Growth and post-spawning survival in capelin (*Mallotus villosus*) on the Northeast coast of Newfoundland

by

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A thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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Abstract

Variation in growth, reproduction and survival drive inter-annual population dynamics of fish; however, information is often limited on these life history traits. Capelin (*Mallotus villosus*) is a small, short-lived forage fish species, which is a key prey species for many top predators. Newfoundland capelin migrate > 350 km to coastal regions to spawn during the summer, after which most are thought to die. We examined post-spawning survival as well as inter-annual variation in growth and environmental factors that impact growth. In Chapter 1, I evaluated the reliability of a spawning zone in the otolith in female capelin by comparing direct (histological) and indirect (otolith-based) indicators of spawning. Using female capelin caught during November - December, 2016, only 50% of individuals in which a spawn check was identified in the otolith had residual oocytes, based on histological examination of ovaries. This suggests that otolith-based determination of post-spawning survival may not be a reliable method of identifying fish that had spawned previously. In Chapter 2, I examined inter-annual variation in growth of male and female capelin and links with various environmental conditions. Capelin were collected at beach and deep-water spawning sites during July-August, 2008-2016 and age-specific annual growth was quantified using otolith-based techniques. Generalized Additive Models revealed that higher growth occurred during 2010-2012 and a Principal Components Analysis on environmental factors indicated that these years were characterized by warmer conditions, with earlier and higher magnitude spring blooms, but the abundance of capelin prey varied widely. This suggests that temperature and bloom dynamics may have a larger influence on capelin growth. We highlight the importance of understanding environmental conditions influencing population dynamics, as well as the importance of further characterizing the life history of capelin.

Acknowledgements

First and foremost, I'd like to thank my supervisor, Dr. Gail Davoren – there's no way I could have completed this project without your support and guidance. Your patience and dedication throughout this entire process has been otherworldly—I don't know how you do it. I have been so fortunate to have been part of your research program.

Thanks also to my advisory committee, D. Gillis and R. Rideout, for your feedback and expertise along the way. Darren, thank you for de-mystifying Generalized Additive Models and for your patience, as it took multiple rounds before I even began to understand it. Rick, thank you for making time to teach me the histological methods required for this project. To my predecessors in the Davoren Lab who have built an extensive historical dataset, and to my fellow students in the lab that have been a constant support as we muddled through this thing called research together. Special thanks to M. Epp, A. Loeppky, and A. Fraser, for your assistance in processing the data.

Lastly, to the everyone I've had the honor of working with at the Department of Fisheries and Oceans in St. John's, Newfoundland. You have been nothing but supportive in my time in Newfoundland. Special thanks for F. Mowbray for helping me co-ordinate my time in order to ensure I got the data I needed.

This project was principally funded by NSERC and the University of Manitoba.

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General Introduction

Life history theory predicts that an individual has limited ‘surplus’ energy, which can be directed into growth and reproduction (Cody 1966, Williams 1966), which leads to a trade-off between the two (Browne 1982, Reznick 1985). The best life history strategy balances this trade-off against natural mortality, in a way that maximizes an individual’s fitness and, thus, population growth rates (Reznick 1985). Optimal life history strategies described for North American fish balance energy between sexual maturation, growth rate and body size, egg size, parity, and parental care (Winemiller and Rose 1992). Forage fish typically have a short life-span with highly fluctuating populations (Schwartzlose et al. 1999). Temperature and prey availability are two of the most important bio-physical factors that affect the growth of forage fish (Brandt 1993), like Japanese sardine (*Sardinops melanostictus*, Itoh et al. 2011) and anchovy (*Engraulis encrasocolus*, Gatti et al. 2017). Owing to high annual mortality, energy allocation to reproduction at earlier ages (i.e. early sexual maturity) is advantageous, because it allows individuals to maximize reproductive output before they die (Cole 1954). Earlier sexual maturity, however, results in reduced energy available for survival and future reproduction (Pianka 1970). Therefore, individuals typically have either one (semelparous) or a few breeding events during their lifespan (MacArthur and Wilson 1967, Pianka 1970, Pitcher 1995), with high fecundity (Schwartzlose et al. 1999).

Fecundity in fish tends to increase with body size (Kozlowski 1996), as such, growth is an important life history trait. The somatic cost of reproduction is evident in fish, as energy directed into reproduction reduces somatic growth, thus potential fecundity in the future is reduced as well (Ware 1980, Roff 1983, Kozlowski 1996). For instance, increased investment in reproduction by Amur sleeper (*Perccottus glenii*), evidenced by a longer breeding season, resulted in reduced growth when older (Grabowska et al. 2011). Reduced growth during reproductive years may be observed in the otolith, known as ‘spawning zones’ or ‘spawn checks (Woodhead 1978). Spawning zones are generally regions of reduced or irregular growth that represent the redirection of energy from somatic growth to reproduction (e.g., spawning migration, gonadal development, Rollefsen 1933). Spawning zones have been described in various fish (e.g., Atlantic cod (*Gadus morhua*), Rollefsen 1933; Arctic char (*Salmo alipunus*), Nordeng 1961), but have not been validated/confirmed using direct methods.

Study Species

Capelin (*Mallotus villosus*) is a small, short-lived (3-6 years) forage fish species that occurs in many northern marine food webs (Carscadden and Vilhjálmsson 2002). Capelin are an important food source for many top predators, such as piscivorous fish (e.g. Atlantic cod, *Gadus morhua*), marine birds and mammals. They help regulate energy flow through marine food webs by providing a link between upper and lower trophic levels (Carscadden and Vilhjálmsson 2002). In coastal Newfoundland, capelin aggregate to spawn on beaches and at deep-water sites (15-40 m; Templeman 1948, Nakashima and Wheeler 2002, Davoren et al. 2008), where eggs adhere to the substrate and remain throughout incubation (Templeman 1948). Males arrive at spawning sites first and remain there throughout the 2-3 week spawning season, where they mate with multiple females; females deposit all their eggs at one time, and then return to deeper water (Templeman 1948, Friis-Rødel and Kanneworff 2002). During the spawning act, males dig into the sand to bury eggs in the substrate, leaving heavily injured anal and caudal fins after the spawning season (Templeman 1948, Saetre and Gjosaeter 1975). Owing to high physical contact with the sediment, post-spawning mortality is thought to be very high, especially for males, because spawning involves physical contact with the seabed, regardless of reproductive mode (i.e. beach versus deep-water spawning). In support, a linear least-squares model revealed that a greater proportion of females (25-50%) survived spawning relative to males (2.5-13%), which was attributed to the high energetic costs of spawning and body damage incurred by males (Shackell et al. 1994).

Overall, female capelin maximize their lifetime reproductive success by spawning multiple times throughout their lifespan, while males maximize their lifetime reproductive success by spawning with multiple females in one year (Huse 1998). Female iteroparity is evidenced by otolith-based observations of a ‘spawn check’ (Winters 1971, Maxner et al. 2016) macroscopic observations of retained oocytes in capelin ovaries (Templeman 1948), recovery of tagged, sexually mature capelin (Nakashima 1992), histological observations of residual eggs from the previous year in the gonads (Burton and Flynn 1998), and model predictions of survival of mature female capelin based on abundance estimates from annual acoustic/trawl surveys from 1982 – 1990 (Shackell et al. 1994). In contrast, males are effectively semelparous, which has been supported for Newfoundland capelin by all males dying after spawning in a laboratory setting (Burton and Flynn 1998) and by a higher proportion of dead males relative to females at spawning beaches (Templeman 1948). Male capelin that survive spawning may spawn again in subsequent years, but the high energetic costs and physical contact (Templeman 1948) during the spawning act lead to low post-spawning survival (1.5%; Christiansen et al. 2008). The extent to which female capelin survive post-spawning, however, has not been well studied, but is important to determine the number of spawning individuals in the population.

Capelin growth is influenced by many bio-physical factors throughout their lifetime. Larval growth and survival are primarily influenced by water temperature and prey availability (Leggett et al. 1984). In the spring/summer of their second year, capelin undergo metamorphosis (Bailey et al. 1977). Feeding slows during the winter (Winters 1970), which is reflected in the otolith by a translucent band (Winters 1969). Feeding resumes in the spring at the onset of sea ice retreat (Buren et al. 2014, Mullowney et al. 2016). Phytoplankton growth is initiated after sea ice retreat (Wu et al. 2007), and is dependent on spring bloom dynamics, such as magnitude, duration, peak timing (O'Driscoll et al. 2001). Feeding intensity of capelin peaks during April – May, resulting in the start of summer growth (Gerasimova 1994). Spring and summer growth is reflected in the otolith by an opaque band (Winters 1969). Capelin remain offshore on the Newfoundland shelf for 2-3 years until they migrate inshore to spawn (Templeman 1948), during which period they stop feeding (Winters 1970, Vesin et al. 1981). The lack of feeding during spawning and energetic costs of reproduction (e.g., spawning migration, development of gonads and secondary sexual characteristics) result in a rapid decline of lipid reserves from overwintering to spawning (Winters 1970, Henderson et al. 1984). This period of lack of feeding and high energetic costs may be reflected in the otolith by a narrow opaque band, and interpreted as a 'spawn check' (Winters 1971, Maxner et al. 2016). If fish survive spawning, feeding intensity increases again during the post-spawning period in the fall prior to overwintering (Henderson et al. 1984).

Changes in capelin biology and behaviour were observed in the early-1990s (Carscadden 2000), which were associated with a population collapse. The change was characterized by: younger age-at-maturity, from three and four years of age to two years of age, (DFO 2013); smaller total length at maturity (females: 140-155 mm; male: 160-175 mm; DFO 2013), and spawning dates up to four weeks later than before 1990 (DFO 2011). This change in capelin biology may be associated in part with changing water temperatures (Carscadden et al. 2001, DFO 2015), favouring early sea-ice retreat (Buren et al. 2014; Mullowney et al. 2016), which leads to earlier zooplankton blooms (Head et al. 2013). Overall, the trend toward later capelin spawning dates appears to create a mismatch between larval emergence and timing of peak larval prey abundance, which has been hypothesized to reduce survival of capelin at the early stages and prolong stock recovery (Mullowney et al. 2016). Similarly, Buren et al. (2014) suggested that the changes in capelin biology may be indicative of a regime shift associated with factors influencing the spring zooplankton bloom. The larval stage has been hypothesized as a ‘critical period’ during which food availability determines the resulting year-class size; scarce food availability results in small year-class, and abundant food results in a large year-class (Hjort 1914). Lasker (1981) builds upon this and highlights the importance of environmental factors. Specifically, a stable environment is crucial to facilitate areas of high food concentration upon which larval fish survival depends on (i.e. Stable Ocean Hypothesis, Lasker 1981). The shift in capelin biology, however, was not attributed to over-exploitation, as directed fishing was minimal before and after the 1990s (Carscadden et al. 2001). Although the 2015 assessment of Newfoundland capelin revealed that the stock may be starting to resemble trends before the regime shift (pre-1990s), capelin spawner biomass was low during 2015 and 2016 and spawning capelin were not found at typical spawning sites (G. Davoren, pers. comm.).

The goal of my thesis is to examine life history traits of capelin on the northeast Newfoundland coast. In Chapter 1, my goal was to determine whether a spawning zone can be reliably detected in female capelin otoliths. To do this, I compared direct, histological techniques with indirect, otolith-based indications of previous spawning. Determining a reliable indirect method to determine previous spawning events and annual estimates of post-spawning survival will provide us with a means to quantify the effective population size of Newfoundland capelin. In doing so, we can provide more accurate life history information to input into stock assessments for this population that collapsed in the early 1990s (Buren et al. 2014). In Chapter

2, my goal was to quantify inter-annual variation in growth of capelin on the eastern Newfoundland shelf to investigate the effects of environmental conditions (e.g., physical oceanography, food abundance). Otolith-based techniques were used to quantify age-specific growth in spawning capelin collected annually on the northeastern Newfoundland coast (2008-2016). This study will allow us to quantify growth since the regime shift in 1990s (Winters 1982), which is an important factor to consider in the stock assessment of capelin.

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Can spawning zones be reliably determined in the otolith of short-lived forage fish species?

Introduction

A fundamental principle of life history theory is that an individual has limited energy available for growth and reproduction (Cody 1966, Williams 1966), leading to a trade-off between the two (Browne 1982, Reznick 1985, Winemiller and Rose 1992, Roff 1983). Short-lived forage fish maximize reproductive output over their lifespan by maturing early, as high annual mortality leads to few lifetime reproductive events (Pitcher 1995). Information on many life history traits have been revealed using otoliths in fish, such as age and growth rates based on annuli formation (Woodhead 1978), as well as determination of migration pathways, reconstruction of previous environmental conditions experienced, and stock or population identification via otolith chemistry (Campana 1999, Davoren and Halden 2014). During reproductive years, increased energy is directed to gonadal development, resulting in reduced somatic growth (Ware 1980, 1982; Roff 1983; Kozlowski 1996), which may be reflected in growth patterns of the otolith, described as ‘spawning zones’ or ‘spawn checks’ (Woodhead 1978, Campana and Neilson 1985). Spawning zones have been used to estimate the number of spawning events in many long-lived species (e.g., Atlantic cod (*Gadus morhua*), Rollefsen 1993; Silver hake (*Merluccius bilinearis*), Pannella 1971; Arctic char (*Salmo alipunus*), Nordeng 1961; South African sparid fish species, Mann-Lang et al. 1996), but few short-lived species (Pannella 1971). A spawning zone in the otolith is generally described as an irregular growth zone, whereby translucent bands, representing slower growth associated with winter and spring, are separated by a narrow opaque band, representing faster growth associated with summer and fall (Pannella 1971, Wells 1981). This narrow opaque band is attributed to energy being directed away from somatic growth for gonadal development and/or spawning migrations, as well as lack of feeding during the spawning season (Cod, Rollefsen 1933; Red Roman (*Chrysoblephus laticeps*), Santer Seabream (*Cheimerius nufar*), Black Musselcracker (*Cymatoceps nasutus*), Blackfish (*Dichistius capensis*), Potts and Cowley 2005; Mann-Lang et al. 1996). Although spawning zones have been described for many species, it has not been compared with direct observations of previous spawning to validate the check.

Capelin (*Mallotus villosus*) is a small, short-lived (3-6 years) forage fish species that occurs in many northern marine food webs (Carscadden and Vilhjálmsson 2002). Capelin are important prey for various predators, such as piscivorous fish (e.g. Atlantic cod), marine birds and mammals. They provide a link between lower and higher trophic levels, which helps to regulate energy flow through marine food webs (Carscadden and Vilhjálmsson 2002). On the Newfoundland shelf, capelin undergo extensive inshore migrations (~350 km) from offshore wintering areas to spawn on coastal beaches and deep-water sites (15-40 m; Templeman 1948, Nakashima and Wheeler 2002, Davoren et al. 2008). Males arrive at spawning sites first and remain there throughout the 2-3 week spawning season (Davoren 2013), where they mate with multiple females, whereas females deposit all their eggs at one time and then return to deeper water (Templeman 1948, Friis-Rødel and Kanneworff 2002). Post-spawning mortality is thought to be high as aresult of physical contact with the seabed, and especially for males, which make multiple spawning runs. Although there is some evidence of post-spawning survival in male capelin (Nakashima 1992, Christiansen et al. 2008), male Newfoundland capelin appear to primarily spawn once and die (i.e. functionally semelparous). In contrast, female capelin appear to survive to spawn in subsequent years (i.e. iteroparous), based on macroscopic observations of retained oocytes in capelin ovaries (Templeman 1948), microscopic observations of residual oocytes (60% of females; Flynn et al. 2001), and model-based prediction of survival of mature female capelin (Shackell et al. 1994) . Overall, differential sex-based parity has been supported theoretically (Huse 1998) as well as by divergent post-spawning mortality of males and females in a laboratory setting (Burton and Flynn 1998) and by a higher proportion of dead males relative to females at spawning beaches (Templeman 1948).

Although histology-based assessments of gonads to determine previous spawning experience are highly accurate, they are time consuming (Flynn 1996). On the other hand, indirect measures, such as macroscopic inspection of gonads or otolith-based determination of spawning zones, are less accurate but are more time efficient and, thus, can be conducted on a larger number of samples. Irregular zones of opaque and translucent bands in the otoliths of female capelin, suggestive of previous spawning, were described previously as a sequence of an accentuated translucent (winter) band, followed by a very narrow opaque (summer) band (Winters 1971). Capelin are thought to metamorphose in the first summer (Bailey et al. 1977) and reach sexual maturity the following summer (i.e. age 2; DFO 2015) and, thus, the second opaque (summer) band is the first opportunity a spawning zone could be observed. Despite the description of spawning zones in capelin otoliths, they have never been validated and have not been used to further elucidate the proportion of iteroparous females (cf Maxner et al. 2016) and instead are often the reason females are not included in otolith-based age and growth studies (e.g. Hedelholm et al. 2010).

The goal of my study is to determine if a spawning zone is a reliable indication of previous spawning in female capelin otoliths by comparing direct (histological) and indirect (otolith-based) indications of previous spawning. We hypothesize that female capelin that spawned during the year of capture, as indicated by the presence of residual oocytes in ovaries, are more likely to have a spawning zone in the otolith. Additionally, we hypothesize that spawning during the year of capture will influence age-specific growth patterns and predict that females spawning during the year of capture will have lower growth during that year relative to non-spawners. Using otolith-based techniques to determine previous spawning experience and annual estimates of post-spawning survival would allow us to quantify the number of spawning individuals in the population of Newfoundland capelin, providing more accurate life history information to input into stock assessments for this population that collapsed in the early 1990s (Buren et al. 2014).

Methods and Materials

Fish collection and processing

Capelin were collected from the Newfoundland shelf during November-December, 2016 using a Campelen trawl aboard a variety of Fisheries and Oceans Canada Research Vessels, including RV *Teleost* (trip numbers 165, 166) and RV *Alfred Needler* (trip number 472; Table 1.1). Samples were collected from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J and 3K. Three samples of 200 – 311 fish per sample (Table 1.1) were frozen onboard the ship for later processing. These samples were supplemented by samples of 25 capelin frozen from 19 sets that were collected from the same region in November-December, 2016 (Table 1.1). In the lab, fish were thawed and the total length (mm) and sex of all fish were measured and recorded. From the three main samples, gonads were removed from a subsample of 5 female fish per 5 mm length category (range: 90 – 200 mm) and preserved in 10% buffered formalin for histological examination. From the supplemental samples, gonads were removed from females whose maturity was macroscopically identified as maturing to recovering, based on Flynn et al. (2001), and preserved in 10% buffered formalin for histological examination. Saggital otoliths also were removed from all subsampled fish, cleaned in a 10% bleach solution and stored dry.

Histology

Histological techniques were used to determine the presence of residual oocytes, following Flynn et al. (2001), as ovaries with residual advanced oocytes indicate that the fish had spawned earlier in the year of capture (Flynn 1996). Ovaries were removed from the 10% buffered formalin, sectioned into thirds and the center section was put through an ethanol dehydration series and cleared in xylene. Ovaries were then embedded in paraffin wax at 60 ^{o}C. Within five regions spaced evenly throughout the gonad, three to five cross-sections of 7 μm were cut, for a total of 15-25 cross-sections per gonad, and placed on microscope slides. Sections were then stained with Ehrlich's haematoxylin and eosin and examined under a microscope (Nikon Polarizing Microscope ECLIPSE 50iPOL) at 10x and 50x magnification.

Histology is the most reliable method to identify evidence of previous spawning in the ovaries of fishes (Rideout et al. 2005) but the amount of information that can be derived from histological preparations is reliant on a quick and suitable fixation technique. Unfortunately, the ovaries used for histology in the current study were collected from fish that had been frozen whole (-20C) as part of regular research collections. The fact that ovaries were frozen and thawed before being placed in formalin resulted in poor fixation, with some aspects of gonad/oocyte morphology and staining characteristics being altered. As a result, some histological characteristics typically used to identify spawning (e.g. post-ovulatory follicles) could not be reliably used here. However, the freezing/poor fixation did not influence the ability to histologically identify residual oocytes so these were used as definitive evidence of previous spawning activity. The presence or absence of residual oocytes (Fig. 1.1) on each slide was determined and recorded. Individuals with the presence of at least one residual oocyte within the gonad were defined as individuals that had spawned during the year of capture (‘spawners’). Individuals in which residual oocytes were not observed may have not spawned during the year of capture (i.e. immature), but also may have been spawners that did not contain residual oocytes in the ovary sections that were examined (or did not contain residual oocytes at all) (Flynn et al. 2001) and were therefore simply referred to as ‘unknown’.

Otoliths

Sagittal otoliths were removed and photographed using a Olympus dissecting microscope (SZX7) (Hedeholm et al. 2010). These photographs were used to determine fish age (years) by counting the number of alternating translucent (i.e. winter) and opaque (i.e. summer) bands, with one pair of summer and winter bands representing one year of growth (Winters 1982, Hedeholm et al. 2010, Davoren and Halden 2014). Two observers independently determined the age and assigned a level of confidence (i.e., poor, fair, or good) (Fig. 1.2). If age could not be estimated consistently between observers or if the confidence level assigned was ‘poor’, the otoliths were not included in further analyses (Hedeholm et al. 2010, Maxner et al. 2016). The presence of a ‘spawning check’ was also recorded, to estimate if each fish had spawned in the year of capture. A spawning check for capelin was primarily identified as a narrow opaque band, with either an accentuated translucent band before (Winters 1971), or a translucent band on either side of varying widths (Maxner et al. 2016). Winters (1971) specifically noted a wide translucent band, but only five otoliths were identified that matched that criteria, so the narrow opaque band was used as the main identifier of previous spawning events (Fig. 1.3). Both observers assigned a level of confidence to the presence or absence of a spawning check (i.e., poor, fair, or good). Otoliths with discrepancies between observers or that were assigned a ‘poor’ confidence level were not included in further analyses. The width of otolith increments(μm) within translucent and opaque bands of each otolith were measured from the photographs using ImageJ, following Hedelholm et al. (2010) and Davoren and Halden (2014). The nucleus region, or center of the otolith, was estimated visually and a line was overlaid on the image from the tip of the rostrum to the bottom of the otolith going through the center (Fig. 1.2). A second line was placed at a 90º angle from the first line, from the center to the outer edge of the otolith (Fig. 1.2). The first year of growth was measured from the center of the otolith to the outer edge of the first winter (translucent) band (Fig. 1.2). Otoliths were measured twice by the same observer. If the measurements differed by <20%, the average of the two measurements was used in the analysis. When the measurements differed by >20%, the otolith was excluded from the analysis.

Once the histology and otolith-based datasets were integrated, we found that some individuals that we had aged as 1+ had residual oocytes (n = 13). As capelin are thought to metamorphose between age 1 and 2 (Bailey et al. 1977), it is unlikely that these individuals would have spawned before turning two-years-old (i.e. age 2+; Flynn et al. 2001). This suggested that these individuals had not been aged properly. Upon re-examining the otoliths of these individuals, we found that the final translucent band was generally very wide with thin opaque bands within the translucent band (Fig. 1.3II), which suggested short periods of higher growth within a year of minimal growth (i.e. mostly translucent banding). Therefore, we defined another spawn check type (Fig. 1.3II). Given these observations and the description of a new spawning check type, one observer(s) blindly re-examined all otolith photographs for age and presence of a spawn check.

Data Analysis

The initial estimations of age and spawn check were compared with the second estimations to determine consistency. We used the second age and spawn check estimates to compare indirect otolith-based and direct histology-based methods of identifying individuals that had spawned in the year of capture. To test the first hypothesis, that individuals with residual oocytes are more likely to have a spawning check present than individuals without residual oocytes, a logistic regression was run using the *stats* library using R v3.3.2 (R core team 2017); significance of variables was evaluated using Wald's z-test. This was conducted for age 2+ female capelin, as this age class represented the majority (84%) of sampled females.

The generalized linear model consisted of three elements: a probability distribution (binomial; eq. 1), a link function (logit; eq.2), and a linear predictor (eta, η; eq. 3). The binomial distribution used for the distribution of the response variable, presence or absence of a spawn check, is described by two variables π, and N; where π is the probability of presence for N independent individuals. The distribution of the response variable, presence or absence of a spawn check was:

$$(1)\ \begin{cases} B(\pi, N) \\ E(Y) = N \times \pi \\ var(Y) = N \times \pi \times (1-\pi) \end{cases}$$

The logit link was:

$$(2)\ ln\left(\frac{\mu}{1-\mu}\right) = \eta$$

Eta (η; eq. 3), was equal to the sum of the intercept, β_0, and the fixed effect term, β_n, multiplied by its estimate, X_n (maturity; i.e. 'spawner' or 'unknown'). This relationship was described as:

$$(3)\ \eta = \beta_0 + \beta_i X_i$$

To determine if a specific maturity (i.e., spawner, unknown) was more likely to have a certain spawn check type (i.e., I, II), a logistic regression was run on individuals in which a spawn check was identified. A separate logistic regression was run for each spawn check type.

To test the second hypothesis, that spawning during the year of capture influences age-specific growth patterns, a generalized linear mixed model was developed using the *lme4* library (Bates et al. 2015). We determined whether there was a difference in seasonal growth patterns between maturity types for age 2+ individuals. The generalized linear mixed models were run using the *lme4* library (Bates et al. 2015).

The generalized linear mixed model consisted of three elements: a probability distribution (normal; eq. 4), a link function (identity; eq.5), and a linear predictor (eta, η; eq. 6). The distribution of the response variable, fish growth was:

$$(4)\ \begin{cases} N(\mu, \sigma^2) \\ E(Y) = \mu \\ var(Y) = \sigma^2 \end{cases}$$

The identity link was:

$$(5)\ \mu = \eta$$

Eta (η; eq. 3), was equal to the sum of the intercept, β_0, and the fixed effect term, β_n, multiplied by its estimate, X_n, and a random effect (a_j; fish ID). This relationship was described as:

$$(6)\ \eta = \beta_0 + \beta_i X_i + \cdots + \beta_n X_n + a_i$$

Otolith increment width (IW), a proxy of fish growth, was described as a function of increment width type and maturity. Increment width type denotes whether the respective increment width was translucent (winter) or opaque (summer), and where the increment width was located in the otolith (e.g., first, second, third) and maturity (i.e. ‘spawner’ or ‘unknown’) is nested within increment width type. Specifically, the first translucent band in the otolith was labeled T1, first opaque band was labeled as O1 and the second translucent band in the otolith was T2 (Fig. 1.2). This accounted for seasonal differences and the age of growth the increment was associated with, as increment widths and growth rates of capelin differ with age (Winters 1982, Hedeholm et al. 2010). Otoliths with spawn check type II (Fig. 1.3II) could not be measured reliably for the translucent band representing the previous winter (T2), the final opaque band representing the summer in the year of capture (O2) and the translucent winter band in the year of capture (T3). As a result, these three regions were summed in all individuals to indicate growth in the year of capture (‘SumFinal’). To account for the variation in growth increments attributed to measuring the same individual multiple times, the individual was treated as a random factor.

Results

Overall, 233 female capelin were sampled for both gonads and otoliths. A total of 52 otoliths were discarded, due to poor confidence in aging (n = 18)**,** spawn check identification (n = 23) and otolith measurements (n = 11), resulting in a final dataset of 181 female capelin. Of the 181 female capelin, 49 were age 1+, 115 were age 2+, 16 were age 3+, and 1 age 4+. We identified the presence of residual oocytes in 48 individuals out of the original 233, but 15 individuals were discarded due to poor confidence in aging (n = 7)**,** spawn check identification (n = 4) and otolith measurements (n = 4), resulting in 33 females with residual oocytes for further analyses (age 2+: n = 30; age 3+: n = 3).

Consistency of aging and spawn check identification

When examining how ageing within the dataset (n = 181) differed between the first and second estimates, we found that 81% (n = 147) of the otoliths were aged the same as the first time. Out of the 19% (n = 34) of the otoliths where age discrepancies occurred, 10% (n = 18) were aged one year older and 1% (n = 1) were aged two years older, while 8% (n = 14) were aged one year younger during the second estimate. After determining the presence/absence of spawn checks in the otoliths a second time, 78% (n = 142) of the individuals were spawn checked similarly to the first estimate, whereby 22% (n = 40) of otoliths had a spawn check identified during both estimates and 56% (n = 102) had no spawn check identified. In contrast, 22% (n = 39) of the individuals were spawn checked differently, whereby 11% (n = 19) of otoliths had a spawn check identified only during the first estimate and 11% (n = 20) of otoliths had a spawn check identified only during the second estimate. Interestingly, a large proportion (53%) of otoliths discarded due to poor age or spawn check identification confidence (during the second estimate) were those with spawn check type II.

Half of the individuals aged as two-year-olds (i.e. age 2+) with residual oocytes had a spawning check (Table 1.2) and, thus, a spawn check was not more likely to be identified in individuals with or without residual oocytes detected ($z = 1.33$, $p = 0.18$). Spawn check type I was not more likely to be identified in individuals with or without residual oocytes detected ($z = -1.51$, $p = 0.13$), nor was type II ($z = 1.51$, $p = 0.13$). Of the 16 age 3+ individuals, 4 had residual oocytes detected, with 50% having spawn checks (n = 1 Type II; n = 1 Type II).

Difference in growth patterns

Increment width did not differ among increment width types (i.e., T1, O1, sum final) of age 2+ females. However, females with residual oocytes detected had a significantly wider first translucent (winter) band relative to females without residual oocytes detected, but differences were not observed for other increment width types (Table 1.3, Fig. 1.4). The mean increment width of ‘Sum Final’ appeared lower for ‘unknown’ relative to ‘spawners’, but the high variation likely resulted in nonsignificant results (Fig. 1.4). The random effect of individual in the linear mixed model did not explain any variance in increment width (Table 1.3), indicating that there was little individual variation. However, the random effect was included by design as the increment width measurements were a repeated measure in the otolith and, therefore, not independent.

Discussion

The spawn check in the otolith does not appear to be a reliable method of identifying previous spawning experience only half of female capelin with residual oocytes had spawning checks of either type. Indeed, even after examining growth patterns in females with residual oocytes and identifying two spawn check types, we still only correctly identified a spawn check in half of the females with previous spawning experience. This may be because spawn checks are typically characterized by periods of reduced growth due to increased energy allocation for gonadal development (cod, Rollefsen 1993; capelin, Winters 1971, Maxner et al. 2016), but instead females that had spawned previously (i.e. residual oocytes present) grew similarly relative to other individuals in the final year of capture. Interestingly, individuals with residual oocytes had significantly higher growth in the first year (T1), suggesting that higher early growth may lead to earlier sexual maturity (Stearns 1992, Trippel 1995). Additionally, findings indicate that irregular growth patterns in the otolith associated with previous spawning experience, may affect accurate age determination in individuals. Indeed, growth patterns associated with spawn check type II, were initially interpreted as one long winter growing season (translucent band), with regions of high growth (narrow opaque bands), which resulted in age being estimated as one year younger.

Growth of females with residual oocytes detected (‘spawners’) in the year of capture (‘SumFinal’) did not differ from those without residual oocytes detected (‘unknown’). This was not expected, as capelin were previously found to experience reduced growth during reproductive years (Winters 1971, Hopkins et al. 1986), similar to other short-lived species (e.g., sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolua*), Brosset et al. 2016) and long-lived species (e.g., cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), Lambert and Dodson 1990; longear sunfish (*Lepomis megalotis*), Jennings and Philipp 1992). So, why did we not observe lower growth in the year of capture for capelin spawners relative to unknowns? This may be due to the high variation in growth of unknowns, which may have resulted from combining a number of maturities within this category (Fig. 1.4). Indeed, individuals without residual oocytes detected may have spawned in the year of capture but residual oocytes were simply not observed in the cross-sections examined. Additionally, fish categorized as ‘unknown’ may have been immature age 2+ individuals, in which growth would be higher than those that had previously spawned as all surplus energy would have been presumably directed toward somatic growth (Roff 1983). Although other characteristics of capelin gonads have been used to determine previous spawning experience (e.g., thickened ovarian wall, double oocyte membrane; Flynn et al. 2001) and immature fish (e.g. all observed oocytes are previtellogenic Flynn 1996), which were observed, our preservation method (i.e. freezing) reduced our confidence in identifying these characteristics. Another possible reason growth differences were not observed in the year of capture between spawners and unknowns, may be due to accelerated growth prior to or after spawning to compensate for reduced growth during the spawning migration and spawning season. Indeed, by including the translucent band (winter/spring) prior to spawning (T2), narrow opaque band (O2) and translucent band (fall) after spawning (T3) in a combined annual growth measure, if spawning age 2+ females grew more in the winter/spring and fall than age 2+ immature fish but less during the summer spawning season, the total growth over the year of capture of immatures and spawners might be similar. In support, when fish reach sexual maturity, they may begin to store surplus energy before spawning (Ware 1980), as evidenced by the accentuated translucent band before the narrow opaque band in capelin spawning zones, as described by Winters (1971). Similarly, capelin may exhibit accelerated growth in the fall after spawning to compensate for the period of growth depression before and during spawning (i.e. compensatory growth, Ali et al. 2003), as observed in other fish species (Atlantic cod, Trippel et al. 2014; three-spined Stickleback (*Gasterosteus aculeatus*), Ali and Wootton 1999). If either or both of these phenomena occur, reduced growth during the spawning season would be masked when growth is measured on an annual scale. This suggests that for individuals that survive spawning, the somatic cost of reproduction are minimal.

Capelin with residual oocytes had higher growth in the first translucent band, representing the year of hatch, than capelin without residual oocytes detected. This suggests that higher early growth may allow capelin to reach sexual maturity at a younger age (Trippel 1995, Yaragina 2010). This finding is consistent with life history theory, which predicts that sexual maturation is dependent on early growth and attaining a certain body size (Stearns 1992). Indeed, sexually mature Atlantic salmon (*Salmo salar*) are larger compared to immature individuals of the same age (Simpson 1992). High early growth may be attributed to competitive ability, which appears to be driven primarily by body size in fish (e.g. Grant 1990, Holbrook and Schmitt 1992) and may be displayed by aggression when competing for prey (Taylor 1991) or foraging in higher quality areas (Hughes and Dill 1990, Deblois and Rose 1996). Alternately, high early growth may be related to temperament (Sih et al. 2004; Reale et al. 2007). For instance, smaller juvenile fish that may be less willing to venture further from optimal conditions to feed have lower competitive ability and are less likely to survive (Ward et al. 2004, White et al. 2013), and therefore will likely remain small as adults. The propensity of an animal to take foraging risks can be described along a shy-bold continuum, whereby bold individuals are more willing to accept more risk for higher foraging gains than shy individuals (Wilson et al. 1993). The growth pattern observed from larval stages into adult stages may reflect an individual's position along the shy-bold continuum. Poor environmental conditions, such as cool temperatures and low prey availability, may inhibit growth in a given year's cohort (Cushing 1972, Houde 1987) and lead to an overall reduced competitive ability. Conversely, high growth as a juvenile resulting from favourable environmental conditions may lead to an overall increased competitive ability. Spawning at an earlier age presents advantages for capelin. Mature females with previous spawning experience have higher fecundity (750 – 2,600 eggs) relative to recruit spawners of the same age (Winters 1971). However, the costs to early maturation may not be represented in the sample as only surviving individuals were considered in the study.

Initial estimates of age, without knowing the presence/absence of spawning experience, resulted in inaccurate age estimates of thirteen females, which were determined to be 1+ but were actually 2+, based on residual oocyte presence combined with age 2+ being the earliest age of sexual maturity. Unless capelin are able to spawn in their first summer, this would indicate that irregular growth patterns associated with spawning checks reduce confidence in otolith-based ageing, as found more generally for low growth periods ('growth checks'; Campana and Neilson 1985). Growth checks may be observed in fish due to sex changes (Walker and McCormick 2004), stress (Payan et al. 2004), metamorphosis (Bailey et al. 1977), as well as spawning (Pannella 1971) and have been found to interfere with accurate otolith-based aging in many species, such as herring (*Clupea harrengus*, Melvin et al. 2010), sablefish (*Anoplopoma fimbria;* Pearson and Shaw 2004), and Colorado pikeminnow (*Ptychocheilus lucius*; Hawkins et al. 2004). Indeed, an observer may incorrectly age a fish one year younger, assuming it is a growth check within a year, or may incorrectly age a fish one year older by interpreting a growth check to be a year of low growth. Additionally, all otolith regions that were characterized by short periods of fast growth (i.e. narrow opaque bands, type I; thin opaque strips within translucent bands, type II) were considered ‘spawning zones’ in age 2+ females, but may have been growth checks not associated with spawning. This could also explain the inaccuracy of identifying spawning zones in capelin.

In conclusion, our findings suggest that previously described spawning checks in capelin otoliths are not a reliable way to identify previous spawning experience. Reliability may be increased in future studies using different methodology. For instance, the preservation method (i.e. freezing) did not allow us to confidently identify other histological indicators of recovering spawners (e.g. thickened ovarian wall; Flynn et al. 2001) or distinguish between mature and immature capelin, which can be identified by the tightly packed arrangement of oocytes, the high proportion of smaller, early stage oocyte development, and a high proportion of Balbiani bodies (Forberg 1982, Flynn 1996). Therefore, future research post-spawning survival on capelin should avoid freezing samples, instead preserve gonads in 10% buffered formalin after capture Although spawn check identification in capelin otoliths appears to be an unreliable indirect estimate of post-spawning survival, confidence may be increased by combining with other indirect methods, such as macroscopic visual examination of ovaries. The latter method appears to be more reliable than spawn checks in the otolith, but macroscopic examination was found to underestimate up to 30% of post-spawning survivors when compared with histological estimates

(Flynn et al. 2001). We conclude that a histological examination of properly preserved capelin gonads should be used when attempting to determine capelin that have spawned previously and survived.

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Table 1.1: Sample sizes and locations of female capelin caught in November-December, 2016 on the Newfoundland Shelf in NAFO Divisions 2J and 3K. [1]Samples were collected on the Research Vessel (RV) *Alfred Needler*, trip 472. Remaining samples were collected on RV *Teleost*, trip 165[2] and 166[3]. Main samples which originally consisted of 200 – 311 fish, frozen on board the RV for processing. All other sets were supplementary sets which consisted of 25 fish before subsampling.

			Location		
Date	**N (males & females)**	**n (females)**	**Latitude**	**Longitude**	**NAFO Division**
Main samples[1]					
December 4	220	45	51°08.3’N	53°17.3’W	3K
December 2	140	64	51°87.8’N	52°51.7’W	3K
November 25	311	37	50°40.7’N	54°64.0’W	3K
Supplemental samples					
December 11[1]	25	5	49°82.0’N	52°74.3’W	3K
December 12[1]	25	3	50°35.3’N	54°33.0’W	3K
December 13[1]	25	5	50°67.7’N	52°70.8’W	3K
December 13[1]	25	11	50°69.2’N	52°36.7’W	3K
December 13[1]	25	9	50°87.3’N	52°41.7’W	3K
November 12[2]	25	2	52°65.8’N	53°09.7’W	2J
November 16[2]	25	4	52°52.8’N	54°81.2’W	2J
November 16[2]	25	3	52°62.5’N	55°03.0’W	2J
November 16[2]	25	7	53°17.0’N	55°53.8’W	2J
November 17[2]	25	8	53°97.5’N	55°89.2’W	2J
November 21[2]	25	3	52°22.7’N	53°85.8’W	3K
November 24[3]	25	2	50°57.5’N	55°41.7’W	3K
November 25[3]	25	1	50°27.5’N	54°94.7’W	3K
November 25[3]	25	6	50°44.0’N	54°45.5’W	3K
November 26[3]	25	2	51°88.7’N	53°62.8’W	3K
December 3[3]	25	2	51°23.7’N	54°27.2’W	3K
December 3[3]	25	6	50°89.3’N	53°60.7’W	3K
December 4[3]	25	7	50°96.8’N	52°84.0’W	3K
December 4[3]	25	1	50°94.7’N	52°55.2’W	3K
Total		**233**			

Table 1.2: Percentages of age 2+ female capelin with and without residual oocytes detected in the ovary that had each spawn check type (Type I and II, as defined in Fig. 1.2). Female capelin were caught in November-December 2016 on the Newfoundland shelf.

	n	% with Spawn Check	% Spawn Check Type I	% Spawn Check Type II
Residual Oocytes Detected	30	50% (n = 15)	23% (n = 7)	27% (n = 8)
Residual Oocytes Not Detected	87	49% (n = 43)	34% (n = 30)	15% (n = 13)

Table 1.3: Coefficients of the predictor variables for the model describing age 2+ growth of capelin captured during November-December 2016 on the northeast Newfoundland coast. Increment Width Type denotes whether the respective increment width was translucent (winter) or opaque (summer), and where the increment width is located in the otolith (e.g., first, second, third)

Random effects:				
Groups	Name	Variance	Std.Dev.	
ID	(Intercept)	0	0	
Residual		7090	84.2	
Number of obs: 345, groups: ID, 115				
Fixed Effects				
	Estimate	Std..Error	t.value	p.z
(Intercept)	288.64	5.18	55.7	0
Increment Width Type	2.43	7.33	0.33	0.74
SumFinal : With Residual Oocytes	9.23	18.52	0.5	0.62
O1: With Residual Oocytes	-11.67	17.4	-0.67	0.5
T1: With Residual Oocytes	40.37	17.4	2.32	0.02

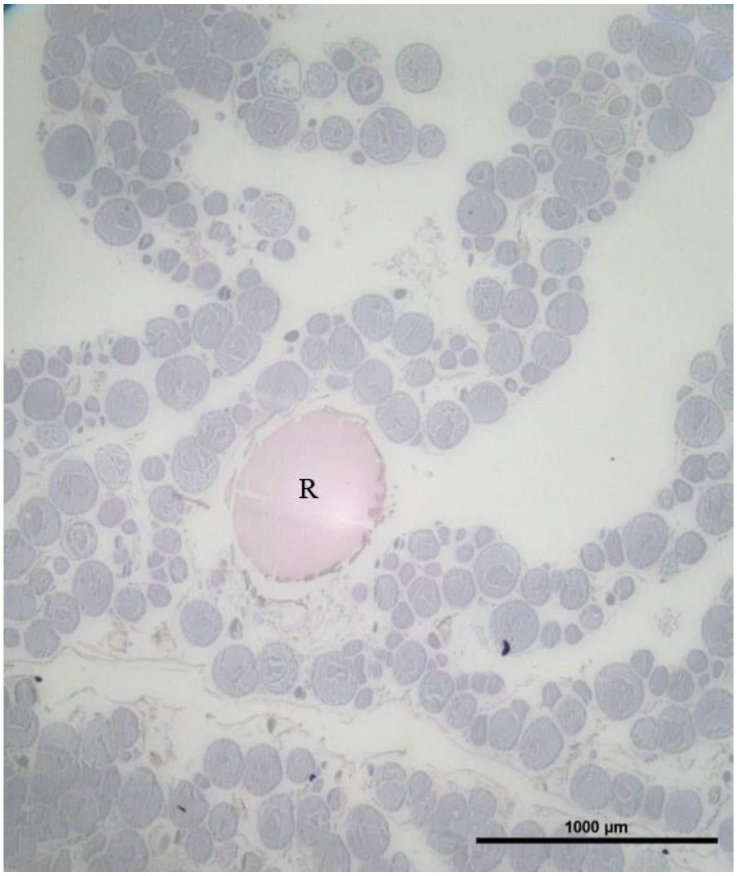

Figure 1.1: Photograph of a transverse section through capelin ovaries of a recovering spawner, captured in December 2016, with a residual oocyte (R) indicated.

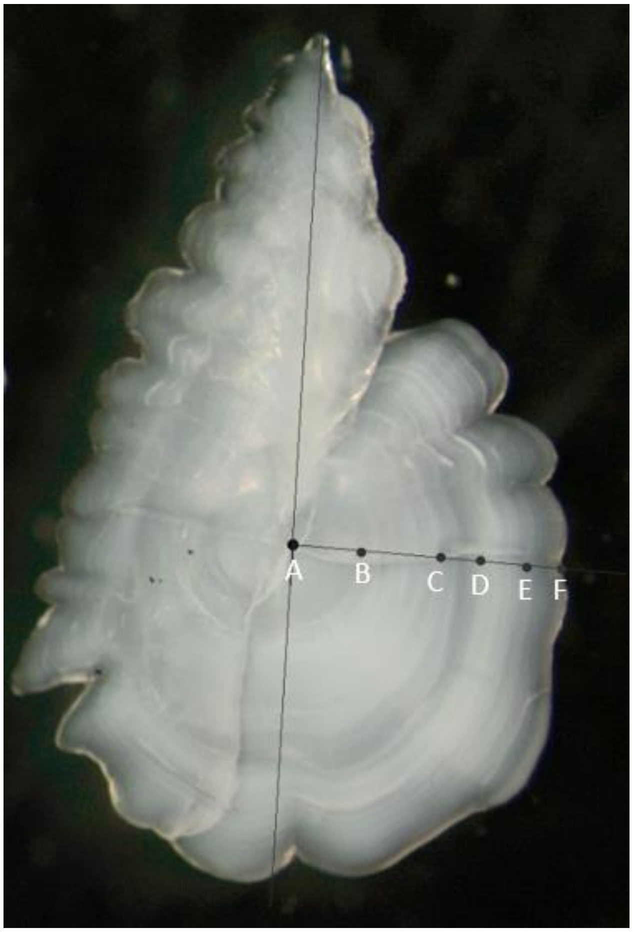

Figure 1.2: A saggital otolith of an age 2+ female capelin without a spawn check or residual oocytes present in the ovary, captured in December, 2016. Age 0+ growth (A-B; T1) with the individual turning age 1 (B); age 1+ opaque summer growth (B-C; O1); age 1+ translucent winter growth (C-D; T2); age 2+ opaque summer growth (D-E; O2); age 2+ translucent winter growth (E-F; T3), during which the fish was captured (F).

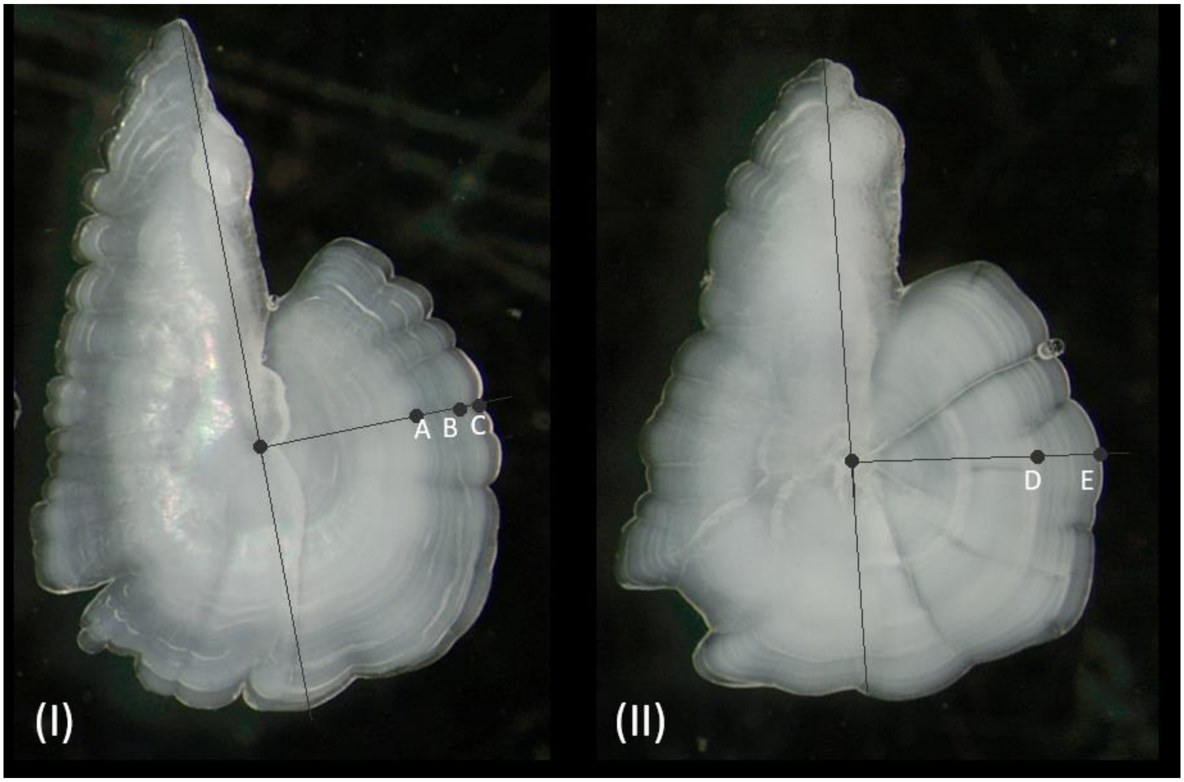

Figure 1.3: Saggital otoliths from two capelin with residual oocytes, with different spawn check types. Spawn check Type I: sequence of translucent band (A-B), narrow opaque band (B-C); II: wide translucent band in the year of capture with opaque banding within the translucent band (D-E).

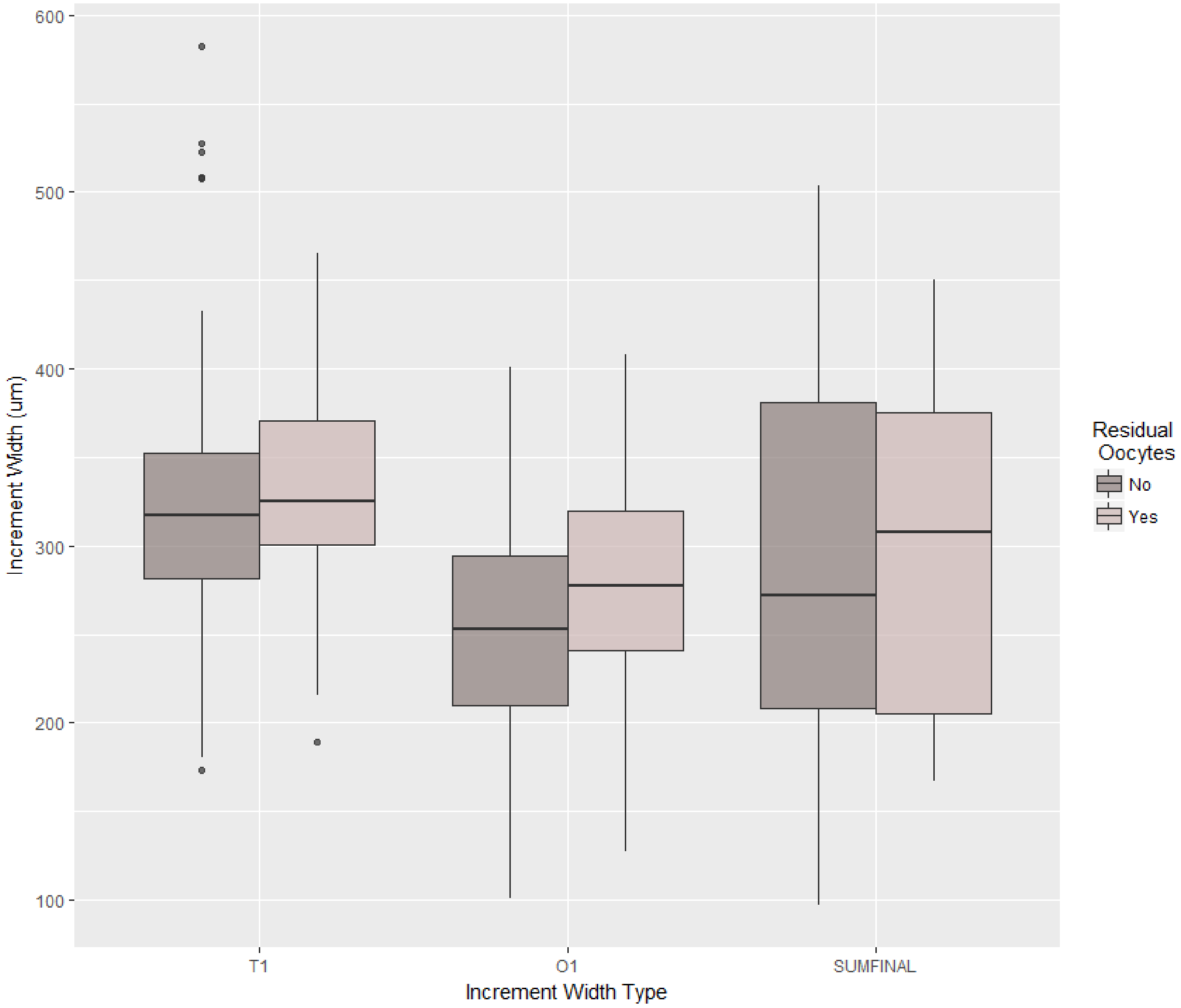

Figure 1.4: Mean (horizontal bar), 25th (lower bar) and 75th (upper bar) percentile (and outliers) for increment width of first translucent band (T1), first opaque band (O1), and the sum of increment widths during the final year of capture ('sumfinal' = second translucent band, second opaque band, and third translucent band, if observed) in age 2+ female capelin with residual oocytes detected (Yes) and not detected (No) caught in November-December 2016 on the Newfoundland Shelf.

Inter-annual variation in growth in capelin (*Mallotus villosus*) on the eastern Newfoundland Shelf

Introduction

The life-history framework for North American fish highlights a trade-off of three crucial life history traits: growth, sexual maturation, and reproductive investment (Winemiller and Rose 1992). For species that exhibit indeterminate growth, such as fish, growth and survival vary with body size, whereby larger individuals have greater fecundity and higher chance of survival (Kozlowski 1996). The life history strategy of forage fish is characterized by a short life-span, high fecundity, may be semelparous or iteroparous (Pitcher 1995) and highly fluctuating populations (up to 40% per year, Schwartzlose et al. 1999). Many bio-physical factors influence growth of forage fish, the most important of which are prey availability and temperature (Brandt 1993, Bacha 2010). For instance, Japanese sardines (*Sardinops melanostictus*) experience higher larval growth in warmer offshore sites compared to cooler inshore areas (Itoh et al. 2011) and anchovy (*Engraulis encrasocolus*) maximize growth and spawning energy reserves in periods of high food availability (Gatti et al. 2017). Fish also often have reduced growth during reproductive years, while energy is directed to gonadal development reducing somatic growth (Ware 1980, 1982; Kozlowski 1996). Indeed, growth tends to decrease after sexual maturity in many fish species (Norwegian herring (*Clupea harengus*) Runnström 1936; Kozlowski 1996b). For females, this is probably due to an increase in energy allocation to gonadal development; however, this is not necessarily the case for males, as male allocation of energy into reproduction is relatively low (Roff 1983).

An important forage fish in many northern marine food webs is capelin (*Mallotus villosus*), a small, short-lived (3-6 years), schooling fish (Carscadden and Vilhjálmsson 2002).

Capelin are key prey for most top predators, including piscivorous fish (e.g. Atlantic cod, *Gadus morhua*), marine birds and mammals, thereby providing an important link between lower and higher trophic levels and regulating energy flow through marine food webs (Carscadden and Vilhjálmsson 2002). In coastal Newfoundland, capelin spawn at and near beaches during the summer, where fertilized eggs adhere to sediment and remain until hatching (Templeman 1948). After hatching, larvae rely on their yolk sac reserves until they reach ~7 mm (Templeman 1948), after which they feed on small zooplankton (i.e. <250 µm; Frank and Leggett 1982b). Larvae passively disperse offshore during the fall, during which growth and survival are primarily influenced by water temperature as well as prey availability, which are important determinants of year-class-strength (Leggett et al. 1984). While in offshore nursery areas, capelin undergo metamorphosis during the spring/summer of their second year (Bailey et al. 1977). During the winter, capelin reduce feeding and growth (Winters 1970) but resume feeding during the spring coincident with sea ice retreat (Buren et al. 2014, Mullowney et al. 2016). Indeed, feeding intensity peaks during April – May, resulting in the start of summer growth (Gerasimova 1994). Sea ice retreat in the spring accelerates stratification in the water column, with warm surface waters promoting high phytoplankton growth (Wu et al. 2007). During this period, the magnitude, duration, and peak timing of spring bloom determine the availability of capelin prey sources, in particular *Calanus finmarchacus* (Gerasimova 1994, O'Driscoll et al. 2001) and *Thysanoessa* sp. (Obradovich et al. 2013) for adults, and *Pseudocalanus* sp. for larval and juvenile capelin (Murphy et al. 2018). Capelin remain offshore on the Newfoundland shelf for 2-3 years until they migrate inshore to spawn (Templeman 1948). Capelin in spawning condition stop feeding during the spawning period (Winters 1970, Vesin et al. 1981) and both the lack of feeding during spawning and energetic costs of developing gonads (primarily females) and secondary sexual characteristics (primarily males), cause male and female capelin to undergo a substantial decline in lipid reserves from overwintering to spawning (Winters 1970, Henderson et al. 1984). If fish survive spawning, feeding intensity increases again during the post-spawning period in the fall prior to overwintering (Henderson et al. 1984).

Changes in Newfoundland capelin biology and behaviour were observed in the early-1990s (Carscadden 2000), which were associated with a population collapse from an estimated at 5,783,000 tonnes in 1990 to 138,000 tonnes in 1991 (Buren et al. 2014). Prior to the 1990s, capelin matured and spawned at three and four years of age (DFO 2013). However, the proportion of age-two spawners increased during the early 1990s (Nakashima 1996, Carscadden et al. 1997) and the majority (37-79%/year) of capelin have continued to mature at age two since 1999 (DFO 2013), with the highest being 80% in 2005 (DFO 2013, 2015). This younger age-at-maturity was accompanied by smaller total lengths for both sexes (females: 140-155 mm; male: 160-175 mm; DFO 2013). Indeed, lengths have stabilized at these lower sizes, but have shown annual variation, with the smallest fish being observed in 2009, one of the cooler years on record (DFO 2011). In contrast, capelin in the eastern Scotian Shelf in Nova Scotia have increased in biomass in the late 1980s to early 1990s, thought to be facilitated by a euphausiid dominant diet, particularly *Thysanoessa* sp. (Obradovich et al. 2013). This increase in biomass was associated with increased growth, condition, and feeding, in comparison to capelin on the northern Grand Banks of the east coast of Newfoundland during and after the population collapse in the early 1990s. Although the reduction in capelin length is associated with cooler temperatures, earlier sexual maturity and delayed annual timing of spawning (DFO 2015), studies have not directly examined inter-annual variation in age-specific growth of capelin throughout this period.

The goal of my study is to quantify inter-annual variation in growth of male and female capelin on the eastern Newfoundland shelf during the post-regime shift period to investigate links with environmental conditions (e.g., physical oceanography, food abundance). To do this, I used otolith-based techniques to quantify age-specific growth in spawning male and female capelin collected annually on the northeastern Newfoundland coast (2008-2016). As males experience higher growth compared to females after their first year, with size differences varying between 20-30 mm in the second and third years (Winters 1982), I examined growth in sexes separately. I hypothesized that age-specific growth in each sex varies in years having anomalous environmental conditions. I predicted that years that have lower food abundance and cooler temperatures result in reduced growth. This study is important, as studies on capelin growth have focused on larval growth, and have focused the period before the 1990 regime shift (Winters 1982), but estimates are critical to interpret inter-annual variation in mean length, which may lead to variation in year-class-strength, based on body size-fecundity relationships (Penton and Davoren 2013).

Methods and Materials

Fish collection and processing

Capelin were collected at known beach (n=5) and deep-water (n=11) spawning sites on the northeast coast of Newfoundland (49–50° N, 53–54°W) during July-August 2008-2016. In each year, samples were collected at the spawning sites whenever capelin was present. At the beach spawning sites, capelin were sampled using dip nets (38 cm diameter, 0.32 cm mesh), whereas a purse seine (26 × 146 m, 0.21 cm mesh) was used at deep-water sites (as described in Maxner et al. 2016). A sample normally consisted of 220 fish, which were frozen for later processing. Of the 220 frozen fish, 5 fish per sex, per 5 mm length increment (range: 90 – 200 mm) were subsampled for otolith removal and growth analyses.

Otolith-based growth

Sagittal otoliths were removed and photographed using a Olympus dissecting microscope (SZX7) (Hedeholm et al. 2010, Maxner et al. 2016). These photographs were used to determine fish age (years) by counting the number of alternating translucent winter and opaque summer bands; one pair of summer and winter bands represent one year of growth (Winters 1982, Hedeholm et al. 2010, Davoren and Halden 2014). Two observers independently determined the age of subsampled fish and each was assigned a level of confidence (i.e., poor, fair, or good). If the estimated age was inconsistent between observers or the confidence level was poor, the otoliths were not included in further analyses (Hedeholm et al. 2010, Maxner et al. 2016). Each growth increment was assigned a year based on the year it was captured (Fig. 1).

Annual growth increments were measured from the otolith photographs using ImageJ (described in Hedeholm et al. 2010, Davoren and Halden 2014). The core region of the otolith was estimated visually and a line was overlain on the image from the tip of the rostrum to the bottom of the otolith going through the core. A second line was placed at a 90° angle from the first line, from the core to the outer edge of the otolith (Fig. 2.1). The first year of growth was measured from the core to the outer edge of the first winter band (Fig. 2.1). Following years were measured from the start of the summer growth band to the outer edge of the next winter band. Otoliths were measured twice by the same observer. If the measurements differed by <20%, the average of the two was used in the analysis. When the measurements differed by >20%, the otoliths were excluded from further analysis.

Data Analysis

Linear additive models were developed to examine age- and sex-specific annual trends in growth increments from 2008-2016. Only three-year-old capelin were included in growth analyses (Fig. 2.1). The general additive models were run using the *mgcv* library (Wood 2011) using R v3.3.2 (R core team 2017). A separate model was developed for capelin at different ages (0+, 1+, 2+), because each age class could potentially respond differently to environmental variation.

The linear additive mixed model consisted of three elements: a probability distribution (normal; eq. 1), a link function (identity; eq. 2), and a linear predictor (eta, η; eq. 3). The distribution of the response variable, fish growth was:

$$(1)\begin{cases} N(\mu, \sigma^2) \\ E(Y) = \mu \\ var(Y) = \sigma^2 \end{cases}$$

The identity link was:

$$(2)\ \mu = \eta$$

Eta (η; eq. 3), was equal to the sum of the intercept, β_0, and the fixed effect term, β_n, multiplied by its estimate, X_n, a smoothing function of the response variable X_n, and a random effect (a_j; fish ID). This relationship was described as:

$$\eta = \beta_0 + \beta_i X_i + f(X_{i+1}) + a_i$$

Growth in capelin was represented by the increment width each pair of opaque and translucent bands.

$$Growth\ increment_{ij} = s(Year, by\ Sex_j) + Sex_j + Previous\ growth + \ \varepsilon$$

Where s is a smooth function of ‘year’, which represents the environmental variation over the years of the study. A separate smooth function was estimated for each sex to account for differences in response to environmental variation over years. For age 0+ capelin however, sex was not considered as capelin have not metamorphosed at this age and sex-based differences in growth are not observed (Winters 1982). Previous growth was the sum of the increment widths of previous years to account for variation among individuals, as a larger individual may be able to grow more than a smaller individual at a given age. For age 0+, previous growth was not included, as it was the first year of growth. Epsilon is the variation in growth not described by the variables considered in the model.

Owing to variation in sampling sites and timing of spawning (described in Crook et al. 2017), there were unequal sample sizes of capelin across years. Samples collected in 2015 and 2016 were omitted from the analysis due to small sample sizes, as they may not be an accurate representation of the population. Samples collected in 2008 were omitted from the model describing adult growth as no males were collected, but were not omitted in 0+ growth as capelin have not metamorphosed and, thus, sex was not an observable factor.

Age- and sex-specific growth was estimated using the abovementioned models to examine growth trends over years of this study and identify years of high and low growth. To do this, I used the *predict.gam()* function in the *mgcv* library (Wood 2011). Growth over the years of the study was predicted using mean values, holding all relevant fixed effects constant (i.e. previous growth) for each age and sex, at the mean value of the respective age and sex (age 1 and 2 only). The resulting annual growth estimates represented the expected growth for capelin of a particular age, sex, and average previous growth, where relevant.

To examine environmental factors that may influence capelin growth, a principal component analysis was conducted on published environmental anomalies developed from several time-series of environmental data to represent the state of bio-physical conditions on the Newfoundland Shelf (DFO 2017, Pepin et al. 2017). An important assumption of PCA is that data are not autocorrelated. Although our data violate this assumption, the PCA is used solely as an exploratory tool to help interpret annual variation in growth (i.e. no statistical inferences were made; Vanhatalo and Kulahci 2016).

Anomalies were calculated as the difference between the annual value for each variable and its long-term mean over a reference period divided by the long-term standard deviation, allowing direct comparison among anomaly values measured on different scales (DFO 2017). The anomalies considered were: chlorophyll-a, *Pseudocalanus* spp. abundance, *Calanus finmarchacus* abundance, magnitude of the spring bloom, peak time of spring bloom, duration of spring boom, a composite index for the physical climate (as described in Pepin et al. 2017, DFO 2017), and an ocean temperature composite, consisting of bottom and sea surface temperatures for multiple locations on the Newfoundland Shelf. The composite index for physical climate integrates many physical parameters, including sea ice extent, surface temperature and salinity, bottom temperature and salinity, and the depth of the cold intermediate layer, from several regions across the Newfoundland Shelf (as described in DFO 2017) to represent general oceanographic conditions (i.e., warm, average, cool) on the shelf. For the composite index for physical climate, the long-term mean was calculated for the reference period of 1950 – 2010, while 1999-2010 was the reference period for all other variables.

Results

Sex, previous growth, and year had a significant effect on growth of capelin of all age classes examined (Table 2.1). Previous growth had a negative effect on age 1+ and 2+ capelin growth, suggesting that higher growth in the previous year resulted in lower growth in the current year. The smooth of Year, which represented annual environmental variation, had a significant effect on capelin growth at all ages (Table 2.1). For age 0+ and 1+ capelin, there were significant changes in growth over the years (Table 2.1; Fig. 2.2a-c). For age 2+ capelin, females did not have a significant change in growth over the years (Table 2.1, Fig. 2.2d), but males did (Fig. 2.2e).

For an average-sized age 0+ capelin, 2006, 2007 and 2013 were years of lower growth, and 2009 – 2012 were years of higher growth (Fig. 2.2a). Average-sized age 1+ female and male capelin had lower growth in 2008 and 2009, but higher growth in 2007, and 2010-2012 (Fig. 2.2b, c). For an average-sized age 2+ female capelin, there was no significant difference in growth across the years (2009 – 2014; Fig. 2.2d). An age 2+ male, however, showed lower growth in 2009-2010 and high growth in 2008 and 2011-2013 (Fig. 2.2e).

A Principal Component Analysis on the environmental variables resulted in three principal components with eigenvalues greater than 1, explaining 84.62% of total variance of environmental variables examined (Table 2.2, Fig. 2.3). The physical climate composite and temperature composite anomalies were both included in the initial analysis; however, the two variables were highly correlated ($r = 0.958$). The PCA was conducted again with only the temperature composite, as together with the other variables, more of the variation in the dataset was explained. The first principal component (PC1) accounted for 47.0% of the total variance, and variables with the highest positive component loadings were temperature and magnitude of the spring bloom, and negative component loadings were peak timing of spring bloom and chlorophyll-a (Table 2.2). PC2 accounted for 24.5% of the total variance (Table 2.2, Fig. 2.3), with *Pseudocalanus* spp. and *Calanus finmarchicus* abundance loading most negatively. PC3 accounted for 13.1% of the total variance and the variable with the highest positive component loading was *Pseudocalanus* spp., while the variable with the highest negative component loading was *Calanus finmarchicus* (Table 2.2, Fig. 2.4).

Discussion

The growth patterns observed in this study were similar to the growth patterns observed for capelin in the Barents Sea (Hedeholm et al. 2010) and a previous study in Newfoundland (Winters 1982), which can be described in three stages: (1) High growth in the first year (age 0+); (2) moderate growth in the second year (1+), and (3) minimal growth during the first possible year of spawning (age 2+) Additionally, male and female capelin showed similar inter-annual growth variation at age 1+ but trends diverged at age 2+, as observed in a previous study (Winters 1982). Capelin growth in all age classes, however, varied among years of this study. Higher growth years were generally represented during 2010-2012 across most age classes. Conditions during 2010-2012 were generally characterized by warmer years, with an earlier and high magnitude spring bloom. Prey abundance for age 0+ capelin (i.e. *Pseudocalanus* spp.) and adults (i.e. *Calanus finmarchicus*), however, varied among these years of higher growth. This suggests that temperature and spring bloom dynamics may be more important for higher growth than food abundance across age classes. The different prey types are negatively correlated, that is, years of low abundance of large copepods (i.e. *Cal. finmarchicus*) have high abundance of small copepods (i.e. *Pseudocalanus* spp). In contrast, lower growth years varied among age classes, occurring in 2006-2007 and 2013 for age 0+, 2008-2009 for age 1+ and 2009-2010 for age 2+. These years were associated with cooler conditions and lower prey abundance (especially 2007 and 2009), along with later timing of peak bloom that had a low magnitude and short to average duration. This suggests that cooler years that are paired with lower prey abundance resulted in lower growth across age classes.

Larval capelin growth (age 0+) was highest during 2010-2012, which were some of the warmest years in the study period, with an early spring bloom of high magnitude but short duration, and prey abundance (i.e. *Pseudocalanus* spp) was moderate (2011) to high (2010, 2012). These findings were not surprising, as high juvenile capelin growth is associated with warmer water and higher prey abundance for capelin (Murphy et al. 2018), as well as other species (e.g., chinook salmon *Oncorhynchus tshawytscha*, lake trout *Salvelinus namaycush*, striped bass *Morone saxatilis*; Brandt et al. 2002). Indeed, a recent study on larval capelin growth on the Newfoundland shelf suggested that both warmer temperatures and higher prey abundance are needed for higher larval growth (Murphy et al. 2018). Other studies have also linked higher larval capelin survival to warmer temperature within the first six months of life, with a primary underlying mechanism thought to be the influence of food abundance on growth (Leggett et al. 1984; cf Carscadden et al. 2000). Years of high age 0+ growth in our study (2010-2012) were also years of high estimated age 0+ capelin abundance since the 1990s regime shift (Mullowney et al. 2016), suggesting that intraspecific competition did not negatively influence growth during these years, as has been observed in other species (Norwegain herring *Clupea harengus*; Husebø et al. 2007). This likely stems from the currently low population sizes of Newfoundland capelin, which have remained since the population collapse in the early 1990s (Mullowney et al. 2016).

The year of lowest age 0+ capelin growth (2013) was characterized by cooler temperatures, but the highest prey abundance (i.e. *Pseudocalanus* spp.) in the time series, suggesting that temperature has a strong inhibitive impact on growth regardless of prey abundance. This is in contrast to other forage fish, which exhibit higher growth associated with high prey availability, even during cooler conditions (e.g. Japanese sardine, *Sardinops melanostictus*; Takahashi et al. 2009). On the Newfoundland shelf, however, the timing of abundant prey, is key to larval survival, whereby a mismatch between larval capelin emergence and timing of peak larval prey abundance appears to have limited survival of larval capelin since the population crash in the 1990s (Mullowney et al. 2016). Indeed, this is supported by the match-mismatch hypothesis, which states that year-class strength is dependent on bloom dates being centered on the long-term median date, as spawning is adapted to this period, and that a particularly late or early bloom will lead to poor recruitment(Cushing 1974, 1975). As growth is often linked to survival, and faster growth is correlated with reduced probably of starvation and predation (‘growth-mortality hypothesis’; Anderson 1988), this mismatch might explain low growth in high prey abundance years. As capelin larvae have high mortality immediately after hatching (Murphy et al. 2018) and only survivors (i.e. spawning adults) were considered here, there were likely other factors affecting growth and survival that were not included in our model, possibly resulting in the low variation explained.

Similar to larval capelin, adult (age 1+ and 2+) growth was highest in 2011-2012, which were among the warmest years in the time series; however, both years had either average or below average prey abundance (i.e. *Calanus* spp). This suggests that adult growth may be influenced more by temperature than prey availability, as suggested for larval growth. Similarly, Hedeholm et al. (2010) reported a primary effect of temperature on growth, with prey availability as a secondary factor, but Obradovich et al. (2013) emphasized the importance of prey abundance for adult capelin growth. This discrepancy may have resulted from our models describing < 30% of the variation in adult growth, which may be attributed to a number of factors. First, shelf-wide bio-physical anomalies used here do not necessarily depict the conditions that individual capelin experienced. Indeed, regional variation in environmental conditions will affect daily, seasonal, and eventually annual growth patterns of individuals (Obradovich et al. 2013). Second, whether individuals spawned at age 2+ was not included in our model, because determining previous spawning experience from capelin otoliths is difficult (Chapter 1, Hedeholm et al. 2010; cf Winters 1971). Female capelin appear to maximize their lifetime reproductive success by spawning multiple times throughout their lifespan (i.e. iteroparous), while males appear to spawn with multiple females in one year and then die (i.e. semelparous; Shackell et al. 1994, Burton and Flynn 1998, Huse 1998, Flynn et al. 2001). As previous spawning events are typically identified in otoliths (i.e. 'spawning check'; Cod (*Gadus* morhua), Rollefsen 1933; Silver hake (*Merluccius bilinearis*), Pannella 1971), based on the assumption of lower growth during the year of spawning (Winters 1971, Ware 1980, 1982, Kozlowski 1996), varying proportions of capelin females that had previously spawned could mask inter-annual variation in growth for females, but not necessarily for males. Previous spawning by females in our model might also explain the divergent growth patterns of males and females observed here and previously (Winters 1982).

Previous growth negatively influenced age 1+ and 2+ growth, suggesting that capelin that experienced high growth at age 0+ had lower growth as adults, whereas capelin experiencing low larval growth had higher adult growth . This suggests that growth patterns of capelin individuals are not set early in life, as found in other fish species where competitive ability is related to body size (e.g., Grant 1990, Holbrook and Schmitt 1992) and/or temperament (Sih et al. 2004; Reale et al. 2007). Instead, capelin appear to accelerate growth after a period of growth depression, induced for example, by poor environmental condition (Ali et al. 2003). This has been observed in other fish species, where fish can achieve the same length-at-age, despite lower early growth (e.g., Herring (*Clupea harengus*), Pedersen et al. 1990; Atlantic salmon (*Salmo salar*), Nicieza and Metcalfe 1997) Pikeperch (*Sander lucioperca*), Mattila et al. 2009). This finding might also be interpreted as high growth in early years leading to early sexual maturity, after which an individual has lower growth because less energy is allocated to somatic growth during reproductive years (Hopkins et al. 1985). Indeed, this would be predicted by life history theory, which states that sexual maturation is dependent on body size, or obtaining sufficient energy stores to reproduce (Stearns 1992) and, thus, achieving a larger size at a young age may allow a fish to spawn at a younger age (Trippel 1995). Indeed, faster growing Atlantic salmon (*Salmo salar*) mature earlier (Saunders et al. 1982). If annual survival is low, spawning earlier is advantageous because it ensures that an individual would spawn at least once during its lifespan before it dies, and would increase the number of reproductive events in its lifespan if the individual survived to spawn again (Stearns 1992). Fecundity may be higher in repeat spawners relative to recruit spawners (Winters 1971), suggesting several advantages to spawning at an early age.

Based on the growth patterns identified here, trends toward warmer temperature in recent years (2012-2014; DFO 2015) may favour higher adult capelin growth, which is supported by increasing mean length-at-age of capelin in 2012 to 2014 (DFO 2015). As larger body size translates into increased fecundity for capelin (Penton and Davoren 2013), these warming trends that favour adult growth, may initiate the recovery of the capelin population on the

Newfoundland Shelf since it collapsed in the 1990s (Buren et al. 2014). Warmer temperatures, however, may lead to earlier sea ice retreat and, thus, earlier peak spring blooms (Buren et al. 2014), resulting in a mismatch between larval emergence and peak larval prey abundance if capelin continue to exhibit delayed spawning (Mullowney et al. 2016). As this will likely inhibit larval growth and survival (Mullowney et al. 2016), the advantage of increased fecundity in adult capelin may be negated by low recruitment into the spawning population. Future research on otolith-based growth should focus on determining previous spawning experience and its effect on capelin growth on the Newfoundland shelf.

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Table 2.1: Coefficients of the predictor variables for the models describing age 0+, 1+ and 2+ growth of three-year-old capelin captured in spawning condition during July-August 2008-2016 on the northeast Newfoundland coast. Sex denotes whether fish were male or female. PG is the sum of all previous growth before the age of interest. [a] Samples collected from 2008 - 2016. [b, c, d] Samples collected from 2009 - 2014.

Model	**Parametric Fixed Effects**					**Approximate Significance of Smooth Terms**					**Variance Explained**
		Estimate	Std. Error	t value	Pr(>|t|)		edf	Ref df	F	p-value	
age 0+ (n=892[a])	Intercept	314.717	2.205	142.7	<2e-16 ***	s(Year)	4.908	5.524	12.31	1.9e-12 ***	8.31%
age 1+ n=(697[b])	Intercept	480.1804	14.33095	33.507	< 2e-16 ***	s(Year): Females	3.376	3.78	8.487	2.57e-06 ***	22.6%
	Sex	37.13512	5.88187	6.313	4.90e-10 ***	s(Year): Males	3.762	3.962	17.82	8.45e-13 ***	
	PG	-0.32618	0.04395	-7.422	3.42e-13 ***						
age 2+ n=(697[c])	Intercept	356.52319	18.58228	19.186	< 2e-16 ***	s(Year): Females	1.490	1.822	0.326	0.69	17.6%
	Sex	44.93086	4.96033	9.058	< 2e-16 ***	s(Year): Males	3.724	3.950	11.027	6.63e-08 ***	
	PG	-0.21301	0.02659	-8.011	4.88e-15 ***						

Table 2.2: Component loadings for Principal Component Analysis on environmental variables expected to affect capelin growth.

Environmental Variable	PC1	PC2	PC3
Chlorophyll-a	**-0.441**	0.381	-0.140
Pseudocalanus spp.	-0.087	**-0.548**	**0.608**
Calanus finmarchacus	-0.162	**-0.415**	**-0.703**
Magnitude Spring Bloom	**0.416**	0.298	0.170
Peak time Spring Bloom	**-0.488**	-0.326	0.089
Duration Spring Bloom	-0.379	0.3942	0.065
Temperature Composite	**0.463**	-0.175	-0.270

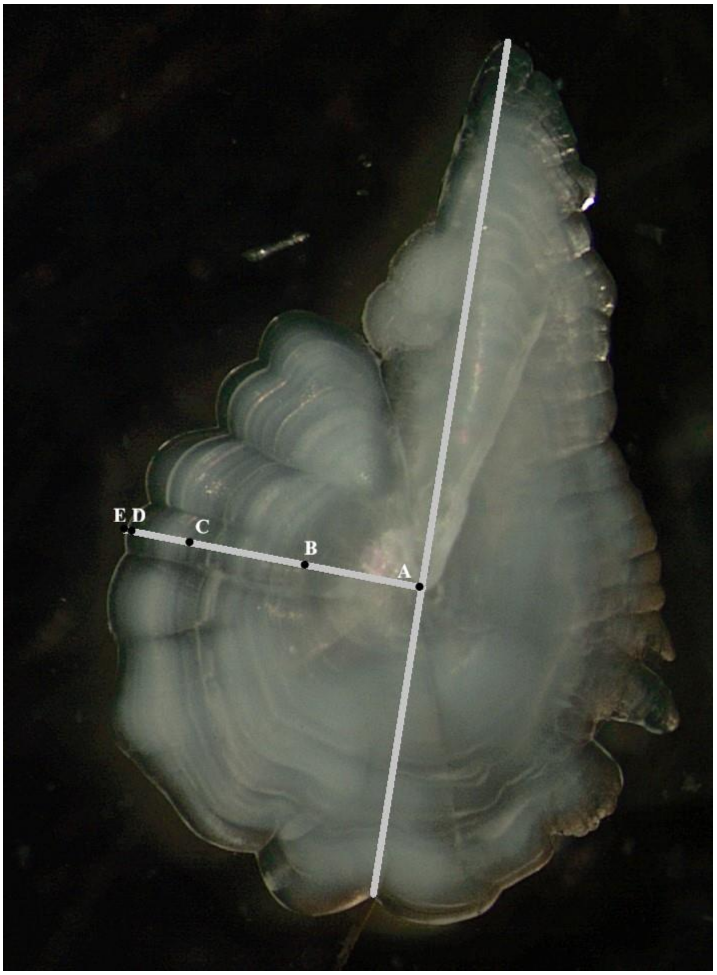


Figure 2.1: Saggital otolith of a capelin captured in July, 2015 (E). Year of hatching is 2012 (A); age 0+ growth (A-B) with the individual turning age 1 on the arbitrary date of January 1, 2013 (B); age 1+ growth (B-C), turning age 2 on January 1, 2014 (C); age 2+ growth (C-D), turning age 3 on January 1, 2015 (D); age 3+ growth (D-E), during which the fish was captured in spawning condition (E). As all capelin were in spawning condition and caught during spawning, growth during the year of capture (i.e. D-E) was minimal and, thus, not measured.

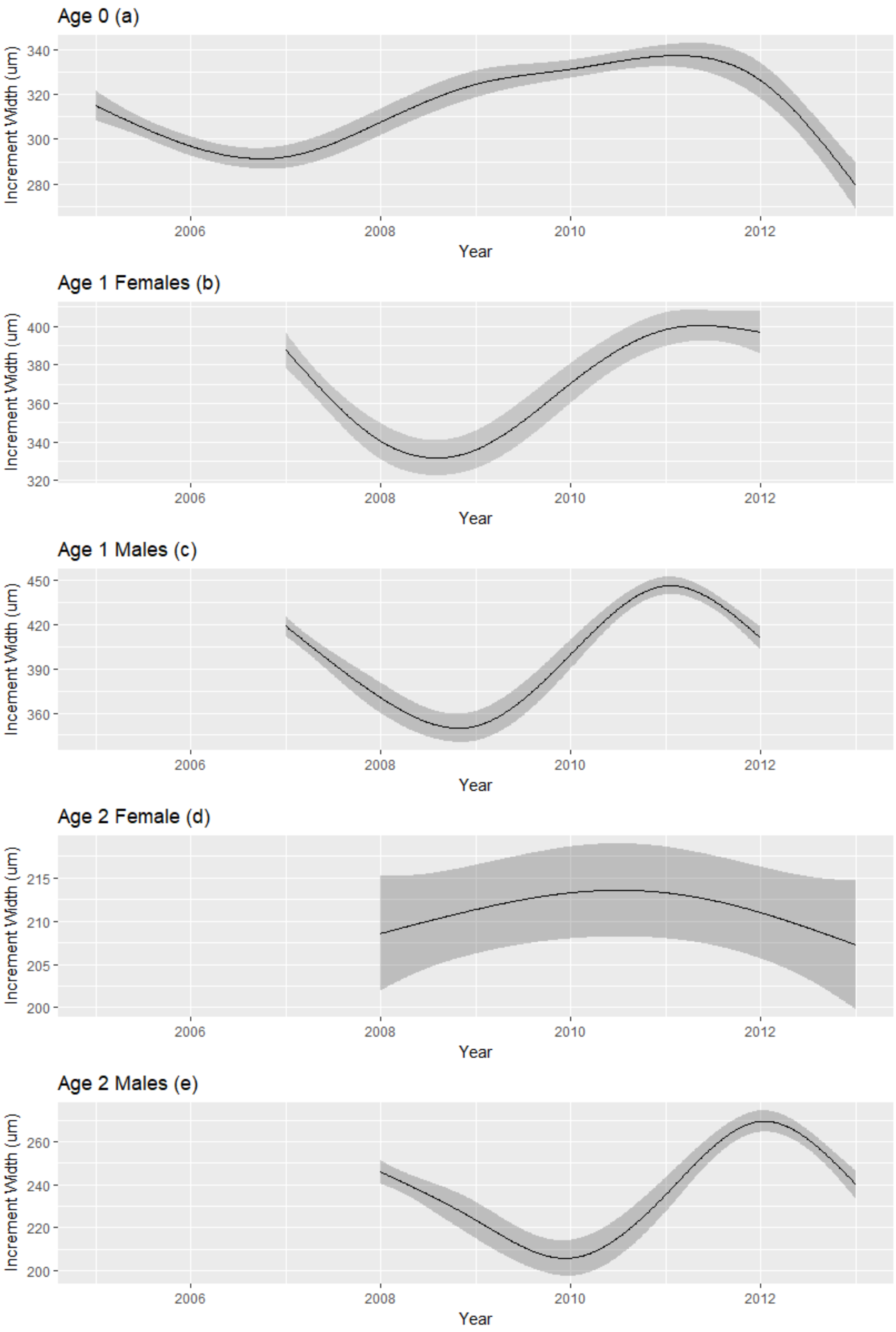


Figure 2.2: Predicted capelin growth from General Additive Models of each age class (age 0+, a; age 1+, b and c; and age 2+, d and e), and sex (female: b and d; male: c and f) for spawning capelin captured during July-August 2008 – 2014 on the northeast Newfoundland coast.

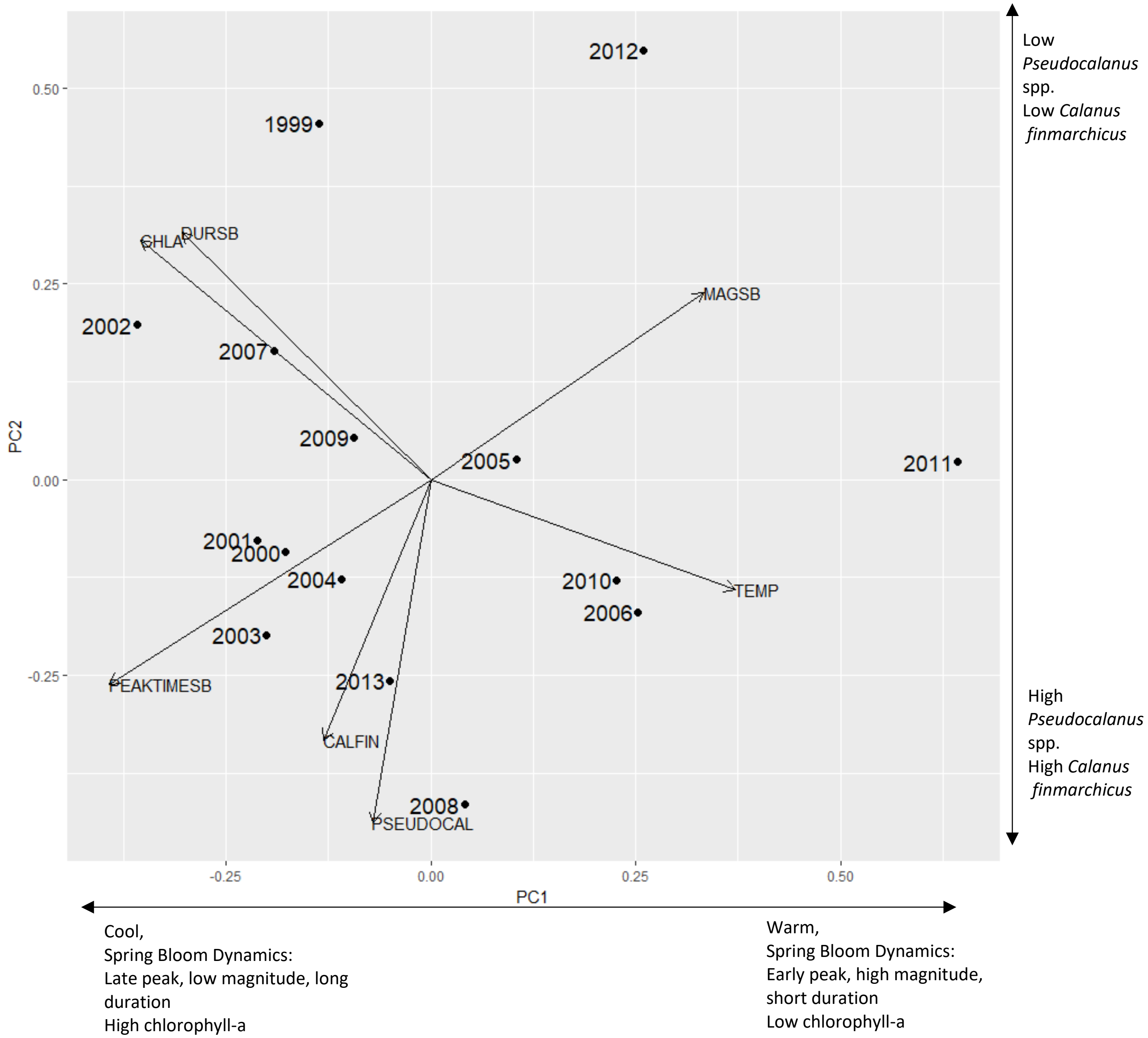
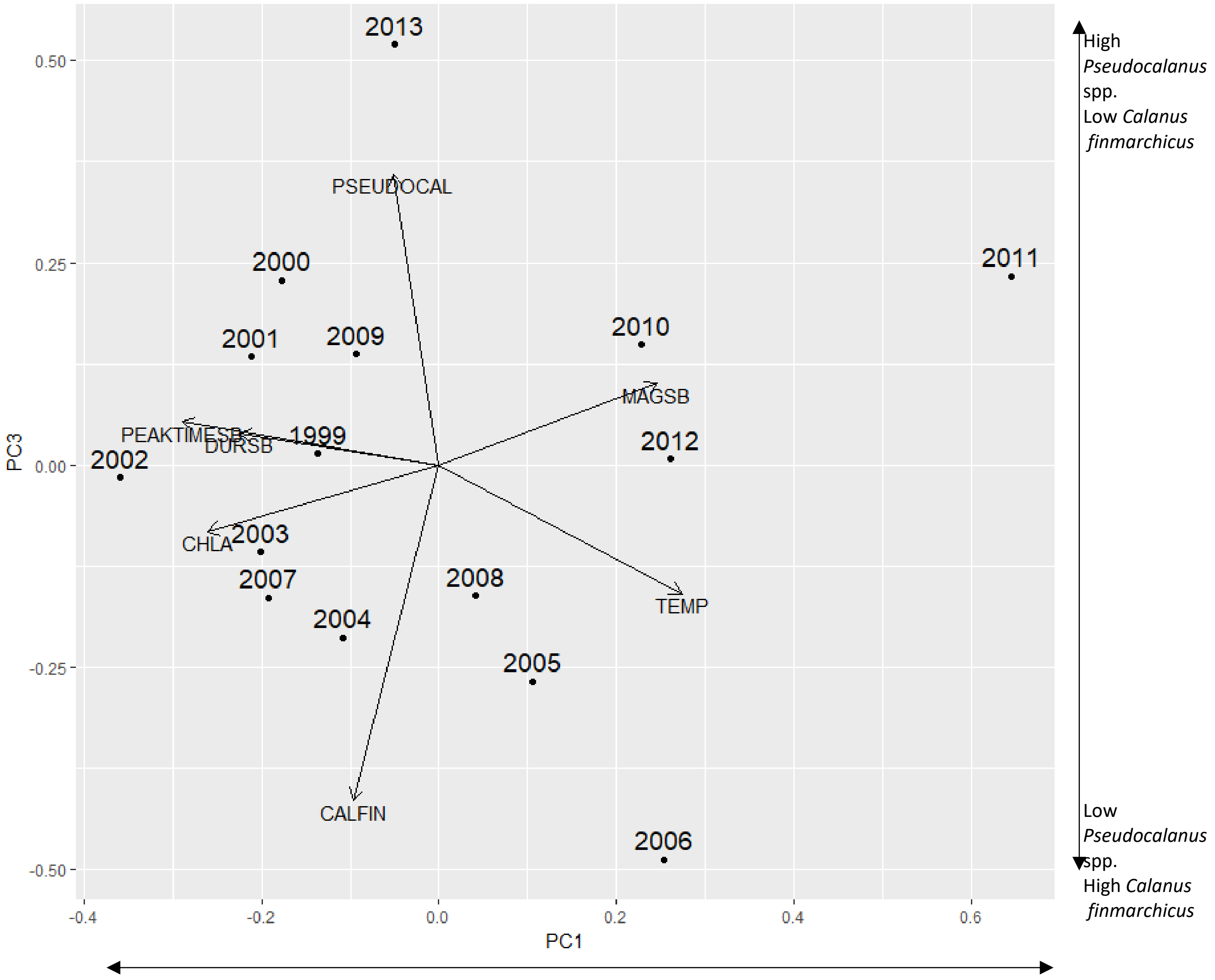


Figure 2.3: Biplot of PC1 and PC2 from the Principal Component Analysis on environmental anomalies of bio-physical conditions on the Newfoundland shelf that likely influence capelin growth. CALFIN is Calanus finmarchicus abundance; PSEUDOCAL is Pseudocalanus spp abundance; TEMP is Temperature composite; PEAKTIMESB is Peak Timing of Spring Bloom; CHLA is Chlorophyll-a Concentration; DURSB is Duration of Spring Bloom, MAGSB is Magnitude of Spring Bloom



High
Pseudocalanus
spp.
Low *Calanus*
finmarchicus

Low
Pseudocalanus
spp.
High *Calanus*
finmarchicus

Cool,
Spring Bloom Dynamics:
Late peak, low magnitude, long duration
High chlorophyll-a

Warm,
Spring Bloom Dynamics:
Early peak, high magnitude, short duration
Low chlorophyll-a

Figure 2.4: Biplot of PC1 and PC3 from the Principal Component Analysis on environmental anomalies of bio-physical conditions on the Newfoundland shelf that likely influence capelin growth. CALFIN is Calanus finmarchicus abundance; PSEUDOCAL is Pseudocalanus spp abundance; TEMP is Temperature composite; PEAKTIMESB is Peak Timing of Spring Bloom; CHLA is Chlorophyll-a Concentration; DURSB is Duration of Spring Bloom, MAGSB is Magnitude of Spring Bloom

General Conclusions

In Chapter 1, my findings illustrated that spawn checks in capelin otoliths do not appear to be a reliable method of identifying previous spawning experience. This may be because spawn checks in other species are typically characterized by reduced growth as a result of energy being directed from somatic growth into reproduction (e.g., spawning migration, gonadal development; Rollefsen 1933, Nordeng 1961, Pannella 1971). My study, however, revealed that females that had residual oocytes in the gonads grew similarly to individuals that did not have residual oocytes present in the year of capture. Similar growth between individuals with and without residual oocytes may have been due to the combination of different maturity levels in the individuals with no residual oocytes observed. Additionally, the lack of difference in growth patterns may be due to increased growth prior to or after spawning, as observed in other fish (Ali and Wootton 1999, Trippel et al. 2014). Accelerated growth in these periods could not be isolated and measured in the year of capture, owing to the irregular growth and banding patterns associated with the spawning check. My findings also revealed that spawn checks and other growth anomalies in the otolith may inhibit our ability to accurately determine the age of individuals. For instance, growth patterns associated with spawn check type II, were initially interpreted as one long winter growing season (translucent band), with regions of high growth (narrow opaque bands), which resulted in age being estimated as one year younger. Growth checks have presented difficulties in otolith-based age determination in other species (Hawkins et al. 2004, Pearson and Shaw 2004, Melvin et al. 2010).

My results suggest that studies that rely on ageing capelin using the otolith may have skewed results, due to the presence of growth checks. Studies that use otolith-based techniques to determine the age of capelin should record the patterns described here as a ‘spawn check’, and classify those otoliths as low confidence, and consider discarding. Determining post-spawning survival from otoliths is not reliable, thus should not be the main indicator for studies that quantify post-spawning survival in capelin. Other indirect methods of identifying post-spawning survivors (e.g. macroscopic visual assessment, Flynn et al. 2001) underestimate post-spawning survival, in comparison to histological examination. Thus, a combination of macroscopic and histological examination of gonads should be used to determine the proportion of capelin that have spawned previously and survived. Additionally, samples that are preserved in 10% buffered formalin should be used, instead of freezing should be used, as freezing hindered our ability to confidently identify other histological indicators of recovering spawners (Flynn et al. 2001) and immature capelin (Flynn 1996). Future research may be able to more definitively show whether or not the spawning check described here is associated with spawning by sampling earlier in the year, shortly after the spawning season. Samples in this study were caught in November and December, giving individuals more time to recover after spawning, which reduced our chance of observing indicators of spawning (Flynn et al. 2001). This study highlights the need to validate spawn checks in otoliths using histological methods.

In Chapter 2, my findings illustrated that capelin growth in all age classes, varied among years of the study (2008 - 2016). Higher growth years were generally characterized by warmer years, with an earlier and high magnitude spring bloom across most age classes. Prey abundance for age 0+ capelin (i.e. *Pseudocalanus* spp.) and adults (i.e. *Calanus finmarchicus*), however, varied among years of higher growth, suggesting that temperature and spring bloom dynamics may be more critical in higher growth than food abundance across all age classes. Lower growth, on the other hand, was associated with cooler conditions and lower prey abundance (especially 2007 and 2009), along with later timing of peak bloom, low magnitude and short to average duration. This suggests that cooler years that are paired with lower prey abundance results in lower growth across age classes.

Our findings suggest that higher early growth may lead to earlier sexual maturity (Stearns 1992, Trippel 1995); this is predicted by life history theory, whereby sexual maturation is dependent on early growth and attaining a certain body size (Stearns 1992). Spawning at an earlier age presents several advantages for capelin. For instance, mature females with previous spawning experience have higher fecundity (750 – 2,600 eggs) relative to recruit spawners of the same age (Winters 1971). Interestingly, male and female capelin showed similar inter-annual growth variation at age 1+ but trends diverged at age 2+, as observed in a previous study (Winters 1982). This may reflect sex-based differences in parity; females spawn multiple times throughout their lifespan (i.e. iteroparous), while males spawn with multiple females in one year and then die (i.e. semelparous; Shackell et al. 1994, Burton and Flynn 1998, Huse 1998, Flynn et al. 2001). Based on the assumption of slower growth in a year of spawning (Winters 1971, Ware 1980, 1982, Kozlowski 1996), inter-annual variation in growth may be masked due the presence of post-spawning survivors for females, which was not considered in the model, but not necessarily for males. Overall, growth patterns suggest that adult capelin will experience accelerated growth as a result of warming temperature as observed in recent years. Increased body size, as a result of accelerated growth, leads increased fecundity in capelin (Penton and Davoren 2013), which may ultimately initiate recovery of the capelin population on the Newfoundland shelf. However, the projected recovery may be limited by low recruitment of larval capelin into the spawning population, resulting from a mismatch between larval emergence and peak larval prey abundance (Mullowney et al. 2016).

Future research on otolith-based growth should further explore the relationship between previous spawning experience and focus on identifying previous spawning experience from otoliths. Previous research on capelin growth in Newfoundland was focused on the period before the population collapse (Frank and Leggett 1982b) and larval capelin (Mullowney et al. 2016, Murphy et al. 2018), with few studies examining adult capelin growth after the regime shift. However, predicting growth is a key factor to consider in a stock assessment. My research provides insight into the relationship between environmental factors and capelin growth. Specifically, which environmental conditions seem to most heavily influence high growth (e.g., warmer temperatures with earlier and high magnitude spring bloom) and low growth (e.g., cooler temperatures, lower prey abundance, later timing of peak spring bloom with low magnitude and shorter duration) across different age classes.

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