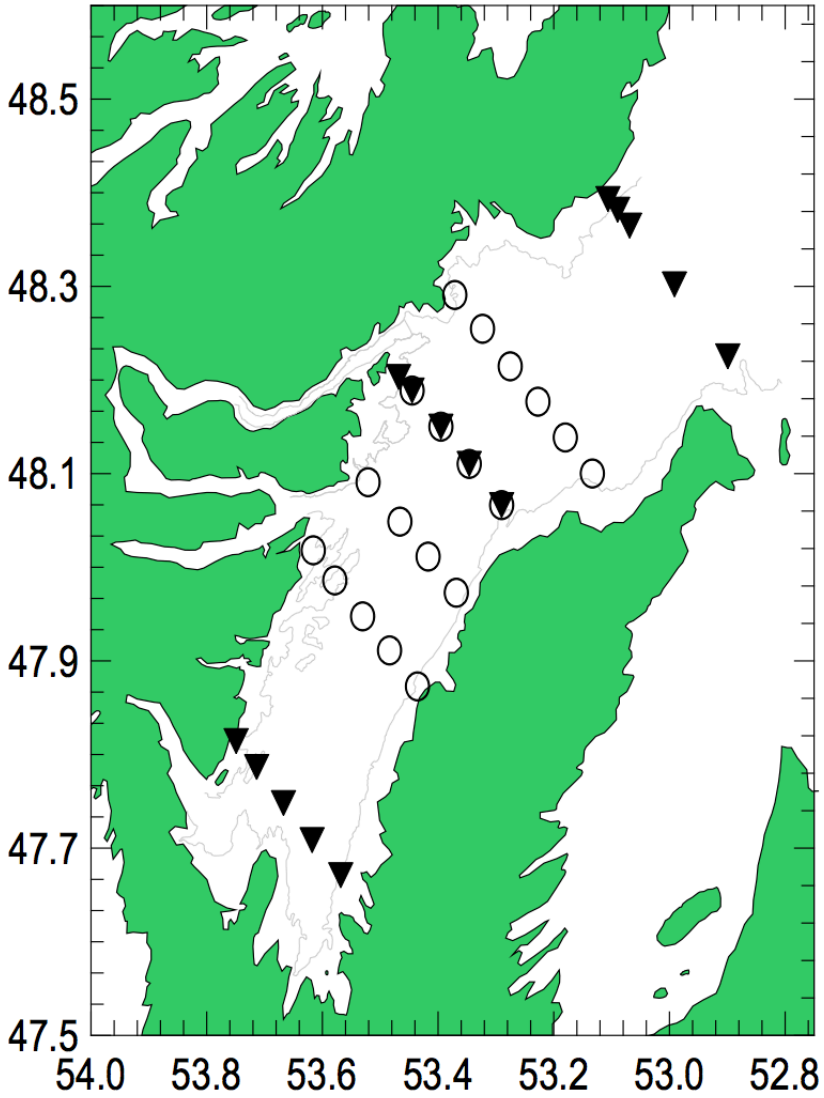


Figure 2.3: Map of Trinity Bay indicating locations of larval tows and CTD profiles occupied during surveys conducted since 2002. Circles indicate stations where bongo nets were fished. Triangles give locations of CTD profiles. Axis labels are in decimal degrees. Retrieved from Nakashima and Mowbray, 2014.

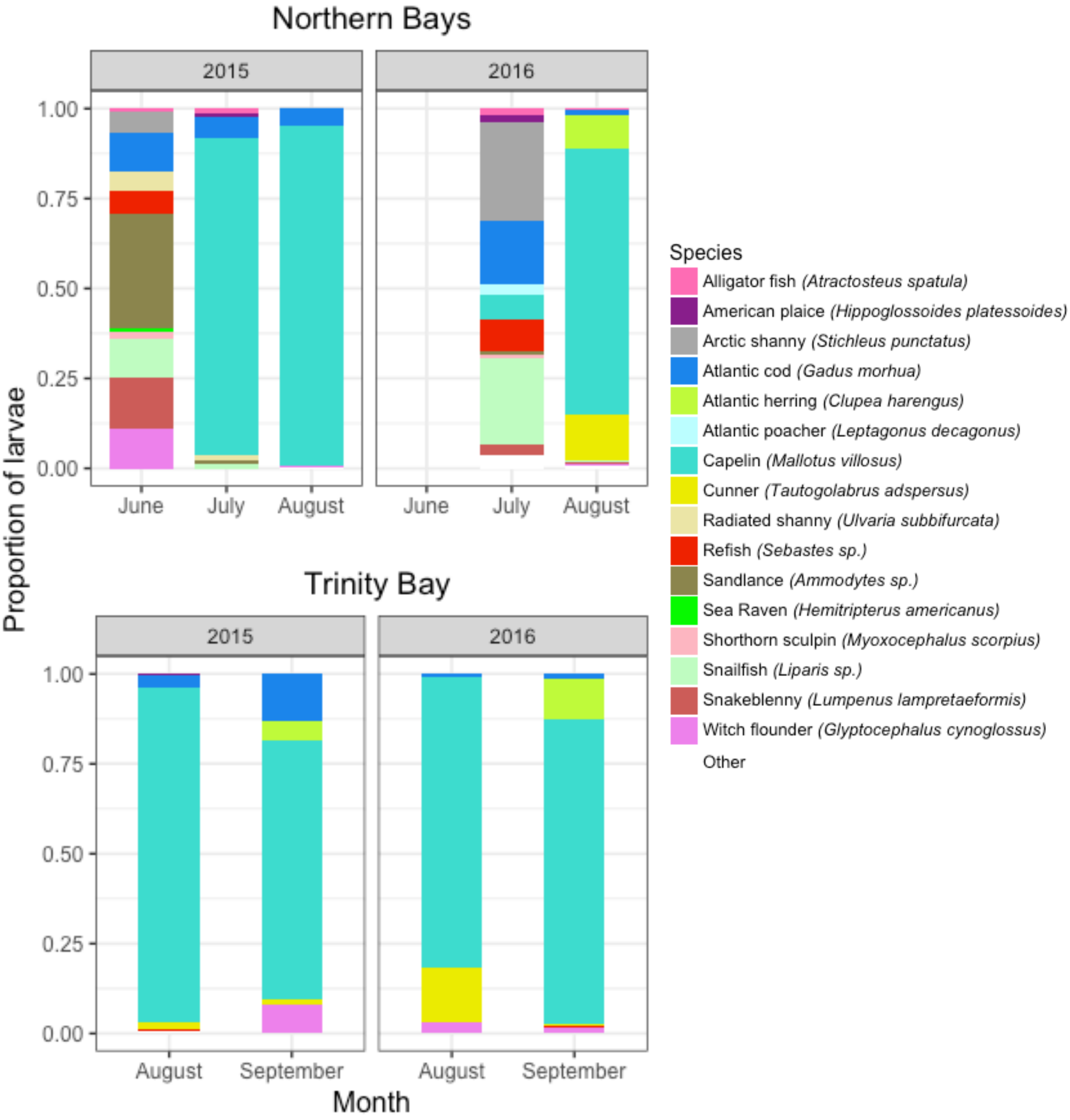


Figure 2.4: Relative contribution of species to the larval fish communities of the northern bays (Notre Dame Bay and White Bay, NL) and of Trinity Bay, NL in summer/fall of 2015 and 2016.

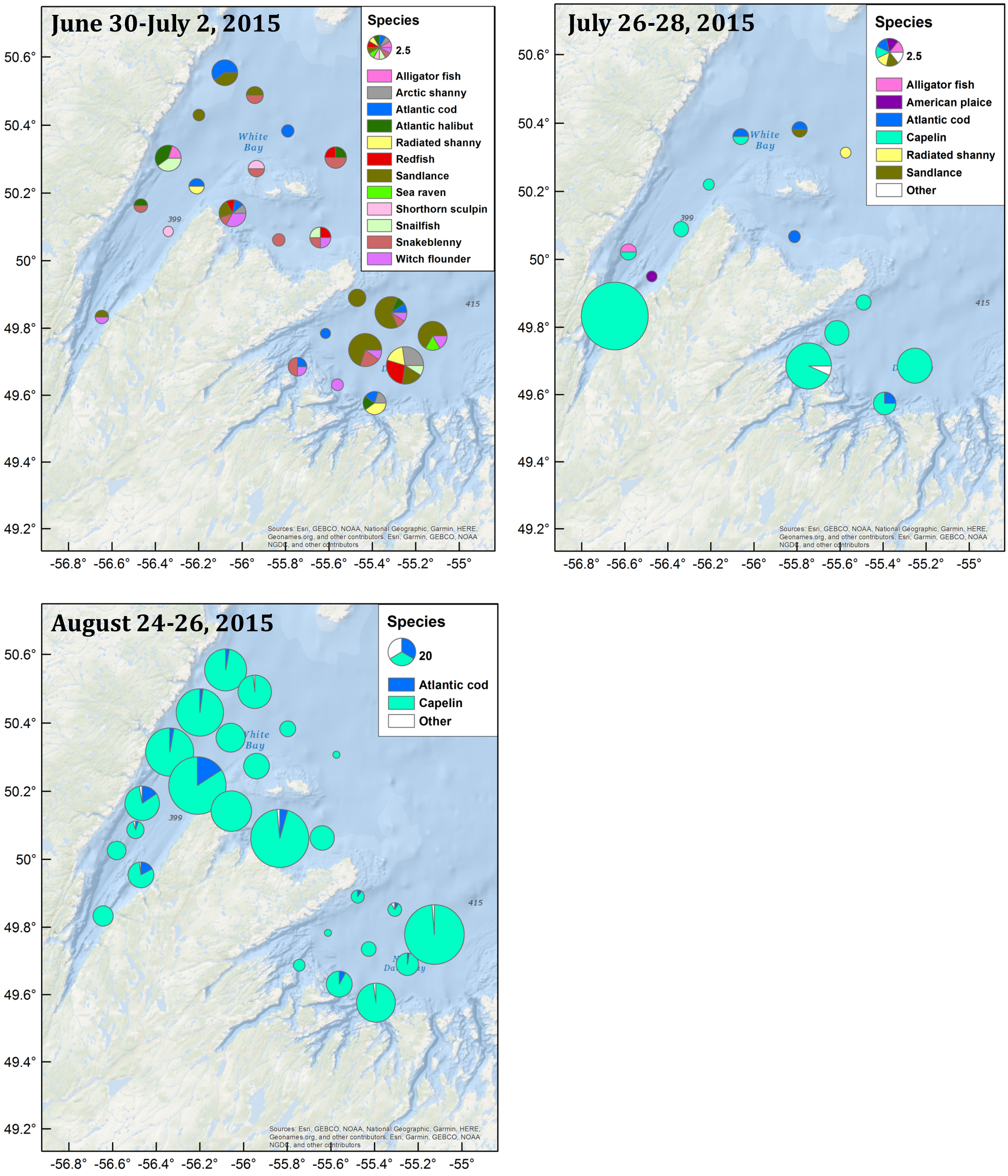
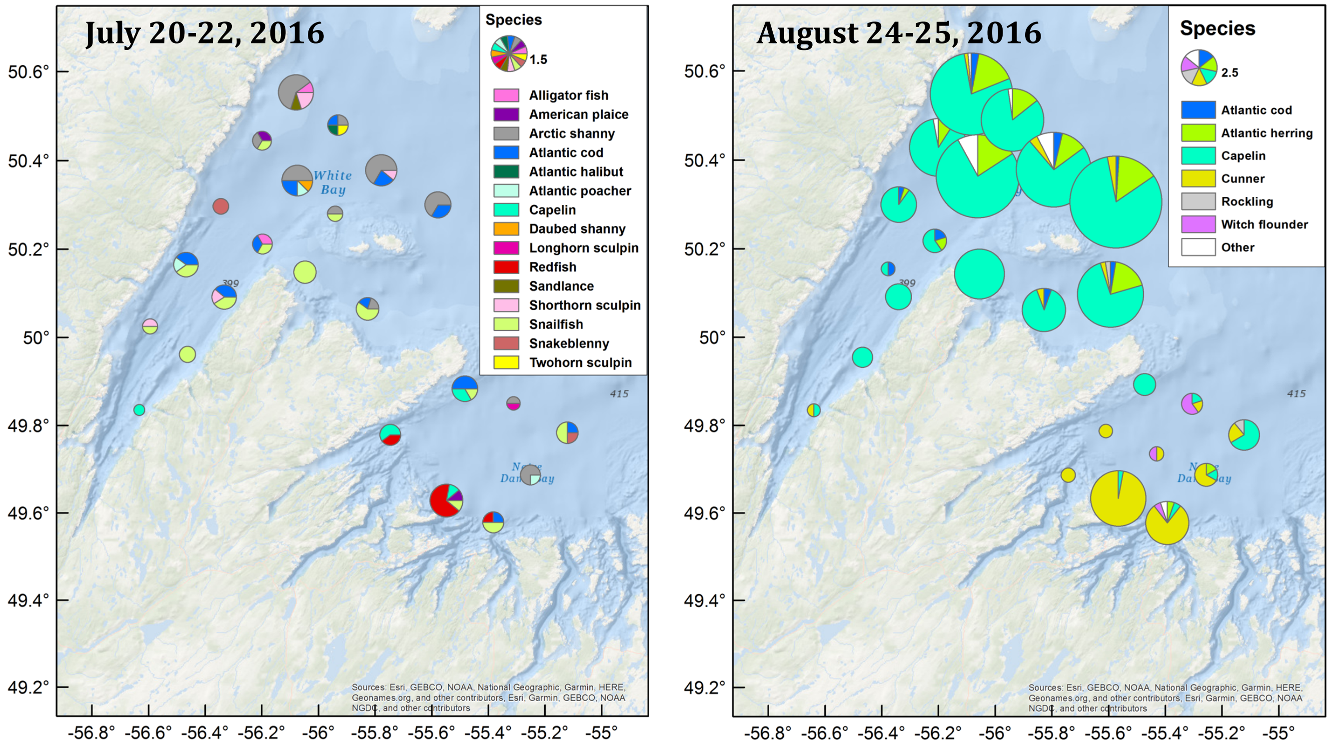


Figure 2.5a: Species composition and relative larval density for the northern bays in 2015. Pie charts scaled by total larval density at a station relative to the highest larval density in a given survey. Median larval density in larvae m^{-2} is shown in the legend.



July 20-22, 2016

August 24-25, 2016

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors. Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure 2.5b: Species composition and relative larval density for the northern bays in 2016. Pie charts scaled by total larval density at a station relative to the highest larval density in a given survey. Median larval density in larvae m^{-2} is shown in the legend.

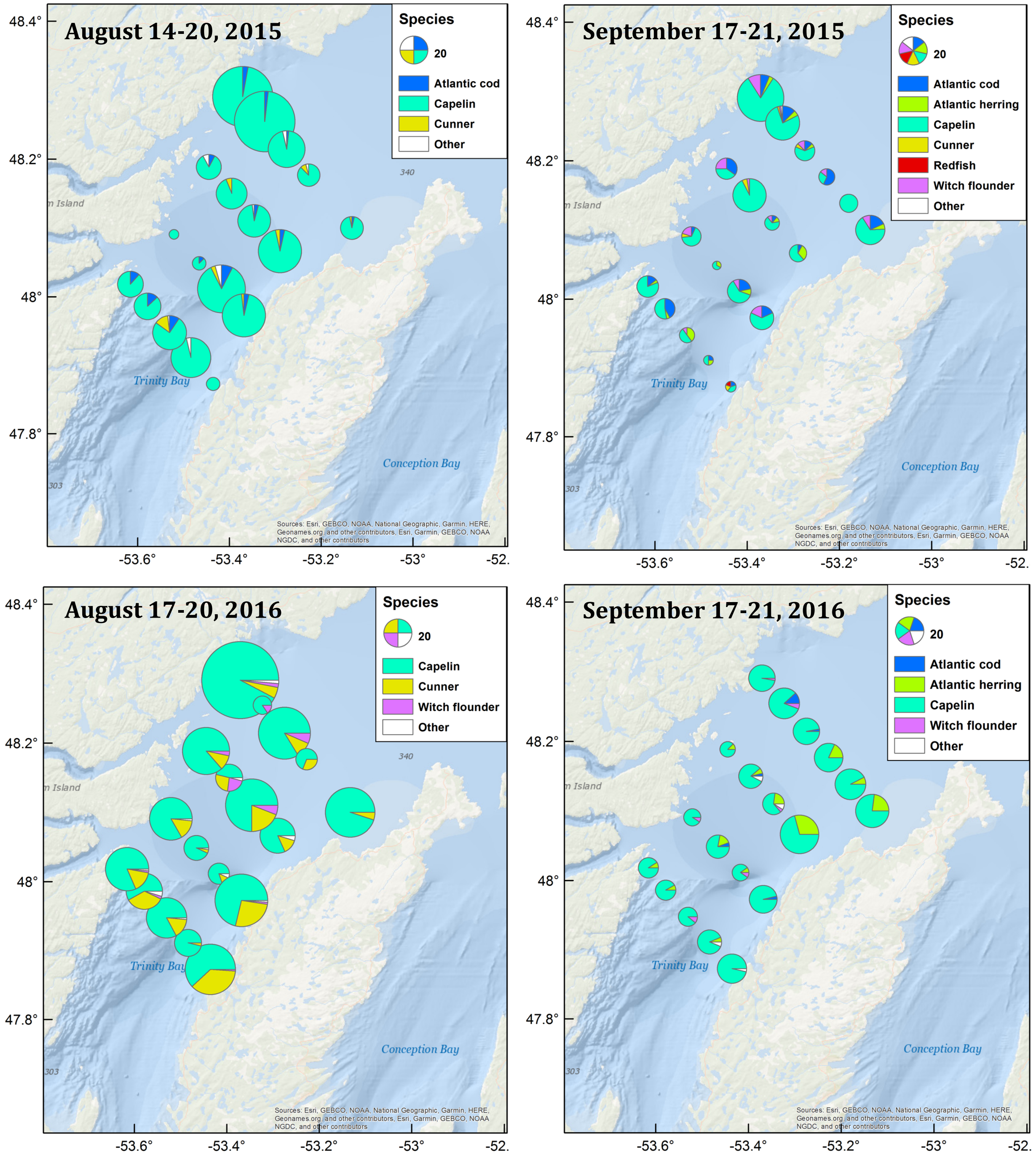


Figure 2.6: Species composition and relative larval density for the Trinity Bay in 2015 and 2016. Pie charts scaled by total larval density at a station relative to the highest larval density in a given survey. Median larval density in larvae m^{-2} is shown in the legend.

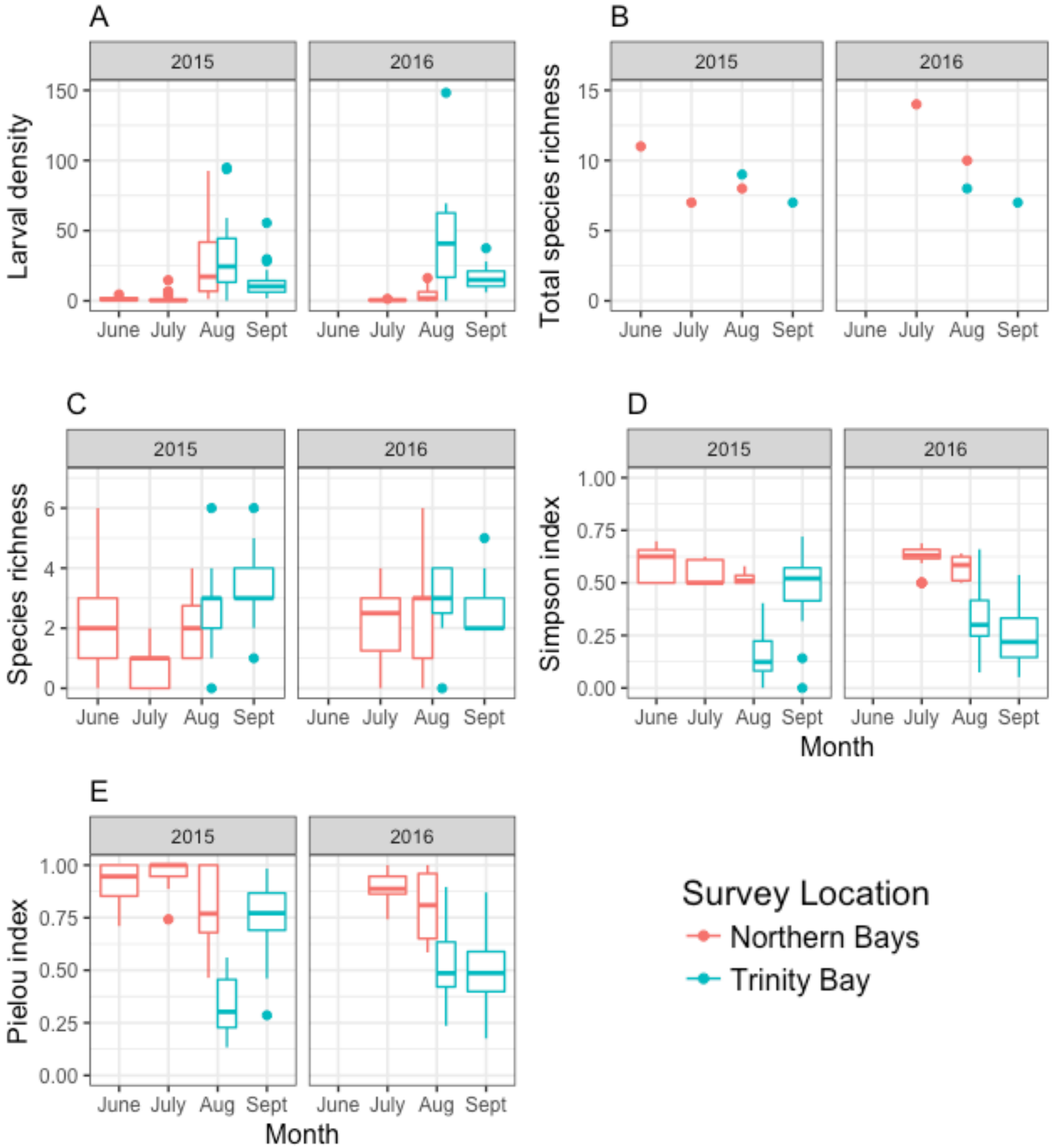


Figure 2.7: Boxplots showing median, first and third quartiles, and outliers. A) Overall larval density in number of larvae m^{-2} for each survey, split by year, B) Total species richness found for each survey, split by year, C) Species richness for each survey, split by year, D) Gini-Simpson species diversity index values for each survey, split by year, and E) Pielou's evenness index values for each survey, split by year.

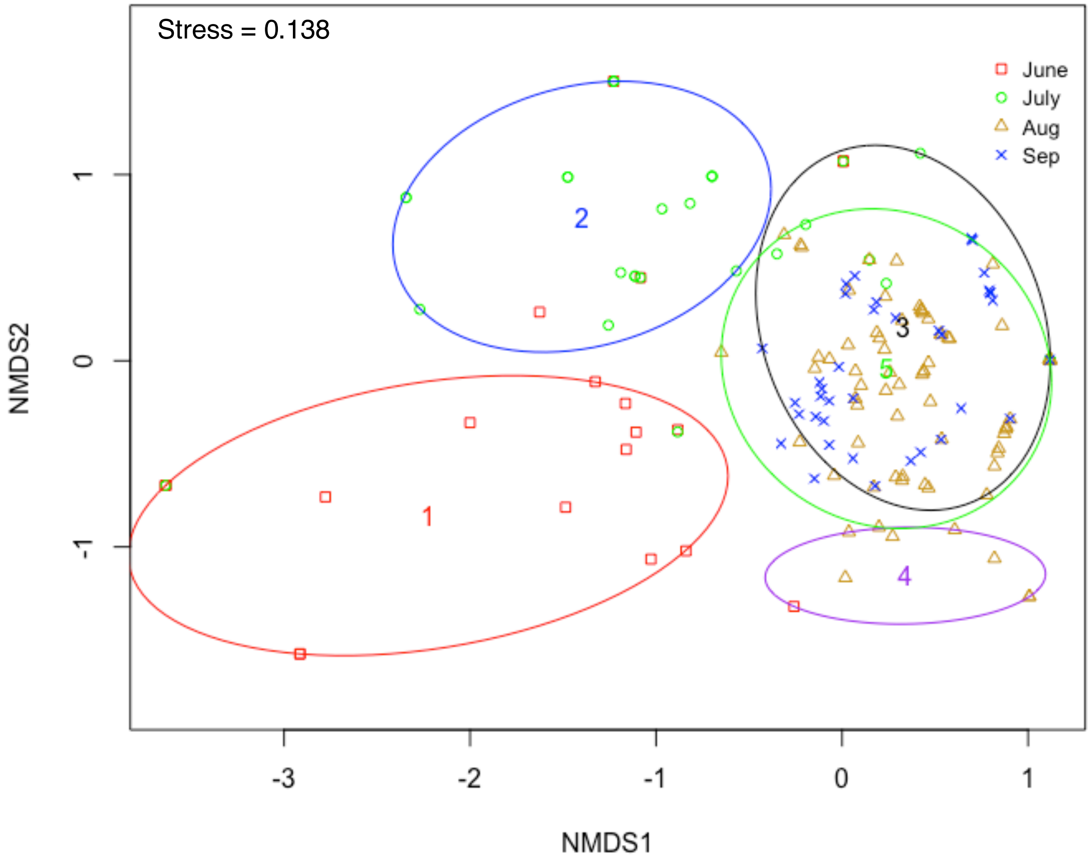


Figure 2.8: NMDS ordination plot for species occurring in at least 3% of sites, with ellipses showing 5 groups derived from hierarchical cluster analysis, and sampling month overlaid onto individual sites.

CHAPTER 3: LARVAL CAPELIN (*MALLOTUS VILLOSUS*) POPULATION DYNAMICS IN COASTAL EMBAYMENTS OF EASTERN NEWFOUNDLAND: AN ANALYSIS OF OTOLITH MICROSTRUCTURE

3.1 Introduction

Capelin (*Mallotus villosus*) is a small pelagic fish that numerically dominates the forage species assemblage in several North Atlantic marine ecosystems (Lavigne, 1996; Gjøsæter, 1998). Capelin plays a crucial role in transferring energy from lower trophic levels to larger vertebrate predators within the pelagic food web of the Barents Sea, waters surrounding Iceland and Greenland, and off the Northeast coast of Newfoundland and Labrador (NL) (Carscadden and Vilhjàlmsson, 2002). In particular, it is a major diet component for piscivorous fish (e.g. Atlantic cod), seabirds (e.g. Northern gannet), and marine mammals (e.g. Minke whale) (Marshall et al., 1999; Carscadden et al., 2001; Vilhjàlmsson, 2002).

The NL capelin stock collapsed in the early 1990s, with estimated abundances dropping to less than 1% of historical values (DFO, 2015). Due to their short lifespan and variable recruitment, capelin stock size can change rapidly and drastically (DFO, 2015), and it has been shown that year-class strength in capelin is determined during the early life-history stages (Frank and Leggett, 1981; Dalley et al., 2002). The larval stage has the highest overall losses of any life stage in fish (Cushing, 1975; McGurk, 1986), and consequently slight changes in survival can result in important fluctuations in recruitment and thus year-class strength (Hjort, 1914; Houde, 1987; Anderson, 1988; Horwood et al., 2000), making it crucial to understand the factors that can affect larval survival. One important such factor is larval growth, as variability in larval growth rates has often been linked to variability in larval survival (Anderson, 1988; Hare and Cowen, 1997; Sirois and Dodson, 2000). Faster-growing larvae typically experience lower mortality due to increased size-at-age (Peterson and Wroblewski, 1984; Folkvord and Hunter, 1986; Miller et al., 1988), decreased duration of the particularly vulnerable larval stage (Chambers and Leggett, 1987; Houde, 1987; Anderson, 1988), and potentially also growth-selective predation resulting in decreased predation mortality (Takasuka et al., 2003, 2004).

Given the impact of growth rates on larval survival, analysis of larval age and growth by use of otolith microstructure is an important tool for exploring population dynamics. Typically, daily growth increments form within larval fish otoliths post-hatch, and can thus be used to estimate larval age, while otolith growth is correlated with somatic growth (Campana and Neilson, 1985). However, the rate of formation of increments, the timing of the "hatch check," and the relationship between otolith growth and somatic growth can vary among species and must be validated (Campana and Neilson, 1985; Moksness, 1992). While otolith microstructure analysis has not been extensively applied to research on larval capelin, fast-growing capelin larvae (somatic growth rates of ~0.3 mm d^{-1}) have been found to deposit approximately one increment per day (Jakobsen et al., 2004; Ivarjord et al., 2008), with the "hatch check" occurring at the age of approximately 12 days post-hatch (Ivarjord et al., 2008). Similar effects of growth rate on otolith increment formation were also found in herring larvae (Geffen, 1982; Folkvord et al., 2000; Fox et al., 2003). Furthermore, it is thought that growth-selective mortality against slow-growing individuals likely increases the accuracy of age estimates on wild-caught larvae (Moksness, 1992; Ivarjord et al., 2008), making the use of otolith microstructure in studies of larval capelin population dynamics both valid and valuable.

DFO conducts an annual larval survey in Trinity Bay to map larval capelin distribution and abundance in order to develop a recruitment index (Nakashima and Mowbray, 2014), and results are extrapolated to encompass the entire stock (Carscadden et al., 1997). However, larval capelin survival can vary spatially with variability in environmental conditions (Frank and Leggett, 1981; Leggett et al., 1984; Carscadden et al., 2001; Dalley et al., 2002), which may differ along the NE Newfoundland coastline. There are important capelin spawning grounds ~300km north of Trinity Bay, yet the assumption that larval population dynamics are consistent throughout eastern Newfoundland has never been tested. To address this issue, larval surveys were conducted in two coastal embayments of NE Newfoundland, White Bay and Notre Dame Bay, and then otolith microstructure analysis was used to compare and contrast larval growth rates, the relationship between otolith growth and somatic growth, and growth rate trajectories between the northern bays and Trinity bay over the course of two years. The objectives of this study were to (1) explore the use of otolith microstructure as a tool for assessing variability in larval capelin growth rates, (2) test the null hypothesis that larval capelin abundance, length-at-age, and growth rates do not differ between areas within the capelin stock spawning distribution, and (3) assess the level of interannual variability in larval capelin growth and abundance.

3.2 Materials and Methods

Field survey

Ichthyoplankton surveys were conducted in August of 2015 and 2016 in three coastal embayments along the eastern coast of Newfoundland (Fig. 2.1). White Bay and Notre Dame Bay, subsequently referred to as the "northern bays," are adjacent bays in northeastern Newfoundland, while Trinity Bay is a more southerly embayment along the same coast (see Chapter 2).

Samples from the northern bays were collected during two surveys (August 24-26, 2015 and August 24-25, 2016), that covered a grid of 26 stations (Figure 2.2). For both surveys, bongo nets measuring 61 cm in diameter with a 333 μm mesh size were deployed in a double oblique fashion and towed at 2.5 knots for ca. 10 minutes at a 45° angle. During these tows, the nets were lowered at 0.5 m s^{-1} to a depth of 50 m, and then raised at the same speed. Upon retrieval, nets were washed with seawater to minimize the potential loss of plankton, and one plankton sample was preserved in 2% buffered formaldehyde and in 2015, the other sample was immediately frozen, while in 2016 it was preserved in 95% ethanol. For all tows, mechanical flowmeters were placed at the mouth of each bongo net to obtain the volume of water sampled (Dalley et al., 2002).

Samples from Trinity Bay were collected during surveys that were part of the annual DFO larval capelin assessment. These surveys cover 19 stations (as shown in Figure 2.3) that were sampled from August 14-21, 2015 and August 17-20, 2016. Oblique tows were completed using 333 μm nets on a 61 cm diameter double bongo frame, with a boat speed of 2-2.5 knots. The bongo was towed to a maximum depth of 200 m, with a target descent rate of 0.33 m s^{-1}, and a target ascent rate of 0.17 m s^{-1}, and mechanical flowmeters were used to determine the volume of water filtered by the nets (Nakashima and Mowbray, 2014). From each tow, one plankton sample was immediately preserved in 2% buffered formaldehyde while the other was preserved in 95% ethanol.

Laboratory analysis

Ichthyoplankton analyses took place at the Centre for Fisheries Ecosystems Research (CFER), Fisheries and Marine Institute of Memorial University of Newfoundland, and at the Northwest Atlantic Fisheries Centre, both located in St. John's, NL, Canada.

For samples from the northern bays, all larvae were extracted from the formalin-preserved plankton samples, as part of a larger ichthyoplankton study, and were then identified to species (Fahay, 2007) with a stereomicroscope. Capelin larvae were measured individually (standard length) using Olympus cellSens imaging software, and overall larval capelin density at each station was determined using the formula:

$$(1)\quad \rho = C * \frac{Z}{V}$$

where larval density in square meters (ρ) is the product of the number of larvae in the sample (C) and the depth of the tow in meters (Z), divided by the volume of water filtered in cubic meters (V), which provides a measure of density that is integrated over the water column (Nakashima and Mowbray, 2014). Previous plankton analyses in coastal Newfoundland have shown that ichthyoplankton are limited to the top 50 m of the water column (P. Pepin, pers. comm.). Thus, the difference in sampling depth between the northern bays and Trinity Bay was controlled for by incorporating both depth and volume sampled into the calculation of larval density.

For samples from Trinity Bay, formalin-preserved plankton samples were strained and reconstituted in freshwater to 1 L volume, then analyzed in consecutive 50 mL aliquots until a minimum of 50 capelin larvae had been extracted from the sample or half the sample had been analyzed. All larvae found were identified to species, the number of larvae recorded, and all capelin larvae up to a total of 50 larvae were measured for standard length. Capelin larval densities for these samples were calculated from the number of larvae, the proportion of the sample analyzed, and the volume of water filtered (obtained from the mechanical flowmeters) as previously described for the northern bays.

Otolith microstructure analysis

To estimate larval age and growth rates, capelin larvae were extracted from a subset of frozen/ethanol-preserved samples. This subset consisted of the six stations with the highest capelin density, as determined from the prior ichthyoplankton analysis, from each survey. The frozen samples from the northern bays in 2015 were re-preserved in 95% ethanol prior to analysis. A subsample of 10 capelin larvae was extracted from each sample, larvae were measured (standard length), and their sagittal otoliths were removed and mounted on glass slides using a cyanoacrylate adhesive as mounting medium (Campana and Neilson, 1985). These were then viewed under light microscopy with immersion oil at 1000 × magnification and photographed. For each larva, the otolith that yielded the clearest image was then analyzed in ImageJ software using the ObjectJ plugin. Daily increments were counted, and increment widths and total otolith radius were measured along the longest axis. Counts and measurements were performed twice for each otolith to ensure precision of aging. If the coefficient of variability between counts was less than 10%, the first count and the average of the two measurements were used for all subsequent analyses. Nineteen otoliths (~ 8%) were discarded, due to the variability between counts being greater than 10%.

Statistical analyses

First, larval growth estimates, derived from length-at-age relationships, were compared between survey locations and years, using an analysis of covariance performed on a general linear regression model of larval length relative to increment number, survey location, and year. Increment number was used, rather than larval age in days, as formation of daily otolith increments in capelin larvae begins at approximately 12 days post-hatch (Ivarjord et al., 2008). Where three-way interaction terms were significant, the model was split by year. However, the model of population growth yielded intercepts that were biologically unrealistic, so a simple general linear model of larval length relative to increment number was conducted, followed by an analysis of variance on the residuals relative to survey location and year. This controlled for larval age and thus focused on the variables of interest: survey location and year. The same procedure was then followed for examining the relationship between otolith growth and somatic growth. Linear model assumptions of normality and homoscedasticity were evaluated for each model by graphical examination of the residuals, and the criterion for significance was set at a level of $\alpha = 0.05$.

Next, in order to assess growth rate trajectories, the relationship between increment width, a proxy for daily somatic growth (Campana and Neilson, 1985), and increment number was examined, with explanatory variables survey location and year. Given that individual larvae may have faster or slower growth rate trajectories, a repeated-measures analysis of variance (ANOVA) was used, as it is an analysis of dependencies. However, the model requires that all individuals (i.e. larvae) have the same number of measurements, which does not occur in field-sampled larvae, as there was a range of ages at capture. To circumvent this issue, three separate repeated-measures ANOVAs were performed. The first model included all larvae that had at least four increments, and analyzed increment width relative to increment number, survey location, and year. The second model included all larvae that had at least eight increments, and analyzed increment widths for increments 5-8 relative to increment number, survey location, and year. The third model contained all larvae that had at least 12 increments, and analyzed increment widths for increments 9-12 relative to increment number, survey location, and year. Where there was a significant three-way interaction term, the model was split by year.

Finally, to assess recent larval growth (defined as the last three days of growth), an index of growth, standardized to zero mean and standard deviation, was computed using the formula:

$$(2)\quad DG_{ij} = \left(G_{ij} - G_j\right) SD_j^{-1}$$

where DG_{ij} is the detrended growth of larva i at age j, G_{ij} is the growth (increment width) of larvae i at age j, and G_j and SD_j are mean and standard deviation for larval growth at age j (Baumann et al., 2003; Robert et al., 2009). An analysis of variance was then performed on this detrended recent growth index relative to survey location and year. The last increment corresponding to the edge of the otolith was not included in the analysis, as it may not have fully formed (i.e. less than 24 hours since deposition). Additionally, edge effects due to refraction of light off the edge of the otolith (Campana and Neilson, 1985) might affect the width measurement of the outermost increment. All statistical analyses were completed in R 3.4.0 with the car and ggplot2 packages.

3.3 Results

Characteristics of larval capelin distribution

Larval capelin abundance and distribution pattern was similar between survey locations in 2015, while abundance differed substantially between the northern bays and Trinity Bay in 2016 (Figure 3.1). Capelin larvae were consistently most abundant near the mouths of the bays, in both the northern bays and Trinity Bay. In 2015, mean larval density was similar between survey locations ($\bar{x} = 26.88$ m^{-2} in the northern bays and $\bar{x} = 30.46$ m^{-2} in Trinity Bay). In 2016, mean density of larval capelin was ~15% higher in Trinity Bay ($\bar{x} = 34.67$ m^{-2}), while the northern bays showed a ~90% decrease in mean larval capelin abundance ($\bar{x} = 3.02$ m^{-2}). This decreased abundance in the northern bays was most predominant in Notre Dame Bay.

Larval length distribution

In both years, mean and modal length of capelin larvae collected in the northern bays was larger than that of larvae collected from Trinity Bay (Figure 3.2). In 2015, larvae collected from the northern bays ranged from 4.5 to 16.2 mm with a mean length of 8.3 mm and ~70 % of larvae between 6 and 10 mm, while larvae collected from Trinity Bay ranged from 3.0 to 21.4 mm, with a mean length of 7.7 mm and ~75 % of larvae between 4 and 9 mm. In 2016, larvae from the northern bays ranged from 4.0 to 29.0 mm, with a mean length of 10.4 mm and ~75 % of larvae within the 6-12 mm size range, while larvae from Trinity Bay ranged from 3.2 to 12.0 mm, with a mean length of 6.0 mm, and ~73 % of larvae within the 4-7 mm size range.

Larval growth estimates

Interannual variation in larval capelin growth rate estimates and length-at-age differed between the northern bays and Trinity Bay (Tables 3.1-3.2 and Figures 3.3-3.4). There was a significant interaction between the effect of larval age (as measured in number of daily growth increments), survey location, and year on larval length (ANCOVA, $F_{1,179} = 12.12$, $p < 0.001$). When the model was split by year, in 2015, growth rate was significantly higher in the northern bays than in Trinity Bay (ANCOVA, $F_{1,91} = 8.71$, $p = 0.004$). In 2016, the slope of length-at-age was higher in Trinity Bay than in the northern bays, although this difference was marginally significant (ANCOVA, $F_{1,88} = 3.81$, $p = 0.054$). Furthermore, when controlling for larval age, there was a significant interaction between the effect of survey location and year on larval length-at-age relative to the overall population mean length-at-age (ANOVA, $F_{1,183} = 40.68$, $p < 0.001$). Median length-at-age of larval capelin in Trinity Bay was close to the population mean, while in 2015 the median length-at-age of capelin larvae in the northern bays was much lower than the population mean, and in 2016 the median was much higher than the population mean (Figure 3.4).

Otolith growth and size

The relationship between otolith growth and somatic growth in larval capelin was linear, and was consistent between survey locations and years (Table 3.3, Figure 3.5). Otolith radius was strongly, positively correlated with somatic length, and the overall mean otolith radius to body length ratio was 1.08, indicating that otolith growth is slightly faster than somatic growth. When controlling for larval length, mean otolith radius of larvae from the northern bays in 2015 was significantly larger than larvae from Trinity Bay in 2015 (ANOVA, $F_{1,93} = 21.62$, $p < 0.001$), while in 2016, there was no significant difference in mean otolith radius between survey locations (Table 3.4 and Figure 3.6).

Daily growth and detrended recent growth

Daily growth, as determined by larval otolith increment width and cumulative otolith radius, differed more between survey locations in 2015 than in 2016 (Tables 3.5-3.7, Figures 3.7-3.8). In 2015, increment widths were similar between survey locations for the first four days of increment deposition, but then diverged as daily growth in the larvae from the northern bays became significantly greater than daily growth of larvae from Trinity (repeated-measures ANOVA, $F_{1,15} = 7.345$, $p = 0.016$ and $F_{1,4} = 10.58$, $p = 0.031$ for increments 5-8 and 9-12, respectively). In 2016, however, there was no significant difference in increment widths between survey locations for increments 1-4 and 9-12, but larvae from Trinity Bay had significantly higher daily growth than the northern bays larvae for increments 5-8 (repeated-measures ANOVA, $F_{1,33} = 4.785$, $\mathrm{p} = 0.036$). This trend was also observed in mean cumulative otolith radius, where otolith growth increased with age in the northern bays in 2015, while it remained constant in Trinity Bay. In 2016, otolith growth rate was constant for larvae from the northern bays, while it increased with age in larvae from Trinity Bay, albeit much less drastically than for larvae from the northern bays in 2015 (Figure 3.8).

Detrended recent growth of individual capelin larvae yielded similar results, where the individual recent growth significantly differed between survey locations in 2015 but not in 2016 (Table 3.8, Figure 3.9). There was a significant interaction

(ANOVA, $F_{1,135} = 7.10$, $p < 0.01$) between the effect of survey location and year on standardized increment width (SIW), a detrended measure of individual recent larval growth. When each year was analyzed individually, SIW was significantly higher in the northern bays than in Trinity Bay in 2015 (ANOVA, $F_{1,70} = 7.04$, $p < 0.01$, effect size of 0.56), while in 2016 there was no significant difference between survey locations (effect size of 0.3).

3.4 Discussion

Otolith microstructure analysis and the accuracy of age measurement

Since daily growth increments were first observed (Pannella, 1971), otolith microstructure analysis has frequently been used to study early life history in fishes as a tool to estimate larval age and growth (Begg et al., 2005). Age estimates, determined from the number of daily growth increments, can be used to estimate growth rates and back-calculate hatch dates (Campana, 1990). However, there are two potential sources of error: 1) error in the accuracy of age estimates relative to true larval age, and 2) precision error arising from the aging technique (Campana, 2001). The first varies interspecifically and can be estimated for a given species by determining the rate of increment deposition from known-age larvae, while the second can be controlled procedurally (Campana and Neilson, 1985; Morison et al., 2005). Various factors can affect ageing accuracy, including the age of first increment deposition (not always coincident with hatching), rate of increment deposition, and image resolution, as narrow increments, particularly in young or slow-growing larvae, may be below the resolution of a light microscope (Campana and Neilson, 1985; Campana et al., 1987; Fox et al., 2003). In capelin, a validation study with known-age larvae showed that increment deposition begins at approximately 12 days post-hatch (Ivarjord et al., 2008), and that fast-growing larvae ($\geq$ 0.3 mm d^{-1}) deposited near-daily increments (0.91-0.96 increments per day). Larval growth rates in the present study, estimated from the slope of length-at-age, varied from 0.21-0.49 mm d^{-1}, falling at the upper end of published growth rates for larval capelin, which range from 0.1-0.4 mm d^{-1} (Frank and Leggett, 1986; Ivarjord et al, 2008; Olafsdottir and Anderson, 2010; Nakashima and Mowbray, 2014). Growth rates measured from capelin larvae raised in a controlled setting yielded lower growth rates, ranging from 0.16-0.33 mm d^{-1} (Frank and Leggett, 1986; Ivarjord et al, 2008), while otolith-derived growth rates in field-caught Icelandic capelin yielded high growth rates (0.3-0.4 mm d^{-1}, Olafsdottir and Anderson, 2010). The highest growth rates from the present study (northern bays in 2015 and Trinity Bay in 2016) and the similarly high growth rates from Olafsdottir and Anderson's study (2010) yielded biologically inaccurate back-calculated hatch lengths. It is possible that larval age was underestimated, thus yielding unrealistic intercepts. The potential for accuracy error in age estimates of larval capelin relative to true age introduces challenges in determining absolute hatch dates. However, precision error in this study was low, because all otoliths were aged blind and by a single reader, and all otolith measurements were performed twice with otoliths yielding a coefficient of variability >10% being discarded prior to statistical analysis to ensure precision and repeatability of ageing results. Given the ability to control for precision error, otolith microstructure analysis applied in the present study is a reliable tool for determining relative differences in length-at-age and growth rates among different groups of larvae.

Spatial and interannual variability in larval abundance

Larval capelin abundance in the northern spawning grounds of White Bay and Notre Dame Bay relative to abundance in Trinity Bay varied between 2015 and 2016. Inshore capelin assessments from 1994-1999 showed that the ratio of emergent larval capelin abundance (derived from surveyed larval abundance and estimates of growth and mortality rates) in the northern bays relative to Trinity Bay ranged from 0.6:1 to 12.4:1 (Anderson et al., 2001). Similarly, in the present study, larval density in the northern bays relative to Trinity Bay varied by an order of magnitude with ratios of 0.91:1 in 2015 and 0.09:1 in 2016.

Larval capelin density is characterized by high interannual variability in Newfoundland systems. Within Trinity Bay alone, mean larval density during the August survey has ranged from 6-70 larvae m^{-2} over the past decade (Nakashima and Mowbray, 2014), and similarly high fluctuations in larval abundance were also found in Trinity Bay, Conception Bay, and Placentia Bay in the late 1990s (Anderson et al., 2001; Carter-Lynn, 2009). However, the high interannual variation in relative larval abundance between the northern bays and Trinity Bay suggests that year-to-year changes are not always synchronous among spawning locations. The interannual variability in the distribution of larval capelin between the northern bays and Trinity Bay suggests that larval capelin survival and subsequently the proportion of recruits from the northern bays relative to Trinity Bay also varied interannually, as recruitment to age 2 in capelin is determined early during the larval stage (Frank and Leggett, 1981; Leggett et al, 1984; Dalley et al., 2002; Murphy et al., 2018).

Spatial and interannual variability in larval growth

When the relationship between otolith growth and somatic growth is linear, as occurred in this study, otolith growth can be used as a proxy for somatic growth (Robert et al., 2007; Olafsdottir and Anderson, 2010; Sponaugle et al., 2010; Murphy et al., 2013). Otolith-derived larval growth trajectory and recent larval growth can vary spatially (Suthers et al., 1989; Sponaugle et al., 2010) and interannually (Olafsdottir and Anderson, 2010; Murphy et al., 2013; Rodriguez-Valentino et al., 2015; Takahashi et al., 2016) within a stock, which in turn can impact larval survival, year-class strength, and consequently, management decisions (Houde, 1987; Anderson, 1988; Pepin, 1991; Bergenius et al., 2002; Fontes et al., 2011; DFO, 2015). Off the NE coast of Newfoundland, larval capelin growth, estimated from mean increment width and detrended recent growth, increased with age in the northern bays in 2015, and in Trinity Bay in 2016, although to a lesser degree. These results concur with the growth rates derived from the larval length-at-age relationship, where the northern bays larvae had a higher growth rate in 2015 while Trinity Bay larvae had a higher growth rate in 2016, indicating that larval capelin growth and subsequent survival potential is spatially and interannually variable.

Factors impacting larval dynamics

While capelin off the NE coast of Newfoundland are known to participate in two possible reproductive strategies, beach or demersal spawning, it is unlikely that the spatial variability in larval capelin growth and density shown in this study is the result of separate stocks. Extensive tagging in the 1980s tested the existence of two stocks off the NE coast of NL and found a high degree of mixing and migration among capelin

(Nakashima, 1992), which, along with meristic analysis of capelin stock structure (Misra and Carscadden, 1984), led to the conclusion that there is a single stock (DFO, 2015). Furthermore, recent genetic analysis found no differentiation between beach-spawning and demersal-spawning capelin, suggesting that reproductive strategy is facultative (Penton et al., 2014) and beach versus demersal habitat selection appears to be related to temperature at spawning sites (Crook et al., 2017). Thus, the variability in larval capelin dynamics observed in the present study is likely a result of environmental factors, suggesting that the quality of the growth environment varies in space and time over the NE coast of Newfoundland. Variations in larval abundance may depend on a combination of several factors: spatiotemporal variability in spawning, larval growth, and predation.

Spatial variability in spawning can occur interannually within a stock due to changing environmental conditions (Bradbury, 2000; Idrizaj, 2014) or spawning stock biomass (Schneider et al., 1997). Low spawning stock biomass can lead to a contraction of spawning distribution (MacCall, 1990; Schneider, 1997), as has been shown in Atlantic mackerel in the southern Gulf of St. Lawrence (Grégoire et al., 2013), and in capelin along the NE coast of Newfoundland (H. Murphy, pers. comm.) Such a contraction of spawning may have occurred in 2016, with spawning centered around Trinity Bay, resulting in the much lower larval density in the northern bays that year.

The interannual variability in larval growth between the northern bays and Trinity Bay may also have contributed to differences in larval abundance, as a result of differential larval survival. Given that larval growth impacts survival (Houde, 1987; Anderson, 1988; Pepin, 1991), it is likely that losses were higher in the northern bays in 2016 when larval growth was lower, resulting in lower larval abundance. Similarly, Trinity Bay larvae had higher growth as well as higher abundance in 2016 than in 2015, suggesting higher larval survival in Trinity Bay in 2016. The interannual variability in larval growth and survival in the northern bays relative to Trinity Bay may reflect differing quality or quantity of prey, factors that, although not measured in this study, have been shown to impact larval growth and survival in numerous marine species (Rilling and Houde, 1999; Zenitani et al., 2007; Robert et al., 2009; Sponaugle et al., 2010; Murphy et al., 2013), including capelin (Frank and Leggett, 1986; Murphy et al., 2018).

Finally, variability in predation mortality may have contributed to differential survival and thus to larval abundance in the northern bays relative to Trinity Bay. While larval predation studies are limited due to challenges posed by the rapid digestion time of larvae (Hunter, 1981; Tanabe, 2001; Takasuka et al., 2003; Schooley et al., 2008), larval predation by invertebrates (e.g. jellyfish, ctenophores) and planctivorous fish is likely a major source of larval mortality (Bailey and Houde, 1989; Takasuka et al., 2004). Thus, interannual variation in the distribution of larval capelin predators, such as juvenile herring (Hallfredsson and Pederson, 2009; Gjøsæter et al, 2016), or variability in environmental conditions that impact invertebrate predator abundance (Frank and Leggett, 1982) may have occurred. If so, this would result in differential levels of predation mortality, which would contribute to the interannual variability in larval abundance in the northern bays relative to Trinity Bay,

The variation in larval growth, abundance, and survival potential found in this study suggests that the proportion of recruits from the northern bays relative to Trinity bay varies interannually, because larval abundance and growth are positively correlated with subsequent recruitment (Dalley et al., 2002), and numerous conceptual and field studies have shown larval growth to be highly correlated with survival and thus recruitment (Anderson, 1988; Bergenius et al., 2002; Jenkins and King, 2006; Houde, 2008; Fontes et al., 2011). Murphy et al. (2018) found that emergent larval density in Trinity Bay alone was sufficient to predict fluctuations in age-2 recruitment of the entire stock, although late larval density was not linked to subsequent recruitment. Murphy et al. (2018) also found that preferred prey density was positively correlated with recruitment success and, for a subsample of three years, higher larval growth rates coincided with years of stronger recruitment, suggesting that factors affecting the late larval stage are also important in determining recruitment. Given that numerous factors, such as prey density, larval growth, and predation mortality, can impact larval survival post-emergence, gaining insight into how these factors differ interannually among the NE coast of Newfoundland may allow for fine-tuning and increased resiliency of recruitment forecasts.

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3.6 Tables

Table 3.1a: Linear regression model for population growth with explanatory variables age (increments), survey location (bay), and year.

Linear model: Length~Increments*Bay*Year				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	243.627	1	243.8952	< 2.2e-16*
Increments	57.317	1	57.3806	1.85E-12*
Year	16.475	1	16.4933	7.29E-05*
Bay	21.547	1	21.5706	6.58E-06*
Increments:Year	0.733	1	0.7335	0.392893
Increments:Bay	8.175	1	8.1844	0.0047283*
Year:Bay	33.628	1	33.665	2.92E-08*
Increments:Year:Bay	12.105	1	12.1187	0.0006272*
Residuals	178.803	179		

Table 3.1b: Linear regression model for population growth with interaction between survey location (bay) and age (increments), split by year.

Linear model for 2015: Length~Increments*Bay				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	243.627	1	259.636	< 2.2e-16*
Increments	57.317	1	61.0838	9.21E-12*
Bay	21.547	1	22.9627	6.40E-06*
Increments:Bay	8.175	1	8.7126	0.004019*
Residuals	85.389	91		

Linear model for 2016: Length~Increments*Bay				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	433.26	1	408.149	< 2.2e-16*
Increments	64.76	1	61.009	1.13E-11*
Bay	12.66	1	11.93	0.0008519*
Increments:Bay	4.04	1	3.809	0.0541576
Residuals	93.41	88		

Table 3.2a: Analysis of variance of the residuals from the population growth linear regression model (Length~Increments), as a function of survey location (bay) and year.

Response: Residuals from lm(Length~Increments) Model: Residuals~Bay*Year				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	34.443	1	31.609	6.95E-08*
Bay	26.409	1	24.235	1.90E-06*
Year	61.993	1	56.892	2.08E-12*
Bay:Year	44.326	1	40.678	1.43E-09*
Residuals	99.41	183		

Table 3.2b: Analysis of variance of the residuals from the population growth linear regression model (Length~Increments), as a function of survey location (bay), split by year.

Response: Residuals from lm(Length~Increments) Model for 2015: Residuals~Bay				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	34.443	1	31.591	1.978E-07*
Bay	26.409	1	24.222	3.702E-06*
Residuals	101.396	93		

Response: Residuals from lm(Length~Increments) Model for 2016: Residuals~Bay				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	27.815	1	25.540	2.259E-06*
Bay	18.356	1	16.856	8.858E-05*
Residuals	98.014	90		

Table 3.3: Analysis of covariance for the relationship between otolith growth and somatic growth, with explanatory variables length, survey location (bay), and year.

Linear model: Radius~Length*Bay*Year				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	22.65	1	9.0372	0.003026*
Length	156.57	1	62.4722	2.66E-13*
Year	3.44	1	1.3718	0.243064
Bay	0.33	1	0.1323	0.716497
Length:Year	0.15	1	0.059	0.8084
Length:Bay	3.22	1	1.2859	0.258319
Year:Bay	0.09	1	0.0355	0.85086
Length:Year:Bay	1.08	1	0.4318	0.511971
Residuals	448.6	179		

Table 3.4a: Analysis of variance of the residuals from the linear regression model of otolith radius relative to total larval body length (Radius~Length), as a function of survey location (bay) and year.

Response: Residuals from lm(Radius~Length) Model: Residuals~Bay*Year				
	Sum Sq	df	F value	Pr(>F)
(Intercept)	54.82	1	21.733	6.02E-06*
Bay	64.61	1	25.613	1.01E-06*
Year	47.22	1	18.72	2.49E-05*
Bay:Year	42.26	1	16.753	6.38E-05*
Residuals	461.59	183		

Table 3.4b: Analysis of variance of the residuals from the linear regression model of otolith radius relative to total larval body length (Radius~Length), as a function of survey location (bay), split by year.

<table>
<tr><td colspan="5">Response: Residuals from lm(Radius~Length)
Model for 2015: Residuals~Bay</td></tr>
<tr><td></td><td>Sum Sq</td><td>df</td><td>F value</td><td>Pr(>F)</td></tr>
<tr><td>(Intercept)</td><td>54.82</td><td>1</td><td>18.342</td><td>4.489E-05*</td></tr>
<tr><td>Bay</td><td>64.61</td><td>1</td><td>21.616</td><td>1.097E-05*</td></tr>
<tr><td>Residuals</td><td>277.96</td><td>93</td><td></td><td></td></tr>
</table>

<table>
<tr><td colspan="5">Response: Residuals from lm(Radius~Length)
Model for 2016: Residuals~Bay</td></tr>
<tr><td></td><td>Sum Sq</td><td>df</td><td>F value</td><td>Pr(>F)</td></tr>
<tr><td>(Intercept)</td><td>5.64</td><td>1</td><td>2.763</td><td>0.09995</td></tr>
<tr><td>Bay</td><td>1.48</td><td>1</td><td>0.724</td><td>0.39711</td></tr>
<tr><td>Residuals</td><td>183.64</td><td>90</td><td></td><td></td></tr>
</table>

Table 3.5: Repeated measures analysis of variance of increment width relative to increment number, year, and survey location (bay), for increments 1-4.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Year	0.077	1	1.904	0.1699
Bay	0.074	1	1.84	0.1772
Year:Bay	0.14	1	3.471	0.0646
Residuals	5.444	135		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.0046	3	0.199	0.897
Year:Increments	0.0282	3	1.229	0.299
Bay:Increments	0.0148	3	0.645	0.587
Year:Bay:Increments	0.0069	3	0.302	0.824
Residuals	3.0951	405		

Table 3.6a: Repeated measures analysis of variance of increment width relative to increment number, year and, survey location (bay), for increments 5-8.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Year	0.0257	1	0.971	0.32948
Bay	0.0016	1	0.061	0.80535
Year:Bay	0.3096	1	11.704	0.00128*
Residuals	1.2696	48		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.0069	3	0.291	0.832
Year:Increments	0.0015	3	0.063	0.979
Bay:Increments	0.0259	3	1.1	0.351
Year:Bay:Increments	0.0005	3	0.02	0.996
Residuals	1.1312	144		

Table 3.6b: Repeated measures analysis of variance of increment width relative to increment number and survey location (bay), for increments 5-8 in 2015.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Bay	0.1806	1	7.345	0.0161*
Residuals	0.3688	15		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.0052	3	0.237	0.870
Bay:Increments	0.0121	3	0.554	0.648
Residuals	0.3261	45		

Table 3.6c: Repeated measures analysis of variance of increment width relative to increment number and survey location (bay), for increments 5-8 in 2016.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Bay	0.1306	1	4.785	0.0359*
Residuals	0.9008	33		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.0032	3	0.130	0.942
Bay:Increments	0.0143	3	0.588	0.625
Residuals	0.8051	99		

Table 3.7a: Repeated measures analysis of variance of increment width relative to increment number, year, and survey location (bay), for increments 9-12.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Year	0.0102	1	0.189	0.671
Bay	0.0006	1	0.012	0.915
Year:Bay	0.3431	1	6.34	0.027*
Residuals	0.6494	12		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.00149	3	0.059	0.981
Year:Increments	0.02998	3	1.183	0.33
Bay:Increments	0.0056	3	0.221	0.881
Year:Bay:Increments	0.03453	3	1.363	0.27
Residuals	0.30406	36		

Table 3.7b: Repeated measures analysis of variance of increment width relative to increment number and survey location (bay), for increments 9-12 in 2015.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Bay	0.18577	1	10.58	0.0313*
Residuals	0.07021	4		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.02392	3	0.638	0.605
Bay:Increments	0.01958	3	0.522	0.675
Residuals	0.15005	12		

Table 3.7c: Repeated measures analysis of variance of increment width relative to increment number and survey location (bay), for increments 9-12 in 2016.

Error: Larva				
	Sum Sq	df	F value	Pr(>F)
Bay	0.1580	1	2.182	0.178
Residuals	0.5792	8		

Error: Larva: Increment				
	Sum Sq	df	F value	Pr(>F)
Increments	0.00755	3	0.392	0.760
Bay:Increments	0.02055	3	1.068	0.381
Residuals	0.15401	24		

Table 3.8a: Analysis of variance of detrended recent growth (three day mean) as a function of year and survey location, where SIW represents standardized (i.e. detrended) increment width.

Model: SIW~Bay*Year				
	Sum Sq	df	F value	Pr(>F)
Year	0.017	1	0.0188	0.891076
Bay	0.736	1	0.828	0.364466
Year:Bay	6.308	1	7.1003	0.008647*
Residuals	119.939	135		

Table 3.8b: Analysis of variance of detrended recent growth (three day mean) as a function of survey location, split by year, where SIW represents standardized (i.e. detrended) increment width.

Model for 2015: SIW~Bay				
	Sum Sq	df	F value	Pr(>F)
Intercept	2.495	1	3.1587	0.079868
Bay	5.560	1	7.0382	0.009865*
Residuals	55.297	70		

Model for 2016: SIW~Bay				
	Sum Sq	df	F value	Pr(>F)
Intercept	0.556	1	0.5596	0.4571
Bay	1.484	1	1.4922	0.2263
Residuals	64.642	65		

3.7 Figures

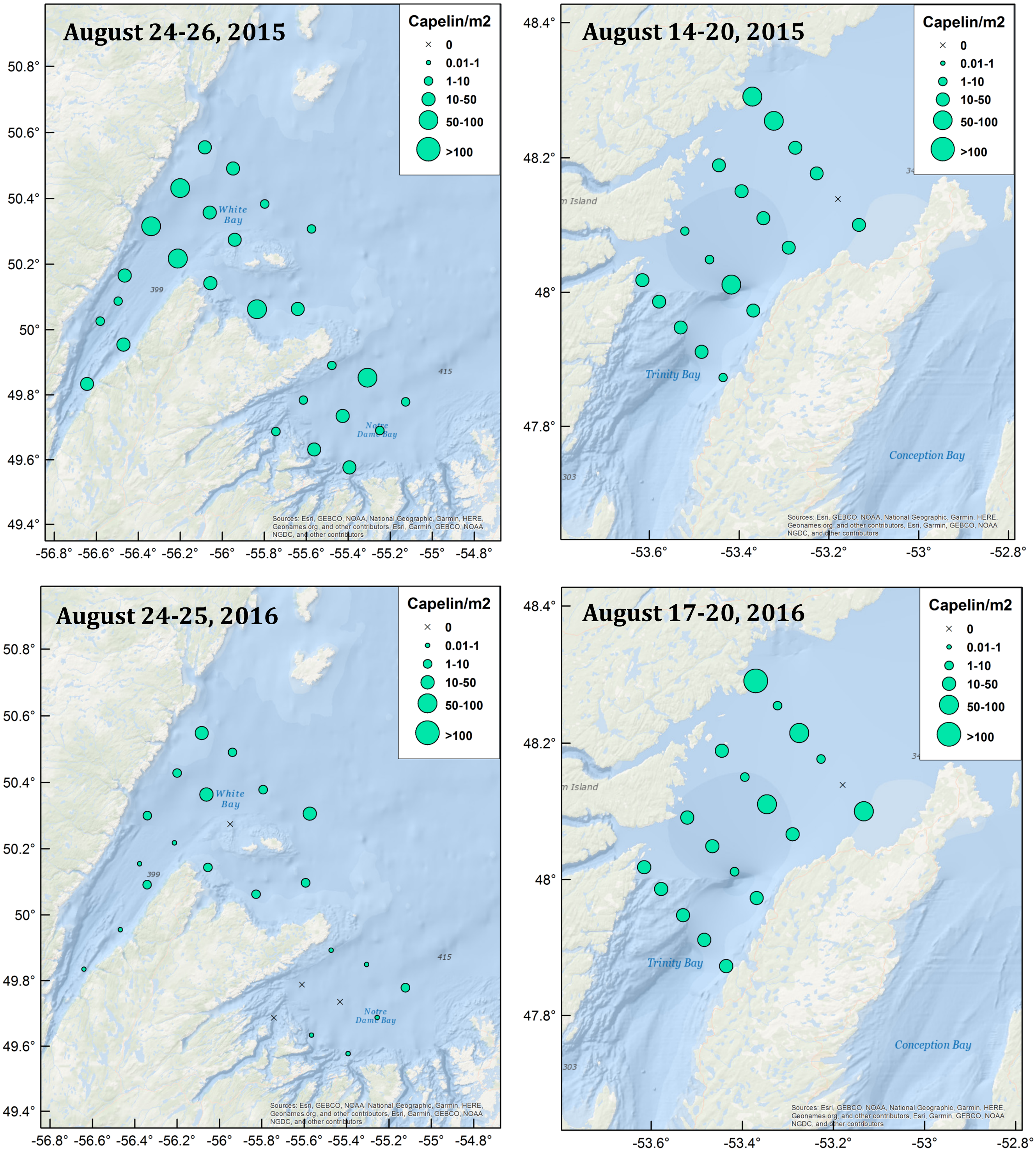

Figure 3.1: Larval capelin density in larvae m^{-2} in the northern bays (left) and Trinity Bay (right) in August of 2015 and 2016.

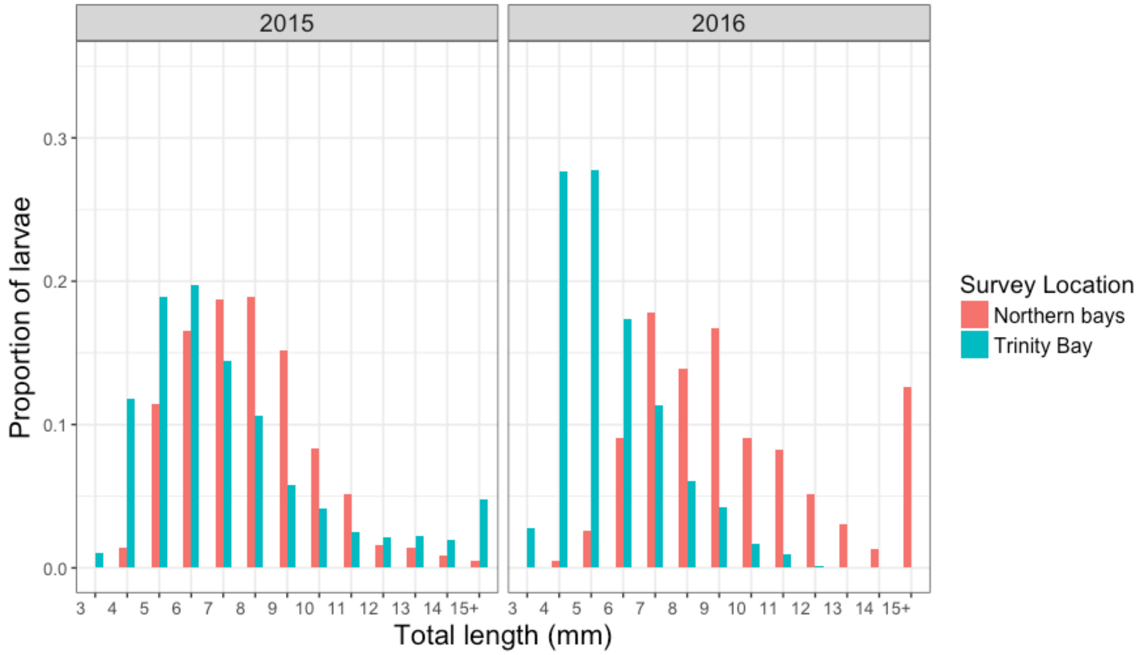

Figure 3.2: Length frequency distribution of capelin larvae collected in the northern bays and Trinity Bay in August of 2015 and 2016.

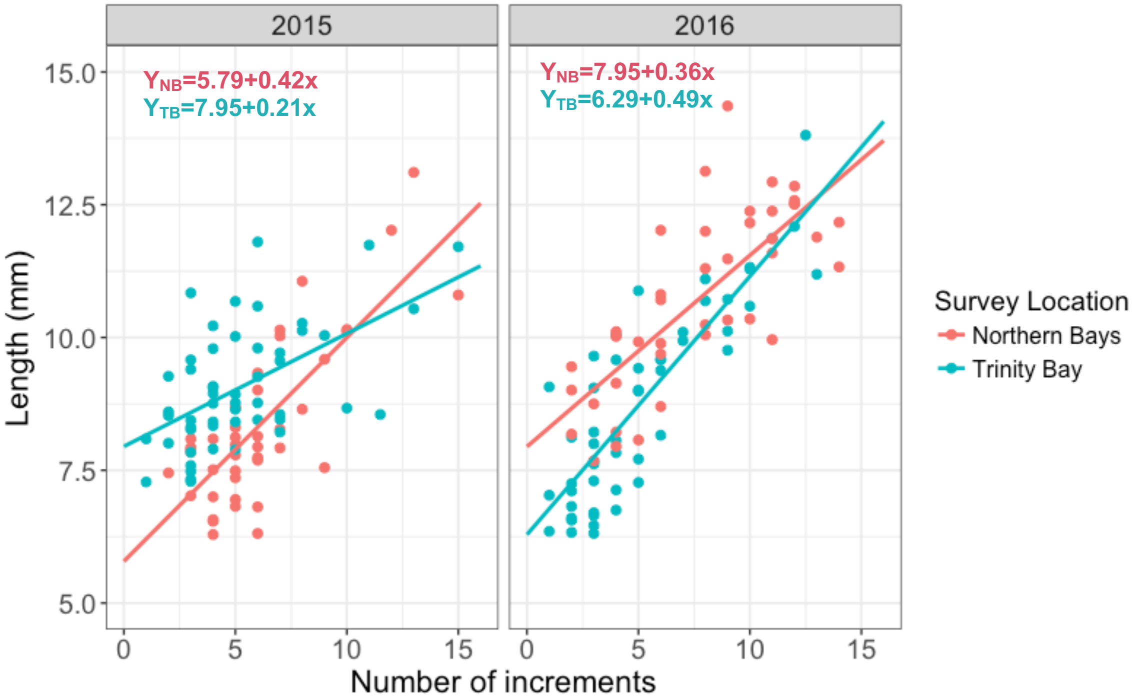

Figure 3.3: Larval capelin population growth in the northern bays and Trinity Bay in August of 2015 and 2016. Linear regression models for trend lines are shown for each survey location and year.

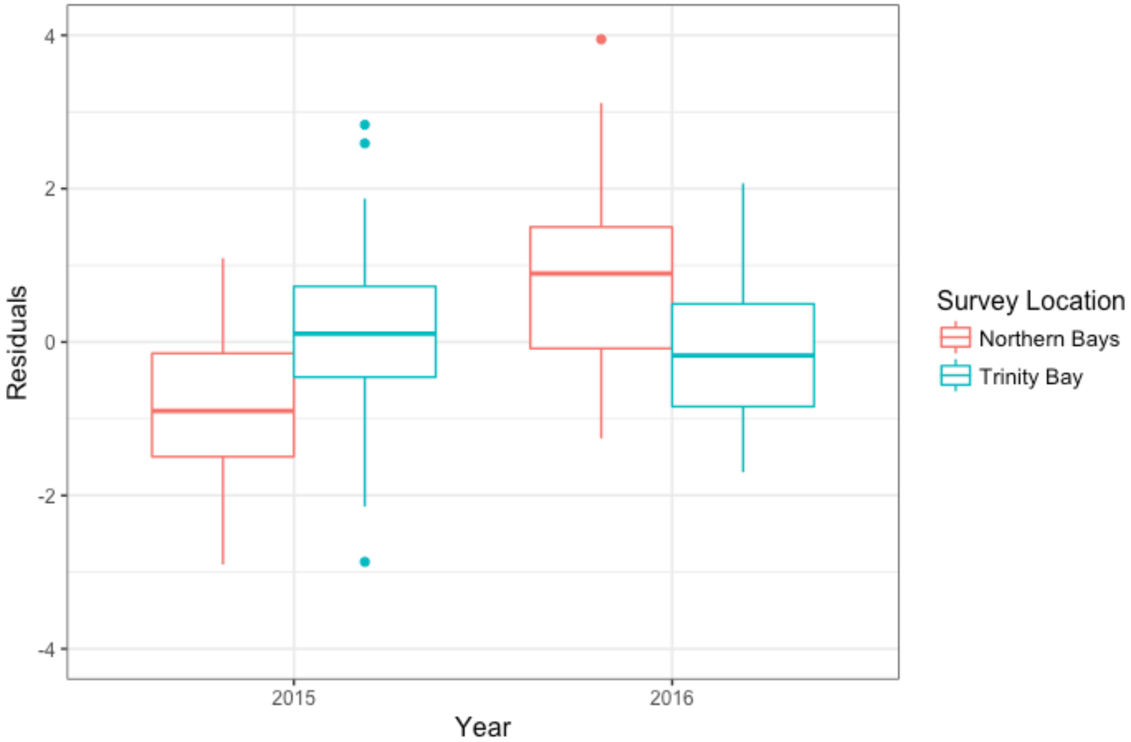

Figure 3.4: Median, first and third quartile, and outliers of the residuals from the linear regression of larval capelin length and increment number, as a function of survey location and year.

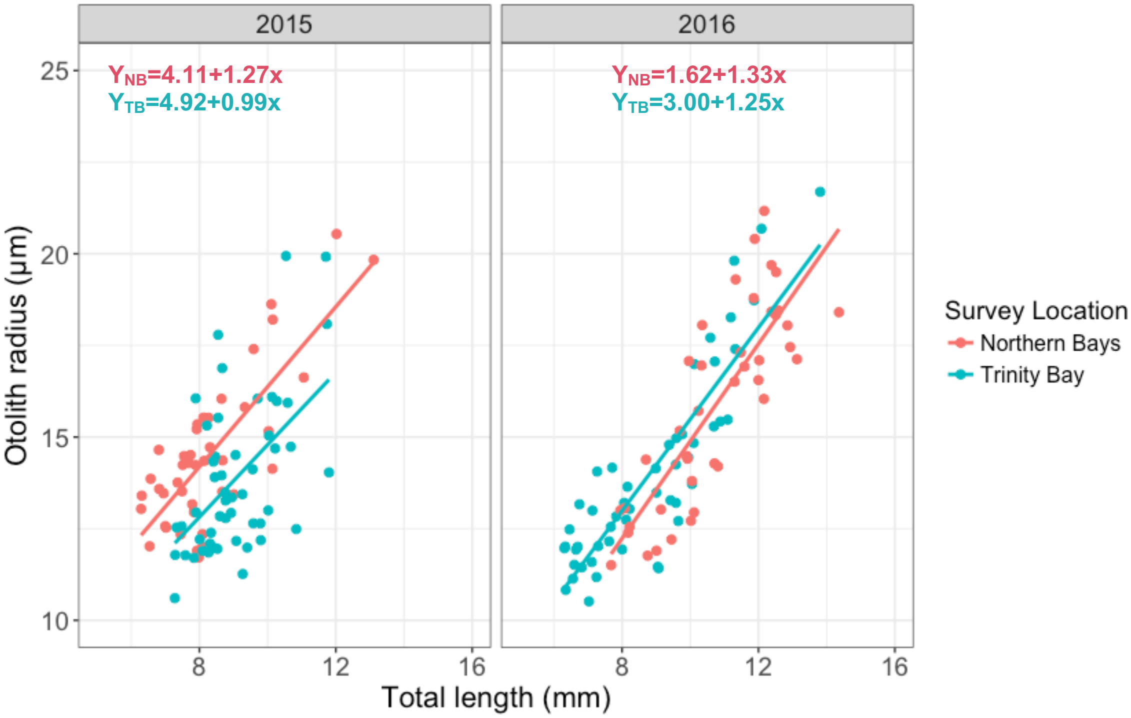

Figure 3.5: Larval capelin otolith growth relative to somatic growth in the northern bays and Trinity Bay in August of 2015 and 2016. Linear regression models for trend lines are shown for each survey location and year.
*** Removing outlier in 2015 NB did not change ANOVA outcome results.

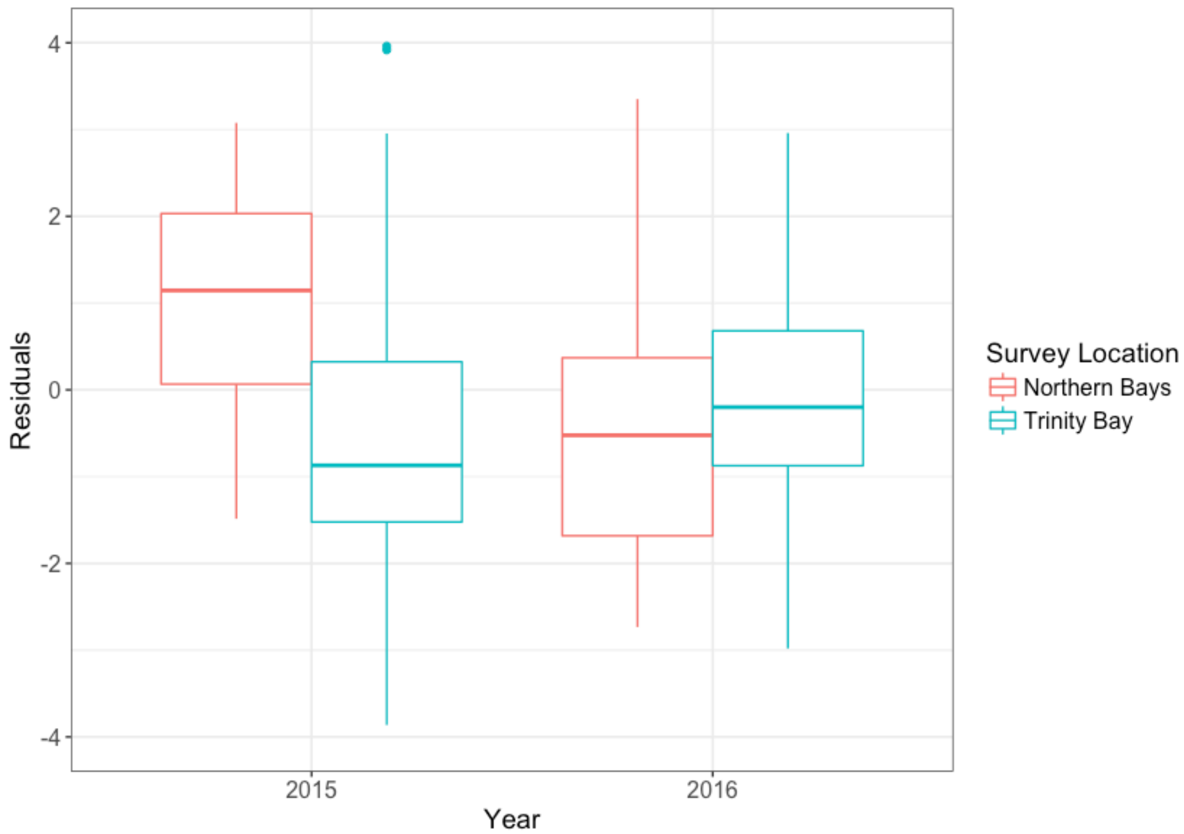

Figure 3.6: Median, first and third quartile, and outliers of the residuals from the linear regression of larval capelin otolith radius (μm) relative to total length (mm), for larval capelin from the northern bays and Trinity Bay, in August of 2015 and 2016.

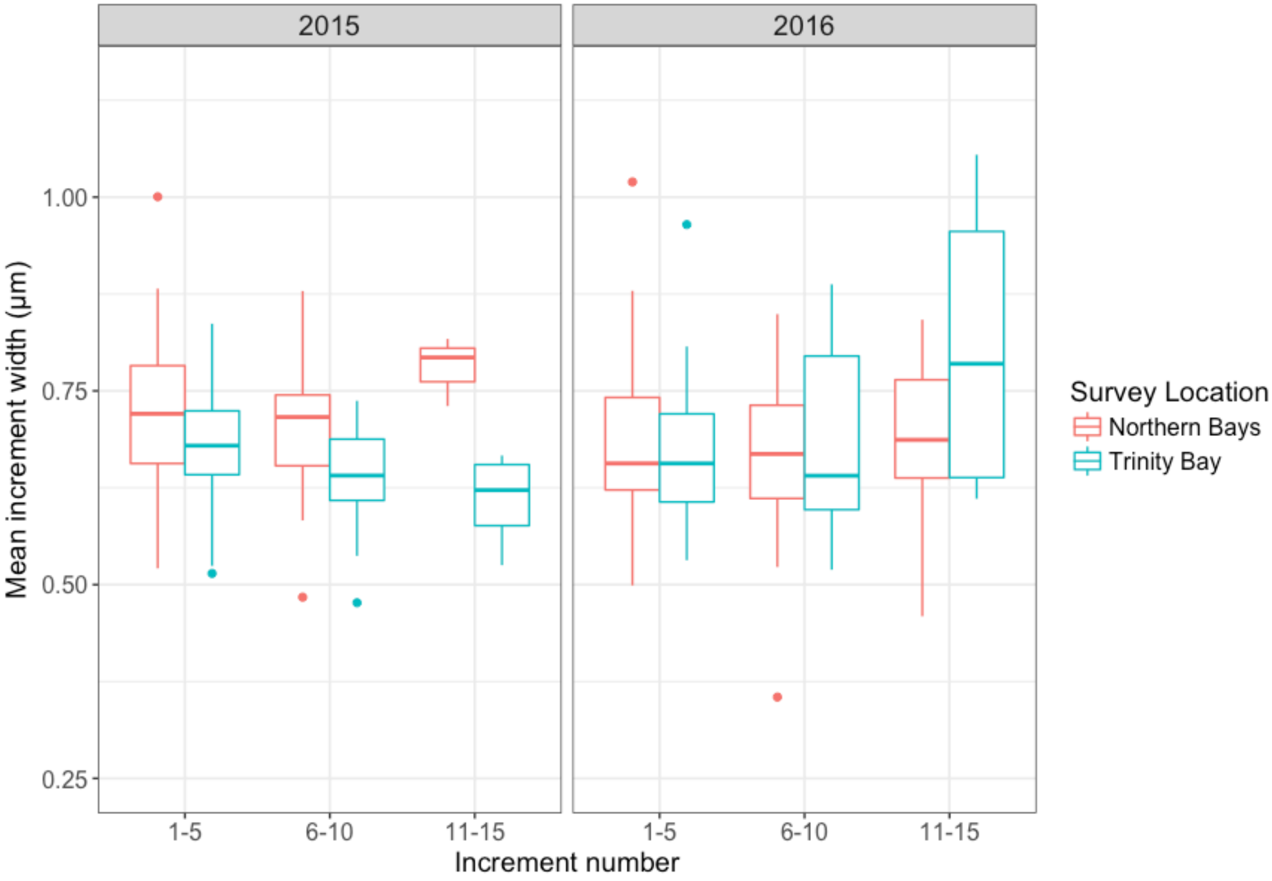

Figure 3.7: Binned mean otolith increment widths for capelin larvae in the northern bays and Trinity Bay in August of 2015 and 2016. Increment widths of individual larvae were averaged by 5-increment groupings. Boxplot indicating median, first and third quartile, and outliers.

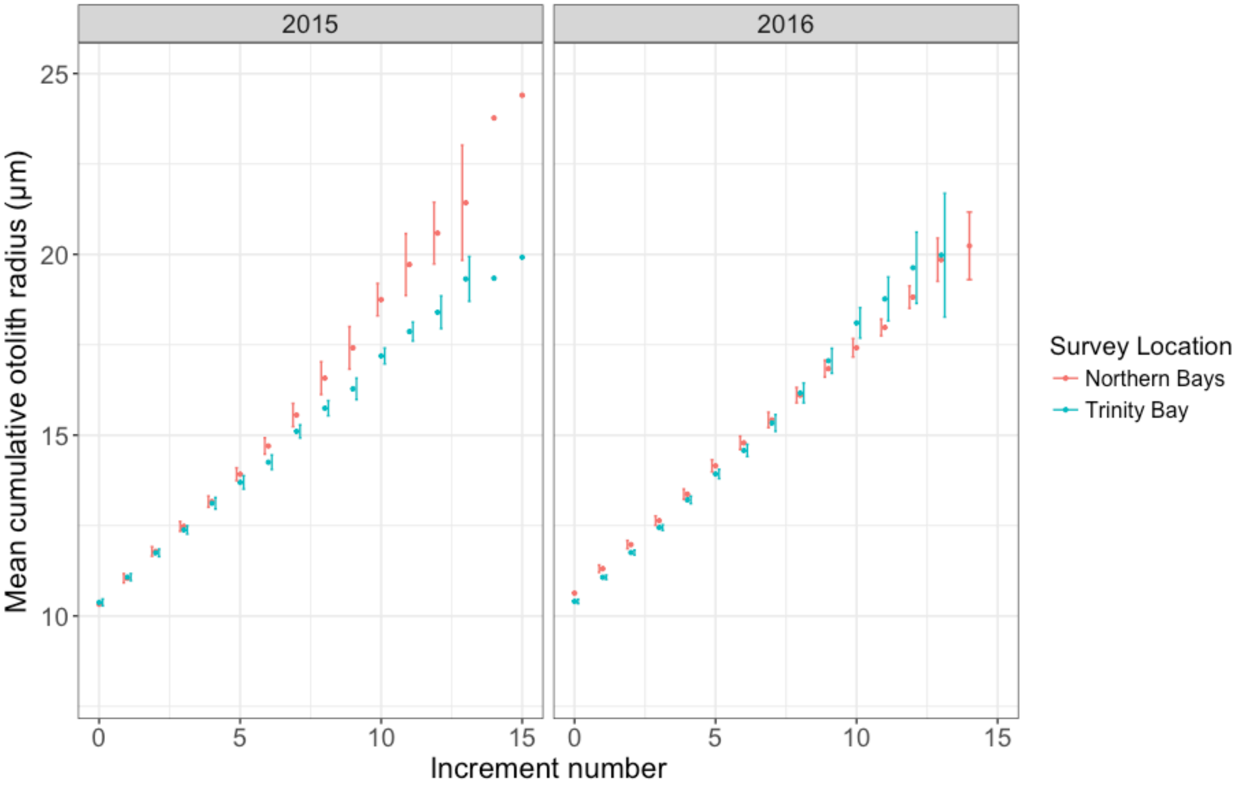

Figure 3.8: Mean growth rate trajectory for capelin larvae in the northern bays and Trinity Bay in August of 2015 and 2016, where error bars represent standard error.

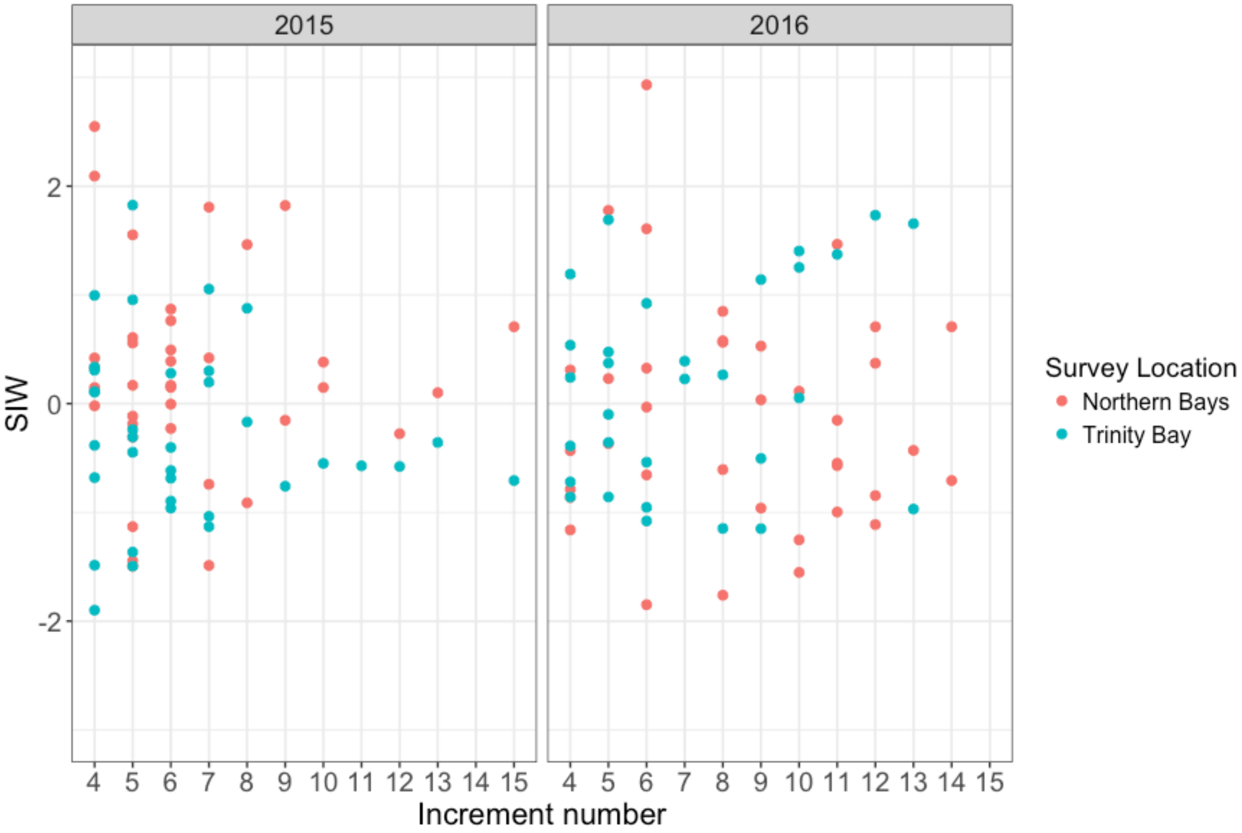

Figure 3.9: Standardized increment widths (SIW) showing detrended recent growth, for individual capelin larvae sampled in August of 2015 and 2016 in the northern bays and Trinity Bay.

CHAPTER 4: GENERAL DISCUSSION

4.1 Thesis overview and discussion

In this thesis, I compared the dynamics of larval fish occurring in two relatively unstudied northeastern coastal embayments (White Bay and Notre Dame Bay) of Newfoundland to the more southerly and annually surveyed Trinity Bay. The aim of this research was to assess previously unstudied larval fish communities in these important northern inshore areas, and to test the assumption that larval capelin dynamics in Trinity Bay are representative of the entire stock's early life history.

The ichthyoplankton community structure described herein provides a baseline for future research, and the analysis of larval capelin growth and population dynamics within these northern bays allowed for a first assessment of variability in larval capelin growth dynamics between the well-documented Trinity Bay ecosystem and White Bay and Notre Dame Bay. However, the lack of prior data from these two northern bays presents a challenge when interpreting results, as little is known of the flow dynamics, predator abundance, and preferred prey abundance within these two bays. Such abiotic and biotic characteristics of the ecosystem can drastically impact larval growth, dispersal, and mortality (Frank and Leggett, 1986; Sinclair, 1988; Takasuka et al., 2004; Gjøsæter et al, 2016; Murphy et al., 2018), and knowledge of how these factors vary within the northern bays and relative to Trinity Bay is extremely limited. Despite these potential limitations, it is evident from the present study that the ichthyoplankton community within White Bay and Notre Dame Bay is consistent with the community found in Trinity Bay, as well as with that found in the more southern Placentia Bay (Carter-Lynn, 2009).

Contrastingly, larval capelin population dynamics differed in space and time along the northeast coast of Newfoundland, where larval abundance and growth rates in White Bay and Notre Dame Bay were lower in 2016 than they were in 2015, while in Trinity Bay they were higher in 2016. Spatial variability in larval capelin density and growth only had minor effects on the ichthyoplankton community, indicating that seasonal trends in community structure are resilient to interannual fluctuations in abundance of a single species (e.g. capelin). Single species frequently have high interannual variation in abundance, making it potentially more difficult to identify long-term trends, while community as a whole is relatively stable – as shown in this thesis – so changes observed in community structure (e.g. changes in species composition or coincidental changes in abundance of groups of species) may be more indicative of actual ecological disturbance or ecosystem regime shift (Villagarcía et al., 1999; Sá-Oliveira et al., 2015).

Several changes were found in the larval capelin population in 2016 relative to 2015. Community structure analysis revealed that spawning, particularly of capelin, appeared to be delayed in 2016, which may have been due to a combination of colder water temperatures in June 2016 and a smaller mean size and condition of spawning adult capelin, two factors that have been shown to delay spawning in capelin (Carscadden and Nakashima, 1997; Carscadden et al., 1997). Furthermore, the assessment of larval capelin density and growth showed that larval density in Trinity Bay was marginally increased in 2016 while it was an order of magnitude less in the northern bays, which may indicate a contraction of the distribution of capelin spawning in 2016 relative to 2015. Such a contraction of spawning has been previously shown to occur in mackerel in the Gulf of St. Lawrence (Grégoire et al., 2013) and in capelin on the NE coast of Newfoundland (H.

Murphy, pers. comm.), and is typically a result of low spawning stock biomass in a given year (MacCall, 1990).

A recent study by Murphy et al. (2018) found that emergent larval density at Bellevue Beach in Trinity Bay was correlated with recruitment variability. However, the authors also found that growth rate and preferred prey abundance later during the larval stage were linked with recruitment, suggesting that factors affecting post-emergent larvae also impact survival and year-class strength. The interannual variation in larval capelin growth rates and larval densities in White Bay and Notre Dame Bay relative to Trinity Bay found in the present study suggests that the prior assumption that Trinity Bay is representative of the stock as a whole is partially inaccurate. Annual surveys including the northern spawning grounds would allow for a more comprehensive view of growth, abundance, and survival within the larval capelin population along the NE coast of Newfoundland. Such an expansion of the current knowledge of the late larval stage northwards to include White Bay and Notre Dame Bay would potentially allow researchers to establish a positive correlation between late larval density and subsequent year-class strength, thus closing the present gap between emergent larval density in Trinity Bay and recruitment.

It is important to monitor larval community structure because changes to patterns of community structure are a potential early indicator of ecosystem shifts. Furthermore, knowledge of community structure can inform on species interactions. The spatial consistency and seasonal variability in community structure shown in this thesis, and similarly found by Carter-Lynn (2009) in Placentia Bay, suggest that monitoring one bay – as presently undertaken annually in Trinity Bay – but with extended sampling effort (e.g. spring through fall) for describing seasonal variability, would be sufficient to detect larval community structure changes at the regional scale. However, relative to the assessment of the 2J3KL capelin stock, results from the present study suggest that there exists asynchronous interannual variability in larval growth and abundance among bays, and thus surveying a single bay may not always yield a reliable recruitment index at the population level. Ultimately, there remains a great deal unknown about larval capelin dynamics and factors affecting survival, especially in the northern portion of the distribution. Predation in particular is thought to be a major source of larval mortality in marine fishes (Hunter, 1982; Bailey and Houde, 1989; Takasuka et al., 2004), and is thus an important component missing from the present study. While there exists little information on larval predation within the Newfoundland capelin stock, Paradis and Pepin (2001), using an individual-based size-dependent model applied to field-based estimates of larval growth and predator abundance from Conception Bay, NL, found that predation by planktivorous fish (e.g. juvenile and adult capelin) was an important source of mortality in several species of larval fish, including capelin itself, while the contribution of predation by macrozooplankton to total losses was minimal. Studies on Barents Sea capelin have shown predation by juvenile herring to be an important source of larval mortality (Hallfredsson and Pederson, 2009; Gjøsæter et al, 2016). Identifying important vertebrate and invertebrate predators of larval capelin, determining the relative importance of predation by planktivorous fish and macrozooplankton, and measuring the effect of predation on recruitment strength is key towards better understanding the drivers of interannual recruitment variability in the Newfoundland capelin stock.

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APPENDICES

Appendix A: Relative contribution of species to the larval fish communities of the northern bays (Notre Dame Bay and White Bay, NL) and of Trinity Bay, NL in summer/fall of 2015 and 2016. Species contributing less than 1% of the total larval abundance are listed as "other."

Northern Bays 2015			
Species	**Relative Abundance in June (%)**	**Relative Abundance in July (%)**	**Relative Abundance in August (%)**
Alligator fish	1.09	1.16	0.00
American plaice	0.00	1.16	0.00
Arctic shanny	5.43	0.00	0.11
Atlantic cod	10.87	5.81	4.69
Atlantic herring	0.00	0.00	0.11
Atlantic poacher	0.00	0.00	0.00
Capelin	0.00	88.37	94.32
Cunner	0.00	0.00	0.06
Radiated shanny	5.43	1.16	0.00
Redfish	6.52	0.00	0.00
Sandlance	31.52	1.16	0.00
Sea Raven	1.09	0.00	0.00
Shorthorn sculpin	2.17	0.00	0.00
Snailfish	10.87	1.16	0.11
Snakeblenny	14.13	0.00	0.00
Witch flounder	10.87	0.00	0.55
Other	0.00	0.00	0.06

Northern Bays 2016		
Species	**Relative Abundance in July (%)**	**Relative Abundance in August (%)**
Alligator fish	1.96	0.18
American plaice	1.96	0.00
Arctic shanny	27.45	0.00
Atlantic cod	17.65	1.65
Atlantic herring	0.00	9.14
Atlantic poacher	2.94	0.00
Capelin	6.86	74.22
Cunner	0.00	12.43
Radiated shanny	0.00	0.00
Redfish	8.82	0.00
Sandlance	0.98	0.00
Sea Raven	0.00	0.00
Shorthorn sculpin	0.98	0.00
Snailfish	23.53	0.73
Snakeblenny	2.94	0.18
Witch flounder	0.00	0.91
Other	3.92	0.55

Trinity Bay 2015		
Species	**Relative Abundance in August (%)**	**Relative Abundance in September (%)**
Alligator fish	0.00	0.00
American plaice	0.13	0.00
Arctic shanny	0.00	0.00
Atlantic cod	3.83	13.08
Atlantic herring	0.00	5.52
Atlantic poacher	0.00	0.00
Capelin	93.04	71.88
Cunner	1.83	1.36
Radiated shanny	0.00	0.00
Redfish	0.56	0.23
Sandlance	0.00	0.00
Sea Raven	0.00	0.00
Shorthorn sculpin	0.00	0.00
Snailfish	0.00	0.00
Snakeblenny	0.00	0.00
Witch flounder	0.18	7.71
Other	0.44	0.23

Trinity Bay 2016		
Species	**Relative Abundance in August (%)**	**Relative Abundance in September (%)**
Alligator fish	0.00	0.00
American plaice	0.00	0.00
Arctic shanny	0.00	0.00
Atlantic cod	0.70	1.59
Atlantic herring	0.00	11.11
Atlantic poacher	0.00	0.00
Capelin	80.78	84.72
Cunner	15.37	0.60
Radiated shanny	0.00	0.00
Redfish	0.17	0.20
Sandlance	0.00	0.00
Sea Raven	0.00	0.00
Shorthorn sculpin	0.00	0.00
Snailfish	0.09	0.00
Snakeblenny	0.00	0.00
Witch flounder	2.67	1.39
Other	0.23	0.40

Appendix B: Similarity of percentages (SIMPER) results for sampling month. Cumulative percentage refers to the cumulative percent contribution of each species to the total dissimilarity in larval fish community between sampling months.

Contrast: June - July

Species	**Mean density in June**	**Mean density in July**	**Cumulative percentage**
Sandlance	0.4877	0.0144	0.2
Capelin	0	0.894	0.391
Atlantic cod	0.1664	0.123	0.533
Snakeblenny	0.2102	0.0114	0.674
Snailfish	0.0742	0.0985	0.776
Arctic shanny	0.0829	0.0997	0.868
Witch flounder	0.1477	0	0.947
Redfish	0.1004	0.0317	1
Atlantic herring	0	0	1
Cunner	0	0	1

Contrast: June - August

Species	**Mean density in June**	**Mean density in August**	**Cumulative percentage**
Capelin	0	23.20806	0.724
Cunner	0	1.75049	0.8
Sandlance	0.4877	0	0.853
Atlantic cod	0.1664	0.75387	0.895
Snakeblenny	0.2102	0.0047	0.926
Witch flounder	0.1477	0.32128	0.955
Atlantic herring	0	0.14439	0.968
Redfish	0.1004	0.05835	0.98
Snailfish	0.0742	0.02933	0.991

Arctic shanny	0.0829	0.00901	1

Contrast: June - September			
Species	**Mean density in June**	**Mean density in September**	**Cumulative percentage**
Capelin	0	11.6493	0.686
Atlantic herring	0	1.2189	0.768
Atlantic cod	0.1664	1.0355	0.849
Witch flounder	0.1477	0.6456	0.897
Sandlance	0.4877	0	0.94
Snakeblenny	0.2102	0	0.961
Redfish	0.1004	0.0288	0.974
Cunner	0	0.1548	0.986
Snailfish	0.0742	0	0.993
Arctic shanny	0.0829	0	1

Contrast: July - August			
Species	**Mean density in July**	**Mean density in August**	**Cumulative percentage**
Capelin	0.894	23.20806	0.786
Cunner	0	1.75049	0.873
Atlantic cod	0.123	0.75387	0.915
Snailfish	0.0985	0.02933	0.936
Arctic shanny	0.0997	0.00901	0.955
Witch flounder	0	0.32128	0.972
Atlantic herring	0	0.14439	0.987
Redfish	0.0317	0.05835	0.994
Snakeblenny	0.0114	0.0047	0.997
Sandlance	0.0144	0	1

Contrast: July – September			
Species	**Mean density in July**	**Mean density in September**	**Cumulative percentage**
Capelin	0.894	11.6493	0.722
Atlantic herring	0	1.2189	0.815
Atlantic cod	0.123	1.0355	0.902
Witch flounder	0	0.6456	0.95
Cunner	0	0.1548	0.964
Arctic shanny	0.0997	0	0.976
Snailfish	0.0985	0	0.988
Redfish	0.0317	0.0288	0.997
Sandlance	0.0144	0	0.998
Snakeblenny	0.0114	0	1

Contrast: August – September			
Species	**Mean density in August**	**Mean density in September**	**Cumulative percentage**
Capelin	23.20806	11.6493	0.74
Atlantic cod	0.75387	1.0355	0.814
Atlantic herring	0.14439	1.2189	0.883
Cunner	1.75049	0.1548	0.95
Witch flounder	0.32128	0.6456	0.992
Redfish	0.05835	0.0288	0.998
Snailfish	0.02933	0	1
Snakeblenny	0.0047	0	1
Arctic shanny	0.00901	0	1
Sandlance	0	0	1

Appendix C: Similarity of percentages (SIMPER) results for the five groupings arising from the average-linkage hierarchical cluster analysis. Cumulative percentage refers to the cumulative percent contribution of each species to the total dissimilarity in larval fish community between groups derived from hierarchical cluster analysis.

Contrast: 1-2

Species	**Mean density in cluster 1**	**Mean density in cluster 2**	**Cumulative percentage**
Sandlance	0.6055	0.04343	0.271
Snakeblenny	0.2884	0.00602	0.479
Snailfish	0.0208	0.19301	0.614
Arctic shanny	0.0153	0.23419	0.746
Atlantic cod	0.1473	0.10452	0.859
Witch flounder	0.1649	0	0.935
Redfish	0.0581	0.09834	0.997
Capelin	0	0.00618	1
Atlantic herring	0	0	1
Cunner	0	0	1

Contrast: 1-3

Species	**Mean density in cluster 1**	**Mean density in cluster 3**	**Cumulative percentage**
Capelin	0	0.79154	0.344
Sandlance	0.6055	0	0.568
Snakeblenny	0.2884	0	0.731
Atlantic cod	0.1473	0.17171	0.853
Witch flounder	0.1649	0	0.916
Redfish	0.0581	0.027	0.949
Atlantic herring	0	0.0535	0.968
Cunner	0	0.03952	0.983

Snailfish	0.0208	0.00426	0.995
Arctic shanny	0.0153	0	1

Contrast: 1-4

Species	**Mean density in cluster 1**	**Mean density in cluster 4**	**Cumulative percentage**
Cunner	0	1.2961	0.344
Sandlance	0.6055	0	0.567
Snakeblenny	0.2884	0	0.732
Witch flounder	0.1649	0.1686	0.854
Atlantic cod	0.1473	0	0.912
Capelin	0	0.0879	0.944
Redfish	0.0581	0	0.969
Atlantic herring	0	0.0447	0.986
Snailfish	0.0208	0	0.995
Arctic shanny	0.0153	0	1

Contrast: 1-5

Species	**Mean density in cluster 1**	**Mean density in cluster 5**	**Cumulative percentage**
Capelin	0	22.97545	0.79
Atlantic cod	0.1473	0.96952	0.836
Sandlance	0.6055	0	0.874
Cunner	0	1.35203	0.909
Atlantic herring	0	0.54623	0.943
Witch flounder	0.1649	0.48664	0.97
Snakeblenny	0.2884	0.00376	0.99
Redfish	0.0581	0.05189	0.996
Snailfish	0.0208	0.02781	0.999

Arctic shanny	0.0153	0.00722	1

Contrast: 2-3			
Species	**Mean density in cluster 2**	**Mean density in cluster 3**	**Cumulative percentage**
Capelin	0.00618	0.79154	0.453
Atlantic cod	0.10452	0.17171	0.602
Snailfish	0.19301	0.00426	0.747
Arctic shanny	0.23419	0	0.889
Redfish	0.09834	0.027	0.939
Atlantic herring	0	0.0535	0.962
Cunner	0	0.03952	0.983
Sandlance	0.04343	0	0.995
Snakeblenny	0.00602	0	1

Contrast: 2-4			
Species	**Mean density in cluster 2**	**Mean density in cluster 4**	**Cumulative percentage**
Cunner	0	1.2961	0.406
Witch flounder	0	0.1686	0.545
Snailfish	0.19301	0	0.683
Arctic shanny	0.23419	0	0.816
Atlantic cod	0.10452	0	0.89
Capelin	0.00618	0.0879	0.93
Redfish	0.09834	0	0.965
Atlantic herring	0	0.0447	0.984
Sandlance	0.04343	0	0.995
Snakeblenny	0.00602	0	1

Contrast: 2-5

Species	**Mean density in cluster 2**	**Mean density in cluster 5**	**Cumulative percentage**
Capelin	0.00618	22.97545	0.817
Atlantic cod	0.10452	0.96952	0.863
Cunner	0	1.35203	0.899
Atlantic herring	0	0.54623	0.934
Witch flounder	0	0.48664	0.959
Arctic shanny	0.23419	0.00722	0.974
Snailfish	0.19301	0.02781	0.989
Redfish	0.09834	0.05189	0.997
Sandlance	0.04343	0	0.999
Snakeblenny	0.00602	0.00376	1

Contrast: 3-4

Species	**Mean density in cluster 3**	**Mean density in cluster 4**	**Cumulative percentage**
Cunner	0.03952	1.2961	0.367
Capelin	0.79154	0.0879	0.723
Witch flounder	0	0.1686	0.842
Atlantic cod	0.17171	0	0.951
Atlantic herring	0.0535	0.0447	0.986
Redfish	0.027	0	0.997
Snailfish	0.00426	0	1

Contrast: 3-5

Species	**Mean density in cluster 3**	**Mean density in cluster 5**	**Cumulative percentage**
Capelin	0.79154	22.97545	0.835

Atlantic cod	0.17171	0.96952	0.886
Cunner	0.03952	1.35203	0.927
Atlantic herring	0.0535	0.54623	0.967
Witch flounder	0	0.48664	0.993
Redfish	0.027	0.05189	0.997
Snailfish	0.00426	0.02781	1

Contrast: 4-5

Species	**Mean density in cluster 4**	**Mean density in cluster 5**	**Cumulative percentage**
Capelin	0.0879	22.97545	0.797
Cunner	1.2961	1.35203	0.887
Atlantic cod	0	0.96952	0.931
Atlantic herring	0.0447	0.54623	0.967
Witch flounder	0.1686	0.48664	0.995
Snailfish	0	0.02781	0.998
Redfish	0	0.05189	1