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Growth and Reproduction of Atlantic Chub Mackerel (*Scomber colias*) in the Northwest Atlantic

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GROWTH AND REPRODUCTION OF ATLANTIC CHUB MACKEREL

(*SCOMBER COLIAS*) IN THE NORTHWEST ATLANTIC

by

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ABSTRACT

Recent efforts to manage Atlantic Chub Mackerel (*Scomber colias*) in the northwest Atlantic have necessitated the description of the stocks life-history characteristics. The purpose of this study was to address the absence of regional information on growth and reproduction. Growth models were fit in a Bayesian framework. The length-at-age relationship was described using four non-linear candidate growth models, which were fit to total length (TL, cm) and age estimates (y). Age estimates were derived from whole otoliths for adults ($n = 422$) and ages of one month were assigned to larval fish ($n = 60$). The three-parameter VBGF was selected as the best candidate model using Deviance Information Criterion ($L_\infty = 33.56$ cm TL, $k = 1.75$ y^{-1}, $t_0 = 0.07$) to describe the weight-at-length relationship ($a = 0.0258$, $b = 2.72$). Sex and maturity were evaluated using histological techniques. A two-parameter logistic function was fit to length measurements (cm) and maturity estimates ($n = 151$) to describe length-specific maturity for females ($r = 0.38$ cm^{-1}, $L_{50} = 27.39$ cm TL). Age-at-50% maturity was estimated as 2.16 (y) by back calculation. Spawning season was estimated to occur during the months of January to April, using histological indicators and evidence of spawning from analysis of historical data on larval fish collections and commercial catch. These results can be used to inform the effective management of the Atlantic Chub Mackerel stock in the northwest Atlantic.

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CHAPTER I – AGE AND GROWTH OF ATLANTIC CHUB MACKEREL IN THE

NORTHWEST ATLANTIC

1.1 Introduction

The absence of biological information on Atlantic Chub Mackerel (*Scomber colias*) in the coastal Mid-Atlantic and New England region of the United States and its recent designation as a "forage fish" by the Mid-Atlantic Fishery Management Council (MAFMC) has had implications for the stock's management. Forage fishes are defined by the MAFMC Ecosystem Subcommittee as small, low trophic level fish that exhibit schooling behavior, and have high variation in recruitment. An increased interest in developing robust approaches for managing forage fish stocks has occurred because of their perceived critical ecological role (Essington et al. 2015). In December 2014, the MAFMC initiated the Unmanaged Forage Omnibus Amendment to protect forage fish stocks from directed harvest until "adequate scientific information is available to promote ecosystem sustainability" (MAFMC 2015). Information on individual growth is essential for the assessment of exploited stocks (Ballagh et al. 2011), and will be necessary for developing an Atlantic Chub Mackerel Fishery Management Plan in the northwest Atlantic.

In this study I address gaps in the description of the life-history characteristics of Atlantic Chub Mackerel in the northwest Atlantic, specifically the length-at-age and weight-at-length relationships. Describing the length-at-age relationship allows ages to be predicted from length measurements and thus length-structured catch information can be used in an age-structured context. Age-structured models permit reconstruction of population dynamics of exploited fish stocks without requiring information on fishing

effort, catchability, or gear selectivity (Francis 2016) and are the primary assessment method used in fisheries science (Cope and Punt 2007). The weight-at-length relationship is useful for transforming observed length measurements into weight in order to calculate estimated biomass, and for comparing the relative condition of the fish (Froese 2006).

The demographic characteristics of Atlantic Chub Mackerel (*Scomber colias*) have been described from populations from the northeast Atlantic (Martins and Gordo 1984; Lorenzo et al. 1995; Martins 1996; Lorenzo and Pajuelo 1996; Carvalho et al. 2002; Vasconcelos et al. 2011; Velasco et al. 2011; Alba Jurado-Ruzafa 2017), Mediterranean Sea (Perrotta et al. 2005; Bayhan 2007; Velasco et al. 2011), and southwest Atlantic (Perrotta et al. 2005), but have not been described for the stock in the northwest Atlantic. Considerable variation exists in length-at-age (Table 1.1) and weight-at-length (Table 1.2) model parameter estimates of Atlantic Chub Mackerel growth among geographic locations.

Uncertainty in growth dynamics can be attributed to several potential sources including selectivity of sampling gear, sample size, geographic distribution, and temporal variability among studies (Tables 1.1 and 1.2). Differences in sex ratios are also potential causes, but unlikely for this species. Most studies reported no difference in mean length-at-age between sexes (Lorenzo and Pajuelo 1996; Kiparissis et al. 2000; Perrotta et al. 2005; Bayhan 2007; Vasconcelos et al. 2011; Velasco et al. 2011); however, slight variations in growth between sexes were reported for Atlantic Chub Mackerel from the Adriatic Sea (Čikeš Keč and Zorica 2012). The majority of studies describing the weight-at-length relationship do not report significant differences between sexes (Lorenzo and Pajuelo 1996; Kiparissis et al. 2000; Santos et al. 2002; Bayhan 2007; Vasconcelos et al.

2011; Velasco et al. 2011). Alba Jurado-Ruzafa (2017) reported statistically significant differences between sexes for the weight-at-length relationship in Atlantic Chub Mackerel caught off the coast of northwest Africa.

Ageing error and model misspecification could also contribute to variation in descriptions of the length-at-age relationship. The use of inaccurate ages can result in erroneous estimates of growth, recruitment, and mortality, leading to serious consequences for fisheries management (Beamish and Mcfarlane 1983). Large discrepancies between age readers from different countries revealed biased age estimates of Baltic Cod (ICES 2006). Reeves (2003) used the case study of Eastern Baltic Cod for a simulation study to quantify the effect of age-reading errors on fisheries management. Fishing mortality (F) and Spawning Stock Biomass (SSB) were estimated under four scenarios where errors occurred from over-ageing, under-ageing, noise only error, and no error (control). A general tendency for age-reading errors to lead to lower estimates of SSB was reported. Regardless of the direction of the bias in ageing error, consistently lower estimates of fishing mortality were estimated; however, over-ageing resulted in the lowest estimates of F (Reeves 2003).

Accurate ages are necessary to define life-history traits applicable to management, including rates of growth and age-at-maturity (Beamish and Mcfarlane 1983). Otoliths are aragonitic structures found in the inner ear of teleost fishes (Campana and Thorrold 2001) and are the most commonly used structure for estimating age (Campana 2001). Otoliths grow continuously throughout ontogeny and are not metabolically active, providing an ideal structure for interpreting growth (Campana 2001). Annuli can be

counted to estimate age of the individual by analyzing the whole otolith or a cross section of the otolith (Campana and Thorrold 2001).

The purpose of the work presented in this chapter is to describe the age and growth characteristics of Atlantic Chub Mackerel from the coastal Mid-Atlantic and New England region of the United States. Age estimates from both whole and sectioned otoliths were evaluated to determine which method results in the greatest precision of age determination. Otolith-derived age estimates were then used to evaluate the length-at-age relationship using a suite of non-linear growth models. The weight-at-length relationship was modeled using a power function. Median growth parameter estimates of Atlantic Chub Mackerel from the northwest Atlantic were then compared with mean parameter estimates reported from other regions in the Atlantic and Mediterranean.

1.2 Methods

Biological information was collected from fish provided by a number of sources to describe the growth characteristics of Atlantic Chub Mackerel in the northwest Atlantic. Atlantic Chub Mackerel were obtained from two commercial fishing companies, Lund's Fisheries Inc. and Seafreeze Limited, in July 2016 ($n = 61$), August 2016 ($n = 145$), September 2016 ($n = 112$), July 2017 ($n = 30$), June 2017 ($n = 75$), and October 2017 ($n = 21$). Additional fish were collected in September 2016 by the National Marine Fisheries Service (NMFS) Northeast Groundfish Survey ($n = 16$) in the northwest Atlantic region. All samples were frozen at time of collection. Measurements for total length (TL, mm), fork length (FL, mm), and wet body weight (g) were recorded, and paired sagittal otoliths were extracted from each fish by making a transverse cut to expose the brain cavity. Otoliths were rinsed to remove the membranous tissue and dried.

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To extend the range of size classes, body length (BL, mm) from smaller individuals ($n =$ 60) reported from SEAMAP plankton surveys in the Northern Gulf of Mexico during the month of January were included in the analysis.

The precision of the age estimates between readers ($n = 2$) was evaluated using percent agreement (PA) for each structure (sectioned vs. whole). Pairs of otoliths from 50 randomly selected fish collected in August 2016 were analyzed for comparison of ageing methodology. This subsample contained samples collected from individuals of various lengths, ranging in size from 264 mm TL to 384 mm TL. Left otoliths were embedded in molds using Epoxicure resin and left to set for 24 hours. A transverse section, approximately 0.3 mm thick, was taken at the core of the otolith using a Buehler IsoMet Slow Speed Saw. The sections were mounted on slides with a coat of Flo-Texx. The right otolith from each pair was left whole and fixed in trays using Flow-Texx as a mounting medium. Age estimates for whole and sectioned otoliths were assigned by counting fully formed annuli at 2X to 5X magnification. Sectioned otoliths were read under transmitted light and whole otoliths under reflected light. PA between readers was calculated for both whole and sectioned otoliths. The structure with the greatest agreement between readers was used for growth characterization.

A stratified sampling plan was used to subsample otoliths from all size classes and months collected for this analysis. A total of 460 whole otoliths were evaluated by two independent readers with no prior knowledge of length or information other than catch date. Otoliths that were deformed or crystalized were eliminated from the analysis without assigning age estimates. PA and CV were reported for between-reader age estimates. After initial interpretation of the annuli was made, readers reevaluated otoliths

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where discrepancies occurred between assigned age estimates. Otoliths where an agreement could not be reached were omitted from analysis. Otoliths were read blind a second time by the first reader to determine within-reader agreement, in order to further evaluate the precision of age estimates. Bowker's test for symmetry was used to evaluate bias of age estimates. All ages were adjusted by date of capture, assuming a hatch date of January 1st (ICES 2015). Ages of one month were assigned to fish captured in January ranging in length of 2.1 to 7.7 mm BL, based on a reported average size at hatching of 3.1 mm (Berrien, 1978).

The length-at-age relationship of Atlantic Chub Mackerel was described using four non-linear models including the two-parameter von Bertalanffy Growth Function (VBGF), three-parameter VBGF, Gompertz growth function, and logistic growth function. These models vary in their structure and are commonly used to describe the non-linear dynamics of growth (Pardo et al. 2013).

The two-parameter VBGF is:

$$L_t = L_\infty(1 - e^{-kt}),$$

where L_t is the TL (cm) at a given age t (y), L_∞ is the average maximum TL (cm), and k is the Brody growth coefficient (y^{-1}).

The three-parameter VBGF (Bertalanffy 1938) is:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

where t_0 is a theoretical age-at-length zero (y).

The Gompertz (1825) growth model is:

$$L_t = L_\infty\, a^{r^t},$$

where a and r (y^{-1}) are parameters that control the structure of the growth curve.

The three-parameter logistic length-at-age model (Ricker 1975) is:

$$L_t = \frac{L_\infty}{1 + a(e^{-bt})},$$

where the parameters a (unitless) and b (y^{-1}) determine the shape of the curve.

The weight-at-length relationship was modeled using a power function:

$$W = aL^b,$$

where W is wet weight (g), L is TL (cm), a is a scaling coefficient, and b is a shape parameter describing change in length relative to weight.

Non-linear growth models describing the length-at-age (Figure 1.1) and weight-at-length relationships (Figure 1.2) were fit using a Bayesian framework. Model fitting and statistical analyses were conducted in R statistical software v. 3.2.3. (R Core Team 2015) using the RJAGS package (Plummer 2016). Age estimates and length measurements from 422 adult individuals, and lengths of 60 larvae assigned ages of one month, were used to describe the length-at-age relationship. Parameter estimation was performed using three Markov chain Monte Carlo (MCMC) chains of 100,000 iterations each and a thinning interval of 10. Weight and length measurements from 1,336 individuals were used as observed data for describing the weight-at-length relationship. The model was run with three Markov chain Monte Carlo (MCMC) chains of 1,000,000 iterations each and a thinning interval of 3000. Convergence was evaluated using the Gelman-Rubin diagnostic and trace plots to visually assess whether the models converged by observing the mixing of chains. The models were checked for autocorrelation. The Bayesian p-value of the mean and standard deviation was used to evaluate model fit and ability to capture the variance of the data. The Bayesian p-value is

the proportion of times that the discrepancy measure for the simulated data sets is more extreme than that for the actual data. A value close to 0.50 exemplifies a good fit, as it indicates that 50% of the predicted values are more extreme than the observed data and 50% are less.

Informative priors were constructed for models using the published mean parameter estimates reported in previous studies (Table 1.1) that described the length-at-age relationship of Atlantic Chub Mackerel using the three-parameter VBGF. A normal distribution was used to describe the distribution of L_∞, k, and t_0. A combination of informative and uninformative parameters was used for the two-parameter VBGF, Gompertz growth function, and logistic growth function. Although parameter estimates from these models were not used in previous studies, L_∞ is common to all. The same informed prior used for L_∞ was used for all models, and uninformative priors with either a normal or lognormal distribution were used for the remaining parameters of each model. The normal distribution of each model was used for the likelihood. Informative priors were used to describe the weight-at-length relationship. Growth models served as the process model, which was combined with data and parameter models to form the joint posteriors for the two-parameter VBGF:

$$(L_\infty, k, \sigma_p \mid L_i) \propto Normal\,(L_i \mid f(L_\infty, k, \sigma_p)),$$

$$Normal \sim (L_\infty \mid 48.21,\ 0.01),$$

$$Normal \sim (k \mid 0,\ 1/\,(100^2)),$$

$$Uniform \sim (\sigma_p \mid 0,\ 100),$$

the three-parameter VBGF:

$$((L_\infty, k, t_0, \boldsymbol{\sigma}_p \mid L_i) \propto \text{Normal }(L_i \mid f(L_\infty, k, t_0, \boldsymbol{\sigma}_p),$$

$$Normal \sim (L_\infty \mid 48.21,\ 0.01),$$

$$Normal \sim (k \mid 0.21,\ 0.01),$$

$$Normal \sim (t_0 \mid -1.47,\ 0.01),$$

$$Uniform \sim (\boldsymbol{\sigma}_p \mid 0,\ 100),$$

the Gompertz growth model:

$$(L_\infty, a, r, \boldsymbol{\sigma}_p \mid L_i) \propto \text{Normal }(L_i \mid f(L_\infty, a, r, \boldsymbol{\sigma}_p)),$$

$$Normal \sim (L_\infty \mid 48.21,\ 0.01),$$

$$Lognormal \sim (a \mid 0.001,\ 1/(100^2)),$$

$$Lognormal \sim (r \mid 0.001,\ 1/(100^2)),$$

$$Uniform \sim (\boldsymbol{\sigma}_p \mid 0,\ 100),$$

the Ricker growth model:

$$(L_\infty, a, b, \boldsymbol{\sigma}_p \mid L_i) \propto \text{Normal }(L_i \mid f(L_\infty, a, b, \boldsymbol{\sigma}_p)),$$

$$Normal \sim (L_\infty \mid 48.21,\ 0.01),$$

$$Normal \sim (a \mid 0,\ 1/(100^2)),$$

$$Normal \sim (b \mid 0,\ 1/(100^2)),$$

$$Uniform \sim (\boldsymbol{\sigma}_p \mid 0,\ 100),$$

and the power function:

$$(a, b, \sigma_p \mid L_i) \propto \text{Normal} (L_i \mid f(a, b, \sigma_p)),$$

$$\text{Normal} \sim (a \mid 0.0038, 1/ (100^2)),$$

$$\text{Normal} \sim (b \mid 3.34, 1/ (100^2)),$$

$$\text{Uniform} \sim (\sigma_p \mid 0, 100).$$

Deviance Information Criterion (DIC) was used to evaluate each non-linear growth model for fit and model complexity. Model complexity is accounted for by penalizing the score based on the number of effective parameters. The model with the lowest DIC value was considered to have the greatest predictive capability and selected as the "best" candidate model (Oravecz and Muth 2017). The 95% (CI) credible intervals were calculated for each of the median parameter estimates of the three-parameter VBGF, which has been used to describe length-at-age in previous studies, and the median parameter estimates of the power function used to describe weight-at-length relationship. Mean growth parameter estimates reported in the existing literature were then compared to the 95% credible intervals of the median parameter estimates of this study to investigate possible significant differences in growth among regions. Differences in predicted growth were also compared by predicting lengths at each age using reported parameter estimates. Predicted lengths were then averaged by region and a curve was fit to the predicted data.

1.3 Results

Whole otoliths were determined to be the most precise method for age determination of Atlantic Chub Mackerel. Age estimates of whole otoliths yielded 72%

PA and sectioned otoliths 64% PA. A subsample of 460 otoliths were selected and

processed whole. Otoliths that were deformed, crystalized, or extremely cloudy were

eliminated without assigning an age estimate ($n = 21$). Between-reader PA was 66% with

a total CV of 19%. Within-reader estimates had a 56% PA and a CV of 24%. After the

readers analyzed each otolith independently, otoliths with disagreements were

reevaluated in a collaborative manner. A final agreement was reached for 422 otoliths and

the remaining 17 otoliths which an agreement could not be reached were omitted.

Assigned age estimates ranged from zero to seven years, from individuals 17.7 to 39.7

cm TL. There was no evidence of systematic disagreement between readers (Bowker's

test of symmetry $\chi^2 = 23.51$, d.f. = 16, $P = 0.10$), indicating there was no significant bias.

Of the four non-linear candidate models used to describe the length-at-age

relationship of Atlantic Chub Mackerel in the northwest Atlantic, the three-parameter

VBGF had the greatest support with the smallest DIC value (Table 1.3). The Gompertz

function had the next smallest DIC value followed by the two-parameter VBGF, and

finally the logistic function. The resulting median parameter estimates of the three-

parameter VBGF were 33.56 cm TL [95% CI = 33.26 to 33.89], 1.75 (y^{-1}) [95% CI =

1.59 to 1.90], and 0.07 (y) [95% CI = 0.06 to 0.08] for L_∞, k, and t_o respectively (Table

1.3). For the Gompertz function the median parameter estimates were 32.71 cm TL [95%

CI = 32.46 to 32.97], 0.002 (y^{-1}) [95% CI = 0.003 to 0.014], and 0.008 (y^{-1}) [95% CI =

0.00009 to 0.00861] for L_∞, a, and r respectively (Table 1.3). For the two-parameter

VBGF the median parameter estimates were 34.15 cm TL [95% CI = 33.79 to 34.51], and

1.35 (y^{-1}) [95% CI = 1.26 to 1.44] for L_∞, and k respectively (Table 1.3). For the Logistic

function the median parameter estimates were 32.66 [95% CI = 32.40 to 32.92] cm TL,

69.54 [95% CI = 41.24 to 134.60], and 8.57 (y^{-1}) [95% CI = 7.58 to 9.77] for L_∞, a, and b respectively (Table 1.3). All models indicate that Atlantic Chub Mackerel exhibit rapid growth from age zero to age one and reach asymptotic length around age two (Figure 1.3). For comparison with other studies the three-parameter VBGF was also fit without the inclusion of larval data resulting in parameter estimates of 37.13 cm TL [95% CI = 35.79 to 39.76], 0.41 (y^{-1}) [95% CI = 0.26 to 0.56], and -2.44 (y) [95% CI -3.81 to -1.64] for L_∞, k, and t_o respectively (Table 1.3).

All four non-linear candidate models used to describe the length-at-age relationship converged well, as indicated by Gelman values of one for all parameter values in each model and adequate mixing of chains trace plots. Minimal autocorrelation was observed after thinning by ten. Despite small differences among models, all fit the mean well as indicated by a 0.51 Bayesian *p*-value of the mean for all non-linear candidate models. In addition, the Bayesian *p*-value of the standard deviation was 0.50 for all non-linear candidate models, indicating that predictions will have more extreme variances 50% of the time.

The mean parameter estimates reported from ten previous studies that described the length-at-age relationship of Atlantic Chub Mackerel, all fell outside the 95% CI of this study when larval data was used to fit the three-parameter VBGF, indicating significant differences in growth (Table 1.1). However, when larval data was not included estimates of k (y^{-1}) in four other studies fell within the 95% CI. The estimate of L_∞ from one study in the Mediterranean (Perrotta et al. 2005) and estimate of t_o (y) from one study in the northeast Atlantic (Martins 1996) fell within the 95% CI of the median parameter estimates reported in this study. This study had the highest k (y^{-1}) and the

lowest L_∞ (cm) parameter estimates when compared to published parameter estimates.

Predicted length-at-age zero was much smaller in the northwest Atlantic than in other

regions when larval data was included and much larger when it was not (Table 1.4).

When lengths were predicted using parameter estimates from the three-parameter VBGF

fit with the inclusion of larval data, predicted lengths were greatest in the northwest

Atlantic region at ages one, two, and three (Table 1.4). The rate of growth in the

northwest Atlantic slows down after age two and the predicted lengths become more

similar at ages three and four, after which predicted lengths in other regions greatly

exceed those in the northwest Atlantic. When lengths were predicted using parameter

estimates from models fit without larval data the predictions were more similar to those

in other regions, particularly the Mediterranean. Regions where individuals were captured

at greater lengths, also had older fish, and did not reach asymptotic growth as quickly

(Figure 1.4).

The median parameter estimates for the weight-at-length relationship were,

0.0258 [95% CI = 0.0203 to 0.0328] and 2.72 [95% CI = 2.65 to 2.79] for a and b

respectively (Figure 1.5). The model passed all checks for convergence, autocorrelation,

and fit. Gelman diagnostics and trace plots indicated the model converged well. The

model fit the data extremly well with a 0.50 Bayesian p-value for both the mean and

standard deviation.

All mean parameter estimates from previous studies used to describe the weight-

at-length relationship were significantly different, falling outside the 95% credible

intervals of the median parameter estimates from this study (Table 1.2). The b parameter

estimate for this study is smaller than other studies.

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1.4 Discussion

Recent efforts by the MAFMC to manage Atlantic Chub Mackerel in the northwest Atlantic have necessitated the description of the stock's life-history characteristics. In this study I applied a Bayesian statistical framework to estimate the parameters of growth models used to describe the length-at-age and weight-at-length relationships. The results of this study address a major gap in the life-history characteristics of this stock by providing the first description of growth for *S. colias* in the northwest Atlantic.

An established protocol has not been developed for ageing Atlantic Chub Mackerel in the northwest Atlantic, requiring an evaluation of methodology. Precision of the age estimates, the reproducibility of repeated measurements on a given structure (Campana 2001), was the main criterion in evaluating the use of whole or sectioned otoliths for age estimation. Whole otoliths were determined to be the best practice for assigning age estimates due to higher PA when compared with the use of sectioned otoliths. Continuation of the use of whole otoliths, which has been the primary technique applied in other studies on Atlantic Chub Mackerel growth, provides the additional benefit of maintaining consistency in methodology among studies. In addition, the use of whole otoliths is more time and cost efficient compared to processing sectioned otoliths for age determination.

PA and CV provide a measure of the precision of age assignment (Beamish and Mcfarlane 1983). PA between readers was 64%, which is comparable to the PA for all readers reported in the 2015 ICES report of the Workshop on Age Reading of Cub Mackerel (WKARCM) of 57%. The total CV of age estimates in this study was 20%.

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This is higher than the suggested reference point of a 5% CV or lower for fishes that exhibit moderate longevity and ease of otolith readability, based on a review of 117 age and growth studies by Campana and Thorrold (2001). The CV in this study is much higher than the suggested level, but is lower than the 30% CV reported from the 2015 WKARCM (ICES 2015). Within reader agreement and CV was only calculated for reader one who read all otoliths twice. Precision was much lower for within reader than between reader agreement. This was likely due to the lack of experience of reader one. Readers in this study experienced difficulty in interpreting otoliths due to false marks or "checks", which has also been reported in other ageing studies on Atlantic Chub Mackerel (Vasconcelos et al. 2011; ICES 2015; Alba Jurado-Ruzafa 2017) and is likely a cause for inconsistent age estimates.

Validation of ages requires an evaluation of the accuracy for all reported age estimates (Beamish and Mcfarlane 1983). Marginal increment analysis is a widely used method of validation where distance between the annulus closest to the edge of the next most recently deposited annulus are measured, to validate the periodicity of growth increment formation (Campana 2001). I was unable to collect samples from enough months in this study to conduct marginal increment analysis, which would require additional sampling in the months of December to April. The absence of commercial and fishery independent catch during this time frame is responsible for the gap in collection data from the northwest Atlantic. Sampling efforts directed in the southwest Atlantic and northern Gulf of Mexico may provide alternative winter and spring collection data that could augment the missing data from the northwest fisheries. Tag recapture studies are another method recommended for validating age estimates, because it allows the true age

of the fish to be determined (Campana 2001). This type of study could be applied in the future, but would require more extensive resources to implement than a marginal increment analysis.

A small number of studies in other regions have validated ageing techniques for Atlantic Chub Mackerel. Vasconcelos et al. (2011) confirmed that one translucent and one opaque band were laid down each year for Atlantic Chub Mackerel collected off Madeira Island and used marginal increment analysis to validate ages zero to four years. Several studies in other regions have used back-calculation models to estimate the past fish length and estimate growth parameters, however this approach is not considered a true validation method (Lorenzo et al. 1995). Until ages can be validated in the northwest Atlantic estimates of growth must be used to inform management decisions conservatively.

The three-parameter VBGF was selected as the "best" candidate model in this work and should be used to describe the length-at-age relationship in future studies. Variations of the VBGF model and other non-linear models were evaluated using objective criteria to reduce errors of model misspecification. The model with the lowest Deviance Information Criterion was considered the best candidate model (Anderson et al. 2000). By selecting for the best model, model misspecification is reduced (Burnham and Anderson 2004). The multi model approach has been used to evaluate candidate length-at-age models of many fish species (Cope and Punt 2007; Thorson and Simpfendorfer 2009; Pardo et al. 2013; Dippold et al. 2016). Previous studies on Atlantic Chub Mackerel have primarily used the three-parameter von Bertalanffy growth function (VBGF) to model the length-at-age relationship (Carvalho et al. 2002; Velasco et al.

2011). Continuing this practice will maintain consistency in modeling methods used to describe the growth of *S. colias*.

Of note, models fit within a Bayesian framework, thereby differing from previous studies that used non-linear regression; however, both methods yield similar results. A noticeable difference between Bayesian and frequentist methods is that the Bayesian approach explicitly incorporates knowledge from previous studies through the use of priors. Priors can help inform the parameter estimation, however, they should have little influence over the final estimates if the data are strong enough. Bayesian statistics provides a framework to model the scientific process and continuously update information as we develop a better understanding of a specie's life-history characteristics, by applying the posteriors to future studies (Ellison 1996). Another advantage of Bayesian statistical methods is in the interpretation of results (Clark 2005). Bayesian methods provide a probability distribution of parameter estimate values where typically the median and 95% credible interval are reported. A credible interval is interpreted as a range of parameter estimates within which 95% of possible values fall. This is a more intuitive interpretation of the results than the common frequentist approach of reporting mean and 95% confidence interval, where 95% of the time, the true parameter value will fall within that interval. The straightforward interpretation of parameter estimates from the Bayesian models is useful when explaining results to managers and stakeholders and provides a framework for informing for future studies.

The description of the length-at-age relationship in this study suggests that individuals in the northwest Atlantic grow faster and reach a smaller average length than in other regions. Spatial and temporal differences among regions exhibit variability in

temperature and productivity, which could be responsible for differences in growth. Although temperature has been reported to effect growth, Perrotta et al., (2005) suggests that quality and availability of food has a greater effect on growth of Atlantic Chub Mackerel. Selectivity likely contributed to differences in reported growth estimates as well. There are a limited number of commercial vessels in the United States that are capable of capturing Atlantic Chub Mackerel. It possible that larger fish are present in this region, but are able to swim at speeds that allow them to evade capture. Length and age ranges varied considerably between studies. Studies with older reported ages, also estimated higher values for L_{∞}. Sampling bias from gear selectivity may result in the underrepresentation of smaller fish reported in some studies.

This study had a much narrower range of sizes of adult fish. However, the inclusion of smaller individuals ranging from 2.1 to 7.7 mm BL captured in ichthyoplankton tows provided a better representation of size classes in this study. Without the inclusion of smaller individuals the three-parameter VBGF predicted length-at-age zero to be 23.48 cm TL. Berrien (1978) reported the size at hatching to average 0.31 cm SL, making the predicted length-at-age zero unrealistically large. Although the inclusion of larval data provides a more biologically realistic description of growth in the northwest Atlantic, other studies on Atlantic Chub Mackerel have not included larval data. In order to allow for a comparison of reported growth parameter estimates among regions I described growth both with the inclusion of larval data and without. Parameter estimates in this study were much similar to those reported in other regions, when only lengths and ages from adult individuals were used to fit the model.

The weight-at-length relationship described in this study differed from previous studies, which showed considerable variation among regions. The scaling exponent *b* estimated in this work is smaller than reported estimates in all previous studies. This suggests that weight does not increase as quickly as a function of length in the northwest Atlantic, compared to other regions where growth dynamics of Atlantic Chub Mackerel have been studied. Given the range of mean parameter estimates, determining the causes of variation (e.g. geographic differences in growth or sampling practices) is challenging.

Differences in growth are likely due to variations in environmental conditions, as a result of spatial and temporal variability. Fish were collected during different months and years among studies, which are likely to vary in temperature and productivity, both factors which effect growth and condition of the fish (Martin 1949; Houde 1974; Powell et al. 2004; Martins 2007). Lower *b* values have been reported during the colder parts of the year, which have implications for understanding growth dynamics studied during different seasons (Čikeš Keč and Zorica 2012). This is supported by reported seasonal fluctuations found in the relative condition factor off the Canary Islands (Lorenzo and Pajuelo 1996). High values were recorded from March to September, and low values from October to February.

This research provides a description of Atlantic Chub Mackerel growth in the northwest Atlantic, including the length-at-age and weight-at-length relationships. Parameter estimates will be used to predict ages from fish length and describe age-at-maturity in Chapter II. The information reported in this study will greatly improve understanding of Atlantic Chub Mackerel life history and directly inform the future management of the northwest Atlantic stock.

Table 1.1

Previous growth studies length-at-age parameter estimates

Study	Region	Months	Years	Gear	Ages (y)	TL (cm)	n	k (y⁻¹)	L_∞ (cm)	t_0 (y)
This study with larval data	NW Atlantic	June to August, October	2016, 2017	Trawl	0 to 7	17.7 to 39.7	422	1.75 (95% CI: 1.59 to 1.90)	33.56 (95% CI: 33.26 to 33.89)	0.07 (95% CI: 0.06 to 0.08)
	Gulf of Mexico	January		Plankton tows	0	0.21 to 0.77	60			
This study without larval data	NW Atlantic	June to August, October	2016, 2017	Trawl	0 to 7	17.7 to 39.7	422	0.41 (95% CI: 0.26 to 0.56)	37.13 (95% CI: 35.79 to 39.76)	-2.44 (95% CI: -3.81 to -1.64)
Perrotta et al., 2005	SW Atlantic	December	2002	Commercial catch	0 to 10	16.3 to 43.5	392	0.32	44.23	-1.39
Alba Jurado-Ruzafa, 2017	NE Atlantic	Monthly	2005 to 2011	Trawl	0 to 7	12.4 to 49.0	163	0.25	48.40	-1.51
Vasconcelos et al., 2011	NE Atlantic	October to December (monthly)	2002, 2003	Purse-seine	0 to 4	17.4 to 41.7	2,191	0.25	50.08	-1.34
(Carvalho et al. 2002)	NE Atlantic	Febuary to Septembe, November	1996 to 2002	Purse-seine, hook and line, dipnets, liftnets	0 to 13	9.6 to 56.6	349	0.20	57.52	-1.09
Martins, 1996	NE Atlantic	January to December (monthly)	1995	Purse-seine, hook and line, trawl	0 to 12	16 to 54	883	0.10	58.52	-3.68

Table 1.1 (continued)

Study	Region	Season	Years	Gear	Age range	Length range	n	K	L_∞	t_0
Lorenzo et al., 1995	NE Atlantic	March to June	1988, 1989	Purse-seine	0 to 7	13.7 to 42.1	470	0.19	52.4	-1.61
Velasco et al., 2011	NE Atlantic	October to September	2003, 2004	Purse-seine, hook and line, trawl	0 to 7	16.4 to 43.0	121	0.27	43.00	-1.10
Velasco et al., 2011	Mediterranean	October to September	2003, 2004	Purse-seine, hook and line, trawl	0 to 6	17.2 to 40.0	98	0.37	40.00	-0.10
Perrotta et al., 2005	Mediterranean	April to July, December	1992, 1997	Commercial catch	0 to 8	11 to 39	158	0.30	39.75	-1.41

Mean parameter estimates from the three-parameter VBGF reported in previous studies compared to the 95% Credible Intervals of median parameter estimates of this study.

Table 1.2

Previous growth studies weight-at-length parameter estimates

Study	Region	Months	Years	Gear	*a*	*b* (y)	TL (cm)	*n*
This study	NW Atlantic	June to October	2016, 2017	Trawl	0.0258 (95% CI: 0.0203 to 0.0328)	2.72 (95% CI: 2.65 to 2.79)	22.4 to 38.6	1,136
Vasconcelos et al., 2011	NE Atlantic	October to December (monthly)	2002, 2003	Purse-seine	0.00231	3.38	13.0 to 41.7	2,212
Alba Jurado-Ruzafa, 2017	NE Atlantic	Monthly	2005 to 2011	Trawl	0.002	3.46	12.4 to 49.0	4,599
Mendes et al, 2004	NE Atlantic	April to September	1994, 1995	Gill-net, trammel net	0.0020	3.44	19.5 to 46.4	323
Santos et al., 2002	NE Atlantic	Monthly	1998 to 2000	Trawl, nets, long-line, traps	0.0021	3.41	15.1 to 47.2	805
Lorenzo et al., 1995	NE Atlantic	March to June	1988, 1989	Purse-seine	0.003	3.31	14.3 to 42.1	1,142
Martins, 1996	NE Atlantic	July, August, October, Novemeber	1995	Trawl survey	0.00278	3.33	19 to 41	3,761
Sinovcic et al., 2004	Mediterranean	January to Febuary	1998 to 2003	Purse-seine, beach seine	0.0066	3.14	19.6 to 38.8	1,607
Moutopoulos & Stergiou, 2002	Mediterranean	Seasonaly	1997, 1998	Gill net, long-line	0.0009	3.70	22.9 to 33.0	46

Values of weight-at-length model parameter estimates from previous studies on Atlantic Chub Mackerel. Parameter *a* is a scaling coefficient, and *b* (y) is a shape parameter describing change in length relative to weight.

Table 1.3

Length-at-age model parameter estimates

Model	Equation	Growth parameters	Median estimates	95% (CI)	DIC	ΔDIC
3-P VBGF without larval data	$L_t = L_\infty(1 - e^{-k(t-t_0)})$	L_∞ (cm)	37.13	35.79 to 39.76	--	--
		k (y⁻¹)	0.41	0.26 to 0.56		
		t_0 (y)	-2.44	-3.81 to -1.64		
3-P VBGF	$L_t = L_\infty(1 - e^{-k(t-t_0)})$	L_∞ (cm)	33.56	33.26 to 33.89	2,157	0
		k (y⁻¹)	1.75	1.59 to 1.90		
		t_0 (y)	0.07	0.06 to 0.08		
Gompertz	$L_t = L_\infty\, a^{rt}$	L_∞ (cm)	32.71	32.46 to 32.97	2,258	101
		a	0.002	0.003 to 0.014		
		r (y⁻¹)	0.008	0.00009 to 0.00861		
2-P VBGF	$L_t = L_\infty(1 - e^{-kt})$	L_∞ (cm)	34.15	33.79 to 34.51	2,261	104
		k (y⁻¹)	1.35	1.26 to 1.44		
Logistic	$L_t = \dfrac{L_\infty}{1 + a(e^{-bt})}$	L_∞ (cm)	32.66	32.40 to 32.92	2,283	126
		a	69.54	41.24 to 134.60		
		b (y⁻¹)	8.57	7.58 to 9.77		

Median parameter estimates of each candidate model used to describe the length-at-age relationship of Atlantic Chub Mackerel. In the logistic function L_∞ is the average maximum total length (cm). The parameters a (unitless) and b (y) determine the shape of the curve. In the Gompertz function L_∞ is the average maximum total length (cm). The parameters a and r are control the structure of the growth curve. In the three-parameter von Bertalanffy growth function (VBGF), L_∞ is the average maximum total length (cm), k is the growth coefficient (y⁻¹) and t_0 (y) is the theoretical age-at-length zero. In the two-parameter von Bertalanffy growth function, L_∞ and are the same as in the three-parameter VBGF.
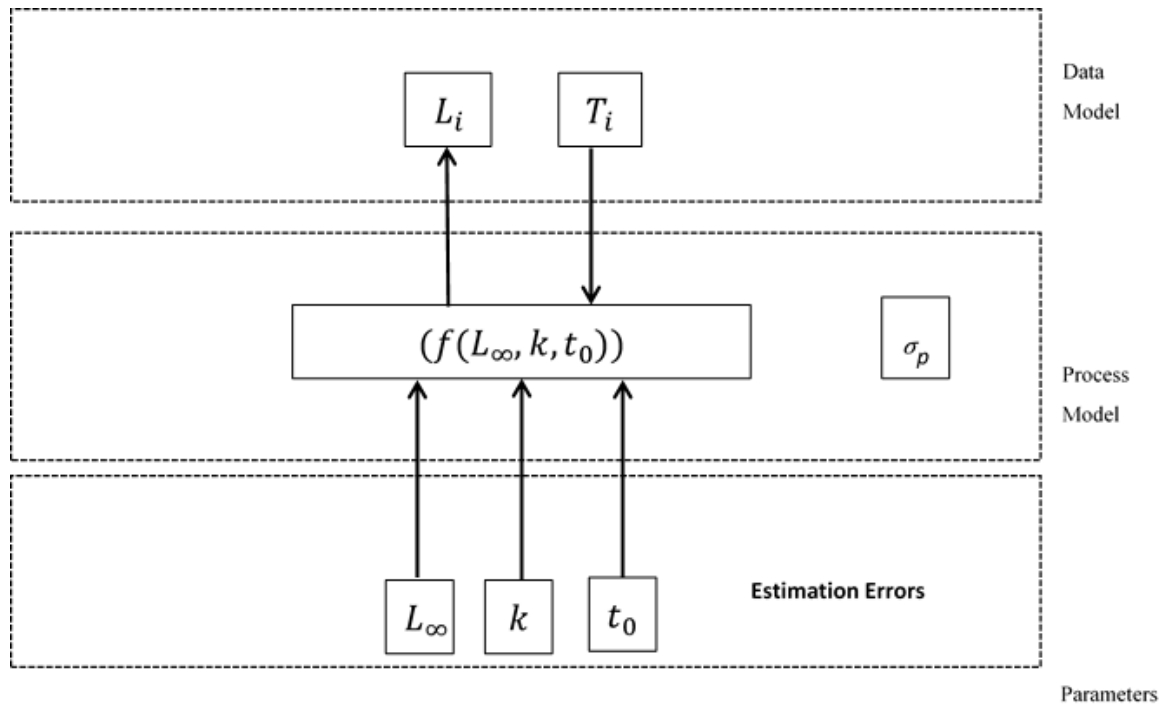
Figure 1.1 Bayesian structure of the three-parameter VBGF model

Bayesian structure of the three-parameter VBGF model used to describe the length-at-age relationship of Atlantic Chub Mackerel in the northwest Atlantic.
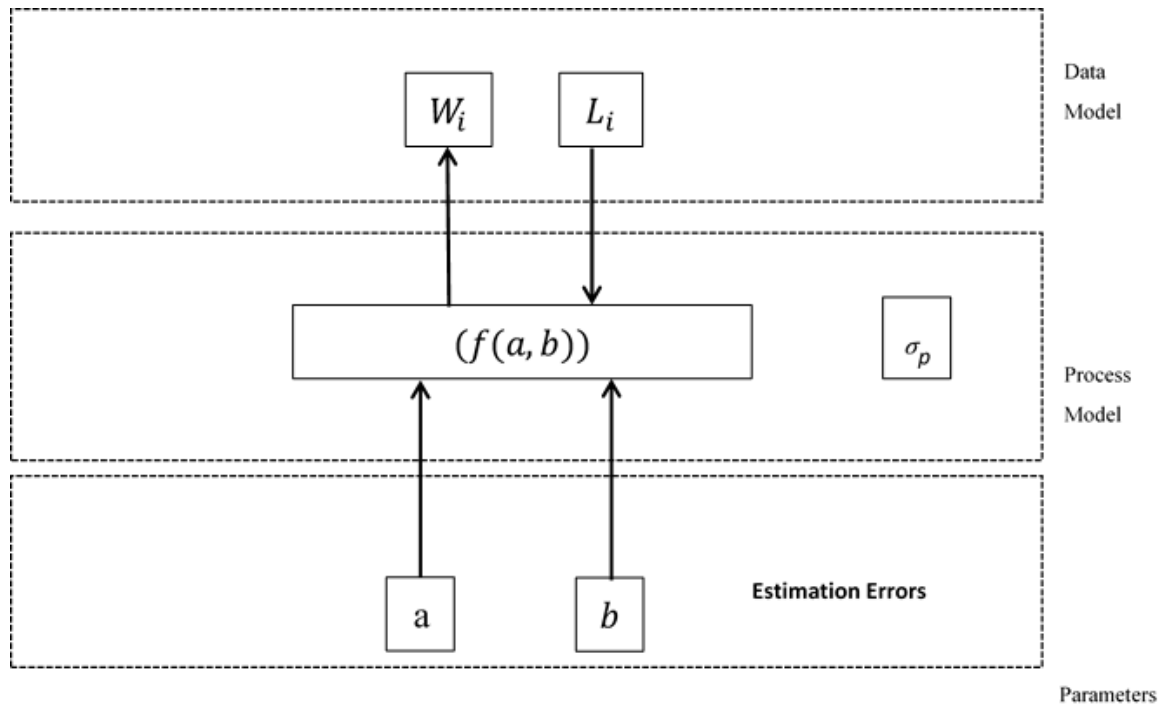
Figure 1.2 Bayesian structure of the power function used to describe weight-at-length

Bayesian structure of the power function used to describe the weight at length realtionship of Atlantic Chub Mackerel in the northwest Atlantic.
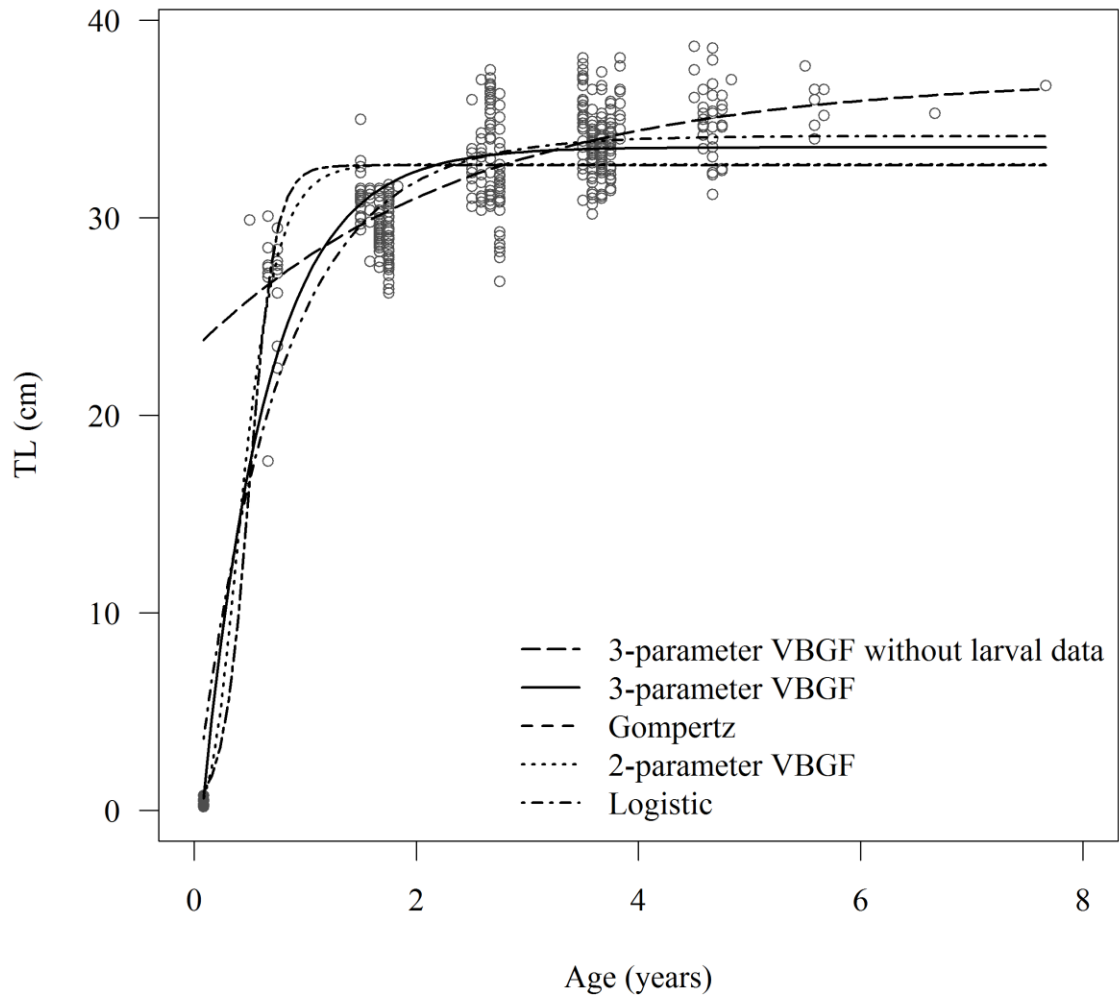
Figure 1.3 Length-at-age relationship

Non-linear candidate models fit using a Bayesian approach to describe the length-at-age relationship for Atlantic Chub Mackerel in the northwest Atlantic. The three-parameter VBGF, Gompertz function, two-parameter VBGF, and logistic function were each fit to total length (cm) and otolith derived age estimates (years) from adults (open circles; $n = 422$) collected in this study and length data body length (cm) from larvae (closed circles; $n = 60$) captured in SEAMAP cruises, which were assigned an age of one month. The three-parameter VBGF was also fit without larval data for comparison with other studies.

Table 1.4

Regional predicted length-at-age

Age (y)	NW Atlantic with larval data TL (cm)	NW Atlantic without larval data TL (cm)	SW Atlantic TL (cm)	NE Atlantic TL (cm)	Mediterranean TL (cm)
0	-4.32	23.48	15.88	13.94	7.58
1	26.84	28.07	23.64	20.89	16.91
2	32.37	31.12	29.28	26.48	23.54
3	33.35	33.14	33.38	30.98	28.23
4	33.52	34.48	36.35	34.62	31.57
5	33.55	35.37	38.51	37.11	33.94
6	33.56	35.96	40.07	39.52	35.63
7	33.56	36.36	41.21	41.50	36.56
8			42.04	44.25	37.39
9			42.64	45.96	
10			43.07	47.44	
11				48.72	
12				49.82	
13				54.08	

Mean predicted lengths of Atlantic Chub Mackerel from this study in the northwest Atlantic, and averaged mean predicted lengths in the southwest Atlantic, northeast Atlantic, and Mediterranean, for the range of ages reported in each region.
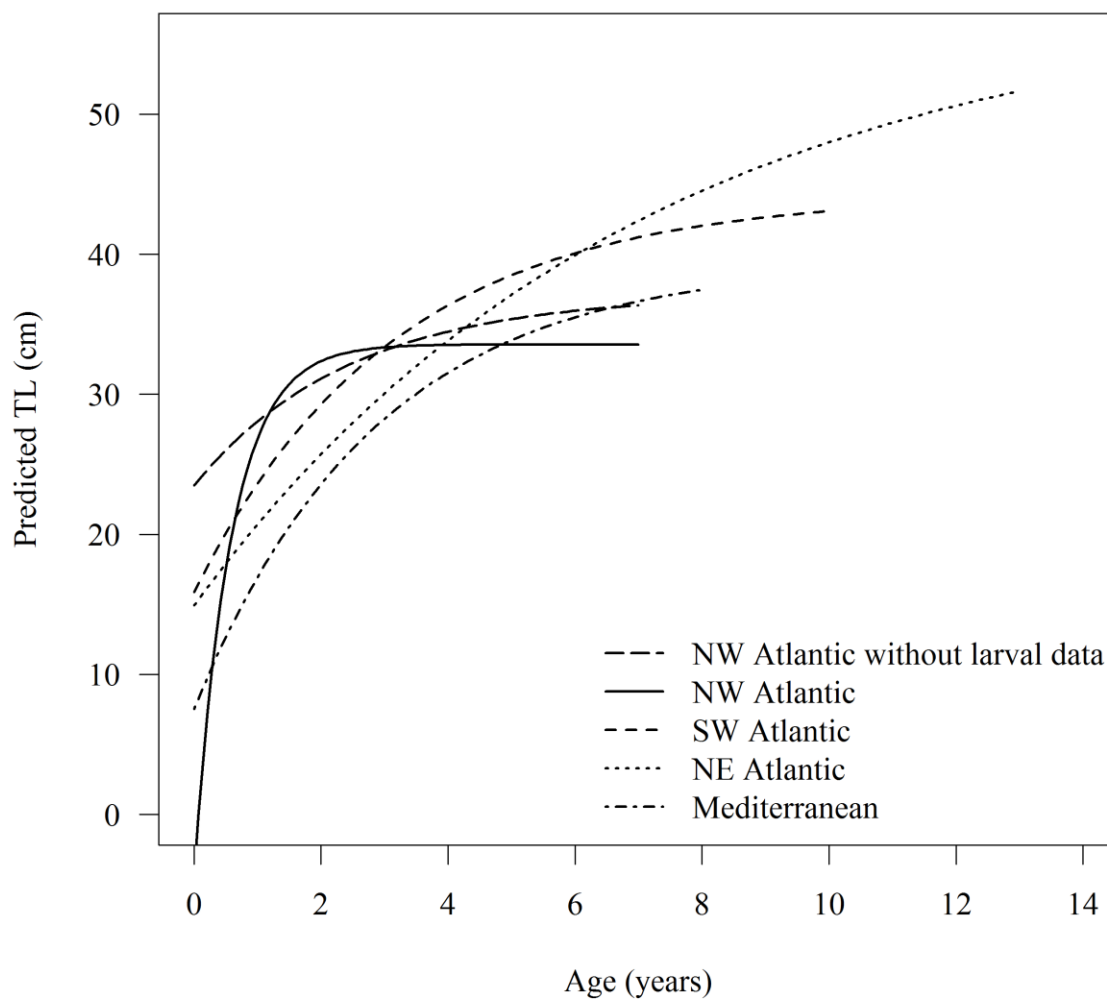
Figure 1.4 Comparison of length-at-age relationship by region

Predicted lengths at ages were calculated from parameter estimates reported for each study in other regions. Predictions were averaged for each region and then a curve was fit to compare average growth among regions. Predicted lengths at ages were also calculated from parameter estimates reported in this study from the northwest Atlantic, estimated with and without the inclusion of larval data.
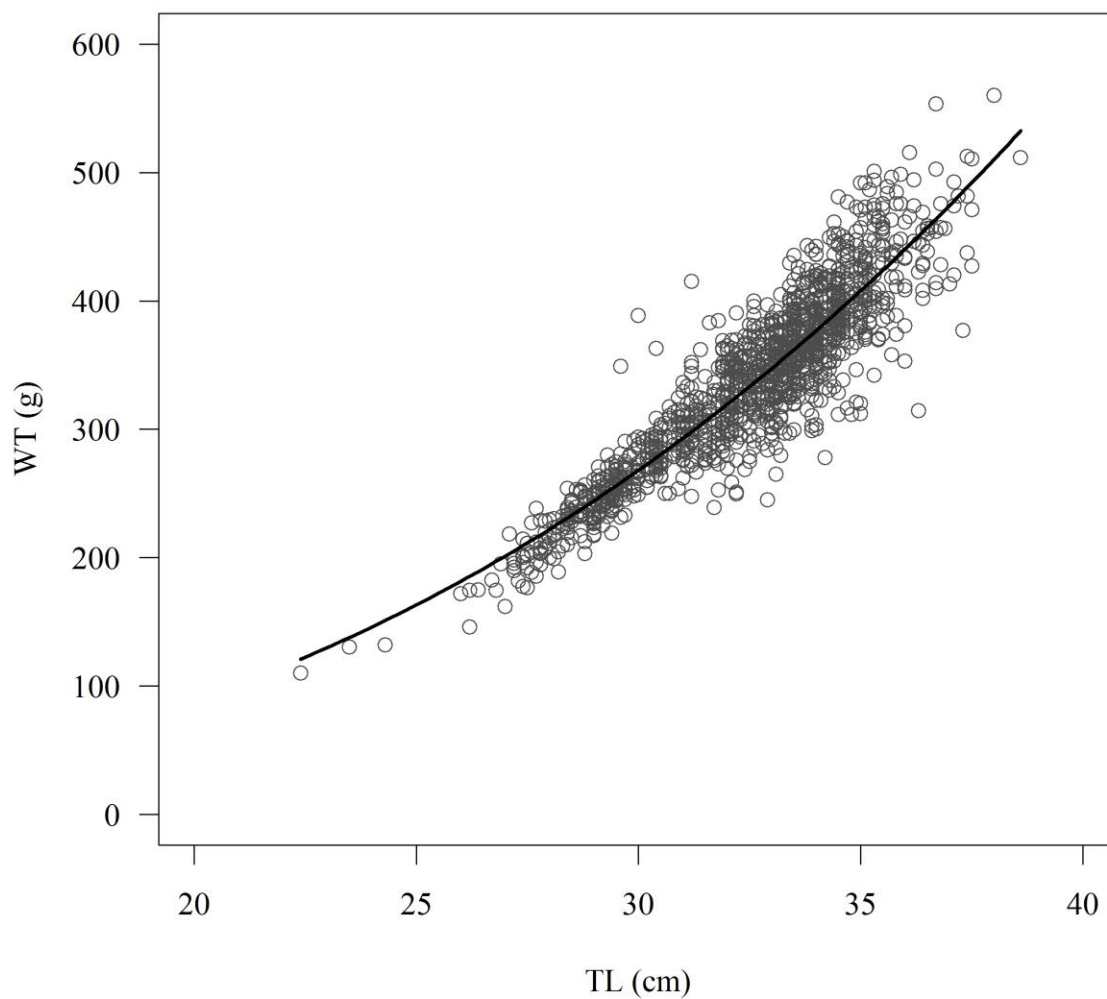
Figure 1.5 Weight-at-length relationship

The weight-at-length relationship of Atlantic Chub Mackerel in the northwest Atlantic. The line is a power function fit to observed

total length (cm) and weight (g).

CHAPTER II – REPRODUCTIVE DYNAMICS OF ATLANTIC CHUB MACKEREL

IN THE NORTHWEST ATLANTIC

2.1 Introduction

Understanding reproductive characteristics of fish stocks is necessary for creating informed management decisions (Juan-Jordá et al. 2013). For example, fishing closures during the spawning season can reduce the risk of over-exploitation of specific spawning components and are frequently used tools in fisheries management (van Overzee and Rijnsdorp 2015). Additionally, an understanding of age- and length-specific maturity can be used to identify whether individuals are being recruited into the fishery before reaching sexual maturity and can be used to predict the vulnerability of exploited fish stocks to different harvest strategies (Denney et al. 2002). Thus, a need exists to identify the temporal and ontogenetic dynamics in age-specific maturity of exploited fish stocks.

Atlantic Chub Mackerel (*Scomber colias)* is a commercially exploited fish that is distributed throughout the north and south Atlantic Ocean. Concerns about the sustainability of an emerging fishery in the northwest Atlantic have been raised, because the stock has been subject to some large harvests and biological information on the individual dynamics of the stock are absent (Figure 2.1). In December 2014, the Mid-Atlantic Fishery Management Council initiated an effort to protect forage fish stocks such as Atlantic Chub Mackerel from directed harvest until "adequate scientific information is available to promote ecosystem sustainability." (Mid-Atlantic Fishery Management Council 2015). Other taxa listed under the amendment include: anchovies (family *Engraulidae*), argentines (family *Argentinidae*), greeneyes (family *Chlorophthalmidae*), halfbeaks (family *Hemiramphidae*), herrings and sardines (family *Clupeidae*), lanternfish

(family *Myctophidae*), pearlsides (family *Sternoptychidae*, sand lances (family *Ammodytidae*), silversides (family *Atherinopsidae*), cusk eels (order Ophidiiformes, bullet mackerel/bullet tuna (*Auxis rochei*), frigate mackerel/frigate tuna (*Auxis thaxard*), Atlantic Saury (*Scomberesox saurus*), pelagic molluscs, except sharptail shortfin squid (*Illex oxygonius*), copepods, krill, amphipods, and other species less than one inch as adults. To address the needs of assessment, describing the reproductive characteristics of Atlantic Chub Mackerel in the northwest Atlantic is necessary.

Reproductive characteristics are not well described for *S. colias*. To date, no published studies have used histological analysis to describe the reproductive characteristics of Atlantic Chub Mackerel. Information derived from macroscopic examination on length-at-maturity (Table 2.1) and spawning season (Table 2.2) has been reported for fish in the northeastern Atlantic. Mean length-at-maturity of females ranges from 19.9 cm TL in the Canary Islands (Lorenzo and Pajuelo 1996) to 29.0 cm TL in the Bay of Biscay (Lucio 1997). Mean length-at-maturity for males ranges from 19.8 cm TL in the Canary Islands (Lorenzo and Pajuelo 1996) to 30.8 cm TL in the Bay of Biscay (Lucio 1997). Reported spawning season is extremely variable depending on the location (Table 2.2), but the spawning season appears to be relatively short, lasting two to three months. Spawning has been reported in January, February, March, May, June, July, August, and December.

Although limited information is available on the reproductive strategies of Atlantic Chub Mackerel, other members of the family *Scombridae* (tunas, bonitos, and mackerels) have been more extensively studied. Scombrids are considered intermediate

strategists within the Opportunistic-Periodic-Equilibrium life history triangle and are batch spawners (Juan-Jordá et al. 2013).

The purpose of this study is to describe elements of the reproductive biology of Atlantic Chub Mackerel in the northwest Atlantic. Histological techniques were used to determine sex and sexual maturity. The length- and age-at-maturity were determined from this analysis. The approximate spawning season was identified using histological indicators and evidence of spawning from analysis of historical data on larval fish collections and commercial catch. These data can be used to inform the effective management of the stock.

2.2 Methods

Frozen Atlantic Chub Mackerel were obtained during the summer and fall of 2016 from two commercial fishing companies, Lund's Fisheries Inc., and Seafreeze Limited, in July ($n = 30$), August ($n = 107$), and September ($n = 103$). Measurements for total length (TL, mm), fork length (FL, mm), and wet body weight (g) were taken from partially thawed fish. Whole gonads were removed from partially thawed fish for histological analysis. Frozen gonad sections less than 1 cm^3 were cut from the center of one gonad and placed in labeled histology cassettes. The cassettes were then placed in a jar of chilled 10% natural buffered formalin and refrigerated to allow thawing to occur slowly. A 20:1 volumetric ratio of fixative to tissue was used to ensure adequate penetration and preservation of the gonadal tissue. Additional fish were collected by Lund's Fisheries Inc. in June ($n = 95$) and October ($n = 15$) of 2017. In addition, gonadal tissue ($n = 30$) collected from one trip in July, 2017 was sampled before the fish were frozen, as well as after freezing. Both frozen and fresh tissues were analyzed to determine whether it is

valid conducting histological analysis on frozen gonadal tissue yields interpretable results. Gonadal tissue samples were used to determine if individuals were reproductively active, using standard histological techniques to determine the reproductive season.

After fixation in formalin for a minimum of one week, samples were rinsed overnight in running tap water, and partially dehydrated through a series of increasingly concentrated ethanol. The jar of cassettes was drained of all water and subsequently replaced by 60% ethanol, followed by 70% ethanol, and finally fresh 70% ethanol. The tissue was soaked in each solution for a minimum of two hours before being drained and replaced. The final solution of 70% ethanol preserves the tissue until it is embedded in paraffin.

The preserved tissue was fully dehydrated, cleared and impregnated with Paraplast Plus automatically using a Shandon Excelsior Tissue Processor (Table 2.3). Complete dehydration occurs through a series of increasingly concentrated ethanols, starting at 70% and ending at 100%. Shandon Xylene substitute was used for clearing, a gradual process where the alcohol is replaced with high refraction liquid that makes the tissue translucent. All steps occurred under vacuum to maximize the penetration of reagents into the tissue. At the completion of the processing cycle, tissue samples were removed from the processor and kept in a paraffin bath to 58 to 60 °C until each specimen was individually embedded using a Shandon Histocentre 2 Embedding Center. The process of embedding took place immediately so that the tissue did not remain in the heated paraffin for more than one hour. To embed, a small amount of Paraplast Plus, heated to at 58 to 60 °C, was poured in the bottom of a stainless-steel mold. The tissue was removed from the cassette and cut using a razor before being oriented in the mold in

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a manner that would result in the best cross section. The tissue was then secured in place by briefly cooling the paraffin, before placing the base of the cassette on top of the mold. The mold was filled with Paraplast Plus and cooled. Once the Paraplast was thoroughly solidified, the block was removed from the mold and excess paraffin trimmed off. Blocks were kept at 40 °C until sectioning.

Sectioning of embedded gonadal tissue took place in a cold room. To prepare for tissue for sectioning, an S/P Brand Tissue Flotation Bath was filled with distilled water and heated to 37 to 42 °C. One cap-full of Surgipath STAY ON, a tissue section adhesive, was added to the bath and gently stirred to mix and remove gas bubbles. Prior to sectioning, the blocks were removed from the refrigerator and placed on ice. Blocks were sectioned at a thickness of 4 μm using an AO Rotary Microtome with a disposable Accu-Edge Low Profile Microtome Blade. Sections were placed in the water bath for no longer than one minute and the best two from each specimen floated onto a labeled slide. Slides were drained of water and left to dry completely on a slide warmer for two hours.

Slides were stained following a regressive method of hematoxylin staining (Luna 1968). The staining process includes removing the paraffin with xylene substitute, rehydrating the tissue in a series of ethanol baths to allow aqueous-based stains to be absorbed, staining basic tissue components using Hematoxylin 2, staining acidic tissue components with Eosin Y (Richard-Allan Scientific), and then dehydrating the section in a sequence of solutions (Table 2.4). Solution baths were rotated or discarded and replaced as needed. Slides were cover-slipped using a mounting medium (Richard-Allan Scientific) and allowed to dry completely.

Gonadal tissue samples were assessed microscopically to determine sex. The presence of oocytes indicate that the sex is female and spermatogonia and lobular structure of the tissue indicate the sex is male. Female individuals were then classified as mature (1) or immature (0) using histological analysis (Table 2.5). This was not possible with tissue samples from males due to the poor quality of the frozen samples. For mature females it was not possible to assign a reproductive phase as described by Brown-Peterson et al. (2011; Table 2.6), due to the quality of frozen tissue. Reproductively inactive females in the regenerating or regressing phases were identified using histological indicators (Table 2.6) and classified as mature inactive.

Each histology slide was read by two independent readers. Analysis of the slides was done with no prior knowledge of the size of the individual. Percent agreement was calculated between readers for sex determination, as well as agreement of maturity for females. In the case of a discrepancy between maturity estimates, the histology slide was reexamined. If an agreement was not reached between readers, the maturity estimate was omitted from the analysis. Percent agreement between the results of histological analysis of fresh and frozen gonadal tissue was also calculated for sex and maturity.

Mean length at 50% maturity was estimated using a two-parameter logistic model:

$$M_{TL} = \frac{1}{1+e^{-r(TL-L_{50})}},$$

where *r* is the instantaneous rate of change (mm^{-1}) and L_{50} is the cm TL at 50% maturity. Age-at-maturity was back-calculated using the length-at-age relationship determined in Chapter I of this thesis.

Spawning season was estimated using a combination of histological indicators to determine if mature individuals are reproductively active, as well as an analysis of larval data in the northern Gulf of Mexico, and historical commercial catches in the northwest Atlantic. Larval and juvenile Atlantic Chub Mackerel collected by the Southeast Area Monitoring Assessment Program (SEAMAP) plankton surveys in the northern Gulf of Mexico across 20 years from 1983 to 2014 were used to infer spawning season. Frequency of Atlantic Chub Mackerel larvae was evaluated to determine what months spawning likely occurred. This was compared to reports of commercial catch from 2007 to 2015 in the northwest Atlantic to determine if evidence exists of individuals migrating south.

2.3 Results

A subsample of 380 Atlantic Chub Mackerel were evaluated using histological analysis for sex and maturity. Fresh samples were used when possible as they were better quality. Of the 380 samples analyzed, 163 were females, which were assigned sex with 100% agreement for identifying females. Maturity was determined for 151 females, with 72% agreement for maturity of females between readers and a final of 97%. Of the females assigned a maturity code, 35 were identified as immature ranging in length from 26.0 to 32.5 cm TL and 116 were identified as mature ranging from 27.2 to 37.7 cm TL. The remaining seven tissue samples identified as female were too degraded to determine maturity and five were omitted from the maturity analysis due to disagreement between readers. These data showed that females mature as small as 27.2 cm TL, and 100% of individuals observed were mature at 32.7 cm TL. From the two-parameter logistic function (Figure 2.7), the r mean parameter estimate was 0.38 cm^{-1} (95% CI: 0.19 to 0.71

cm^{-1}) and the L_{50} mean parameter estimate was 27.39 cm TL (95% CI: 24.53 to 28.47 cm

TL) for females. The age-at-50% maturity was estimated as 2.16 by back calculation

using the three-parameter von Bertalanffy growth function mean parameter estimates

reported in Chapter I.

In this study, I determined if females had reached maturation by identifying

specific histological markers that could be distinguished in the damaged tissue samples.

The presence of perinucleor oocytes is often used to distinguish reproductive activity,

with mature females having a greater perinucleor to chromatin nucleor oocyte ratio

compared to immature females (Table 2.6). However, the quality of the tissue samples

often prevented observation of the nucleoli. We found the best indicator of maturity was

the presence of blood vessels and muscle tissue, followed by oocyte size, thickness of

ovarian wall, and spacing of primary growth oocytes (Figures 2.2 and 2.3). Reduced

interstitial tissue, macrophage aggregates, and muscle bundles were also useful indicators

of maturity. Immature fish were identified by closely packed oocytes of uniform size, the

presence of interstitial tissue, and a thin ovarian wall (Figure 2.4). Although it was not

possible to clearly distinguish between phases, it was clear that all individuals collected

during this study were reproductively inactive. Only primary growth oocytes were

observed (PN), indicating that mature females were in either the regenerating or

regressing phase Vtgs and CAs, which would indicate maturity, were not present.

Of the 380 Atlantic Chub Mackerel evaluated using histological analysis for sex,

188 males were identified by the basic underlying lobular architecture of the gonad tissue

and presence of spermatocysts (Figure 2.5). Gonad tissue was difficult to identify

macroscopically in the fish after freezing, resulting in non-gonadal tissue being sampled

from 25 fish and preventing sex from being determined. In some cases, the poor quality of the tissue made it difficult to determine if the tissue was taken from a male gonad or another type of tissue (Figure 2.6). Three samples were degraded beyond recognition and were eliminated, without determining tissue type. Agreement on distinguishing between male and non-gonadal tissue was 95% for a subsample ($n = 167$). Readers came to a final agreement of 148 males and 16 non-gonadal tissues. Two samples, which readers could not reach an agreement, were omitted. An additional 48 tissue samples were analyzed by reader one, who identified 39 male and nine non-gonadal tissue samples. Spermatocysts were not present in most slides and could rarely be identified to spermatogenic stage which is used to determine maturity and phase. Males were not identified as mature or immature except for four, which were identified as spawning capable by the presence of spermatozoa in the lumens (Figure 2.7), and therefore mature. Mature males ranged in size from 31.6 to 36.5 cm TL, which is an insufficient range of lengths to fit a maturity curve.

A small number of gonad tissues ($n = 30$) were sampled both before and after freezing to validate the use of frozen tissue. Samples which were not frozen were much clearer and easier to read (Figure 2.8 and 2.9). Twelve tissue samples were identified as female with 100% agreement for both fresh and frozen samples. One fresh sample was eliminated from the maturity analysis due to poor quality and two of the frozen samples. Of the 11 viable female tissues, which were not frozen, agreement on determination of maturity was 91%. After reevaluating slides, readers reached a final agreement on all samples, with two immature females and nine mature females. Of the ten viable female tissues, which were frozen, agreement on determination of maturity was 90%. Final

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agreement was 90% with nine mature females and one tissue sample where an agreement

could not be reached. Agreement on maturity of females between fresh and frozen

samples was 89%. For the fresh samples, readers agreed 94% of the time in

distinguishing between male and non-gonadal tissue, which can look similar in tissue

samples of poor quality. Agreement of frozen samples was 72%. Final agreement for

both was 100% with one non-gonadal tissue and 17 male gonad tissues. Agreement

between fresh and frozen samples was 100% on distinguishing between male and non-

gonadal tissue.

Spawning season was estimated using histological indicators to determine if

mature individuals were reproductively active, as well as an analysis of larval data in the

northern Gulf of Mexico, and historical commercial catches in the northwest Atlantic. No

actively spawning or spawning capable female fish were sampled from June to October.

Four males collected in October were spawning capable. Commercial catch decreases

strongly in the northwest Atlantic during December, with no reported commercial

landings of Atlantic Chub Mackerel during the months of January to February (Figure

2.10). SEAMAP plankton surveys in the northern Gulf of Mexico recorded the highest

occurrence of Atlantic Chub Mackerel larvae and juveniles in January, February, March,

and April (Figure 2.11). These results indicate that Atlantic Chub Mackerel are winter

spawners.

2.4 Discussion

Understanding reproductive dynamics is critical for understanding the resilience

of fish stocks (Lowerre-Barbieri et al. 2011a). With the MAFMC considering adding

Atlantic Chub Mackerel to the Atlantic Mackerel, Squids, and Butterfish Fishery

Management Plan (FMP), descriptions of the stock's reproductive biology are needed to inform future management decisions (Mid-Atlantic Fishery Management Council 2015). In this work, I describe length- and age-at-maturity and identify the approximate spawning season. Estimates of length-at-maturity can be used to evaluate selectivity and age-at-maturity is used to calculate spawning stock biomass per recruit and maximum spawning potential.

Results indicate that Atlantic Chub Mackerel mature around age two, which is consistent with reported age-at-50% maturity of 2.23 (y) in the Azores (Carvalho et al. 2002). Most information on the reproductive biology of the species comes from studies in other regions. Two studies conducted in the Azores and Portuguese continental coast reported L_{50} estimates, which fell within the 95% CI of this study (Martins 1996; Carvalho et al. 2002). Three other studies from the Madeira Islands, Canary Islands, and Bay of Biscay reported estimates which indicate significant differences in maturity. Previous studies used macroscopic evaluation to determine sex and maturity. Macroscopic evaluation was not used in this study, as the frozen gonads lost their shape and coloration. Instead, histological analysis was used to determine sex and maturity. Histological analysis also provides additional information on phase, although this was difficult to evaluate due to tissue quality.

The approximate spawning season of Atlantic Chub Mackerel was determined to occur in the northern Gulf of Mexico during the winter. No females collected in the northwest Atlantic during the months of June, July, August, and October provided any indication of spawning activity. Males are known to enter the spawning capable phase before the females in the population (Lowerre-Barbieri et al. 2011b). The four males

determined to be spawning capable suggests that the spawning season occurs after October. Low commercial catch of Atlantic Chub Mackerel in the northwest Atlantic coincides with the peaks in frequency of larval fish in the Gulf of Mexico which suggests that the fish are migrating south to spawn around November and December, returning north after the spawning season around May. Based on my analysis of Atlantic Chub Mackerel larval data collected from SEAMAP plankton surveys in the northern Gulf of Mexico, the spawning season for Atlantic Chub Mackerel occurs during the winter in the northern Gulf of Mexico. Larvae are first observed in the month of January with high occurrence over the following three months.

Evidence of Atlantic Chub Mackerel spawning activity in the winter reported in the southwest Atlantic and Gulf of Mexico is consistent with my analysis of the spawning season. Berrien (1978) found evidence of spawning activity from Cape Hatteras to Florida during January to July. Icthyoplankton surveys specifically targeted collection of eggs and larvae of *Scomber scombrus* and *Scomber japonicas* (now classified as *Scomber colias),* in the continental shelf waters between Massachusetts and Florida. *Scomber colias* eggs were collected south of Cape Hatteras, in the outer half of shelf waters, during winter and spring cruises. Along the southeast coast, 14 locations were sampled four times from Cape Fear to Palm Beach, from May 1967 to February 1968, and 14 locations along the northeast coast were sampled eight times from Cape Lookout to Martha's Vineyard. The absence of Atlantic Chub Mackerel eggs and larvae north of Cape Hatteras, despite extensively sampling provides a definitive range for the northern extent of the spawning region. Richardson et al. (2010) also documented Atlantic Chub Mackerel larvae in the nearshore waters of the Straits of Florida from January to May.

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Based on these studies, the geographic range of Atlantic Chub Mackerel spawning activity occurs from Cape Hatteras to the northern Gulf of Mexico.

The winter spawning season estimated in this study from January to April is consistent with reports of Atlantic Chub Mackerel in the northern hemisphere spawning during the first half of the year, and during the second half of the year in the southern hemisphere (Hernández and Ortega 2000). Water temperature has been reported to be a major factor in triggering the spawning activities of Atlantic Chub Mackerel and occurs most often at water temperatures of 15 to 20 °C (Collette and Nauen 1983). Differences in water temperature is likely to be a major contributing factor for variation in the seasonality of spawning activity, among geographic locations (Lorenzo and Pajuelo 1996; Lucio 1997; Carvalho et al. 2012; Joana Vasconcelos, Manuel Afonso-dias et al. 2012). Berrien (1978) reported surface temperature associated with egg occurrence ranging from 20.4 to 25.4 °C and larvae to occur at temperature of between 16 and 29.4 °C along the east coast of the United States.

Autolysis, degradation, and freezing damaged the gonadal tissue, making it difficult or sometimes impossible to observe histological indicators typically used to determine maturity and phase. Emphasis was placed on identifying female maturity, due to the relevance of this information for fisheries management and the presence of specific histological markers that could be distinguished despite damaged tissue and being outside the spawning season. Challenges in sample quality were addressed by placing a different emphasis on certain histological indicators. A greater ratio of PN to CN is an indicator of maturity, however the nuclei could not be observed in all samples. Closely packed oocytes indicate that the fish is immature. The degraded tissue made it difficult to

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distinguish cells spaced apart as an indication of maturity or an artifact. Degraded tissue also made identifying interstitial tissue difficult. Large amounts of interstitial tissue are an indicator that the fish is immature. The ratio of the nucleus to cytoplasm is greater in mature fish, however gaps in tissue left very little tissue that could be analyzed in some samples. Criteria that are the same and could usually be observed include blood vessels, muscle, and thickness of wall; therefore a greater emphasis was placed on these indicators in this study. The presence of macrophage aggregates and parasites are common in older fish suggesting maturity. It is possible to observe macrophage aggregates and parasites in immature fish, but a high frequency is unlikely. This is not traditionally used to evaluate maturity; however we included this information in our analysis.

Although fresh tissue is preferred for histological analysis, the comparison of the precision of results using frozen and fresh tissue from the same individual indicates that histological analysis of frozen tissue is a valid method for determining sex, as well as maturity of females. Degradation and autolysis appear to be a major problem, however the quality of many of the samples which were not frozen was still poor. Likely, degradation occurred in this batch as samples were kept on ice for about two days after capture, until the commercial vessel reached shore and tissue samples could be taken. We had a limited sample size for this comparison ($n = 30$) because sampling fresh fish is challenging due to the opportunistic nature of the fishery.

During the spawning season, maturity estimates and possibly determination of phase should be possible for both males and females, even with the degraded and frozen samples. Determining maturity is more difficult outside the spawning season than when

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the fish are spawning capable. During the spawning season, more obvious histological indicators are present that can be used to differentiate between phases, as well as mature and immature fish. The presence of spermatozoa in four male fish was very clear and provided a strong indicator of maturity that could not be observed in males outside the spawning period. Mature males from other months were either regressing or regenerating but it is difficult to tell. Similarly, in female fish Vtgs or CAs are a clear indication of maturity. Further evidence of maturity is the occurrence of POFs and atresia which indicate spawning has occurred recently. In this study, all mature females were reproductively inactive, which can be difficult to distinguish from immature fish.

This research provides a description of Atlantic Chub Mackerel reproduction in the northwest Atlantic, including a female-specific estimation of length- and age-at-maturity, and estimation of the spawning season duration. Additional research is necessary to provide a more comprehensive description of the reproductive biology of Atlantic Chub Mackerel in the northwest Atlantic. Collection of actively spawning females during the suspected winter spawning season would provide a more reliable and specific estimation of the spawning season. Histological indicators of maturity are more obvious during this time, which would make it possible to determine maturity for males, as well as provide a more reliable estimation for females. The collection of females during the spawning season would also allow for estimation of fecundity and spawning frequency, as well as classification of fecundity type. The information reported in this study is a first step to understanding reproductive characteristics of Atlantic Chub Mackerel and can directly inform future assessment efforts of the northwest Atlantic stock.
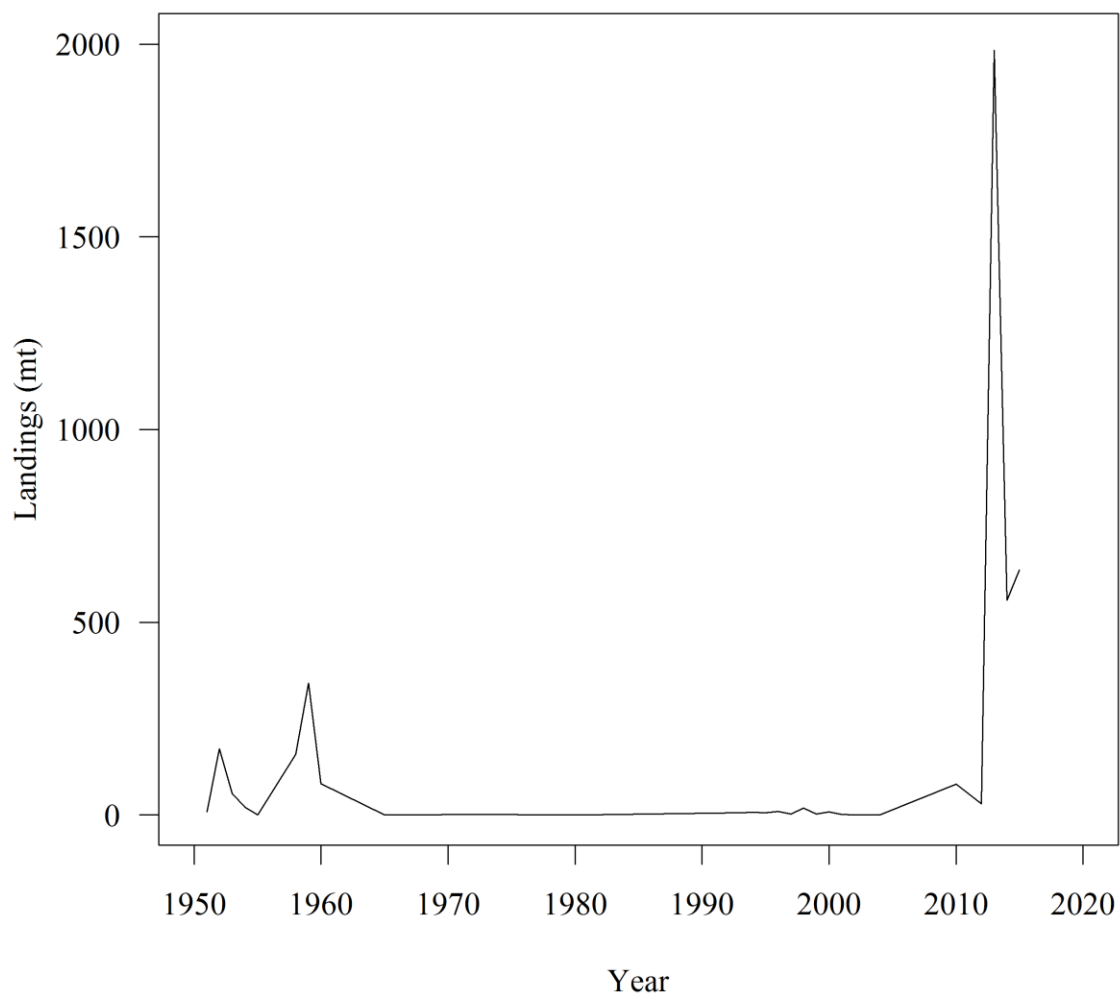
Figure 2.1 Historical commercial catch

Commercial catch of Atlantic Chub Mackerel from 1951 to 2015.

Table 2.1

Summary of reported length-at-maturity estimates

Study	Location	L_{50} TL (cm) F	L_{50} TL (cm) M	L_{50} TL (cm) Combined sex	Evaluation
This study	NW Atlantic	27.39 (95% CI: 24.53 to 28.47)			Microscopic
Vasconcelos et al. (2012)	Madeira Island	21.55	22.12		Macroscopic
(Carvalho et al. 2002)	Azores Archipelago			27.78	Macroscopic
Lorenzo & Pajuelo (1996)	Canary Island	19.9	19.8		Macroscopic
Lucio (1997)	Bay of Biscay	29.0	30.8		Macroscopic
Martins (1996)	Portuguese continental coast			27.0	Macroscopic

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Table 2.2

Summary of reported spawning season

Study	Location	Months
This Study	NW Atlantic	January to April
Cengiz (2012)	Aegean Sea	June to August
Vasconcelos et al. (2012)	Madeira Island	February to March
Lucio (1997)	Bay of Biscay	May to June
Lorenzo & Pajuelo (1996)	Canary Island	December to January
Martins (1996)	Portuguese continental coast	February to March and April to May

Table 2.3

Histological processing sequence

Step	Solution	Duration
1	Xylene substitute	3 min
2	Xylene substitute	3 min
3	Xylene substitute	3 min
4	100% EtOH	10 dips
5	100% EtOH	10 dips
6	95% EtOH	10 dips
7	95% EtOH	10 dips
8	80% EtOH	10 dips
9	80% EtOH	10 dips
10	50% EtOH	10 dips
11	Distilled water	1 min
12	Hematoxalyin 2	3-6 min
13	Water	Rinse
14	Acid water	2 dips
15	Water	Rinse
16	Blueing water	30 sec
17	Water	Rinse
18	95% EtOH	10 dips
19	Eosin Y	30 - 90 sec
20	Paper towel	Bolt Blot Blot
21	95% EtOH	10 dips
22	95% EtOH	10 dips
23	95% EtOH	10 dips
24	100% EtOH	1 min
25	100% EtOH	1 min
26	100% EtOH	1 min
27	Xylene substitute	1 min
28	Xylene substitute	1 min
29	Xylene substitute	1 min
30	Xylene substitute	1 min

Histological processing sequence completed using a Shandon Histocentre 2 Processor.

Table 2.4

Outline of tissue staining process

Step	Solution	Duration
1	Xylene substitute	3 min
2	Xylene substitute	3 min
3	Xylene substitute	3 min
4	100% EtOH	10 dips
5	100% EtOH	10 dips
6	95% EtOH	10 dips
7	95% EtOH	10 dips
8	80% EtOH	10 dips
9	80% EtOH	10 dips
10	50% EtOH	10 dips
11	Distilled water	1 min
12	Hematoxalyin 2	3-6 min
13	Water	Rinse
14	Acid water	2 dips
15	Water	Rinse
16	Blueing water	30 sec
17	Water	Rinse
18	95% EtOH	10 dips
19	Eosin Y	30 - 90 sec
20	Paper towel	Bolt Blot Blot
21	95% EtOH	10 dips
22	95% EtOH	10 dips
23	95% EtOH	10 dips
24	100% EtOH	1 min
25	100% EtOH	1 min
26	100% EtOH	1 min
27	Xylene substitute	1 min
28	Xylene substitute	1 min
29	Xylene substitute	1 min
30	Xylene substitute	1 min

Table 2.5

Indicators of maturity

Mature	Immature
Large blood vessels	Small or no blood vessels
Presence of muscle bundles likely	Presence of muscle bundles unlikely
Ratio of cytoplasm < nucleus	Ratio of cytoplasm > nucleus
Diversity in oocyte sizes	Homogeneity of oocyte sizes
Thick ovarian wall	Thin ovarian wall
Space between oocytes	Closely packed oocytes
Little or no interstitial tissue	Interstitial tissue present
Lots of Perinucleor (PN) in primary growth oocytes (rarely seen in poor quality samples)	More Chromatin Nucleor (CN) than Perinucleor present (absence of PN does not mean immature)
Presence of macrophage aggregates and/or parasites likely	Macrophage aggregates and/or parasires are possible

Histological analysis used to determine maturity in female Atlantic Chub Mackerel based on frozen tissue. Criteria are listed in order of usefulness.

Table 2.6

Female reproductive phase terminology

Phase	Definition	Histological Description
Immature	Never spawned	Contains only oogonia and PG oocytes with a higher concentration of CN than PN. No atresia, muscle bundles. Ovarian wall is thin and interstitial tissue is present. Oocytes are closely packed and uniform in size.
Developing	Ovaries are preparing for spawning.	Contains PG, CA, Vtg1, and Vtg2 oocytes. Some atresia may be present, but no POFs or Vtg3 oocytes.
Early Developing	Subphase of developing.	Contains PG and CA oocytes. Atresia may be present.
Spawning Capable	Fish is physiologically able to spawn in this cycle.	Contains Vtg3, Vtg2, and Vtg1 oocytes. Atresia of vitellogenic oocytes, hydrated oocytes, early stages of OM, and/or POFs may be present.
Actively Spawning	Subphase of spawning capable. Fish has either spawned within 12 hours or will spawn within 12 hours.	Oocytes undergoing late GVM, GVBD, hydration, or ovulation. POFs may be present.
Regressing	Spawning has ceased for the season.	Contains atresia (any stage) and POFs. Some CA and/or vitellogenic oocytes may be present.
Regenerating	Fish is sexually mature, but reproductively inactive.	Contains oogonia and primary growth oocytes with a higher concentration of PN than CN. Ovarian wall is think. Atresia, degenerating POFs, enlarged blood vessels, reduced interstitial tissue, and muscle bundles may be present.

Female classification terminology adapted from Brown-Peterson et al. (2011).

Microscopic descriptions of the phases in the reproductive cycle of female Atlantic Chub Mackerel (CA = cortical alveolar; GVBD = germinal vesicle breakdown; GVM = germinal vesicle migration; OM = oocyte maturation; PG = primary growth; POF = postovulatory follicle complex; Vtg1 = primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic; Perinucleor (PN); Chromatin Nucleor (CN).
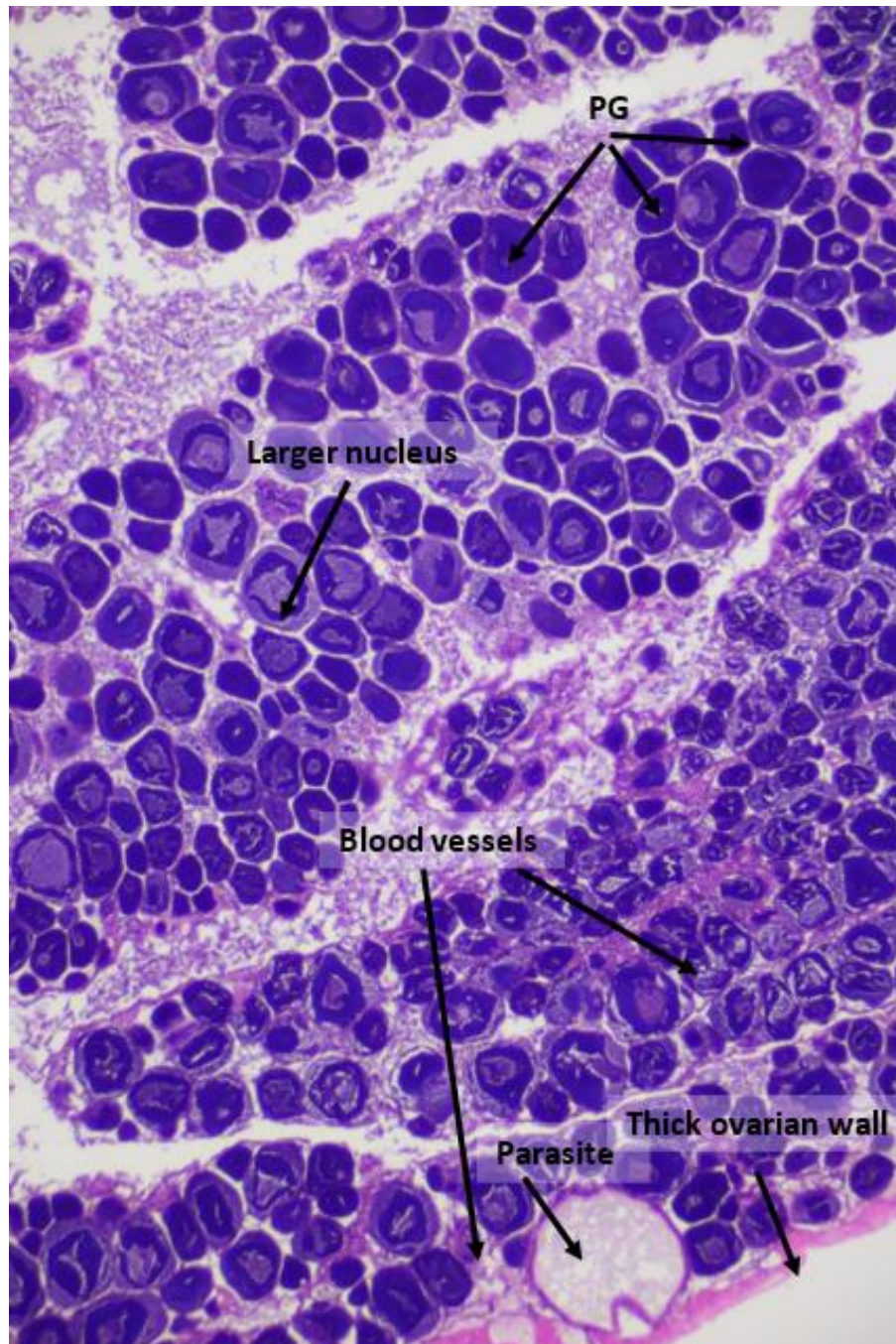
Figure 2.2 Mature female histology image

Histology sample imaged at 10x magnification from a mature female Atlantic Chub Mackerel (35.8 cm TL) caught in October 2017.

Mature females were identified by the presence blood vessels, loosely packed primary growth oocytes (PG), diversity of PG size, and
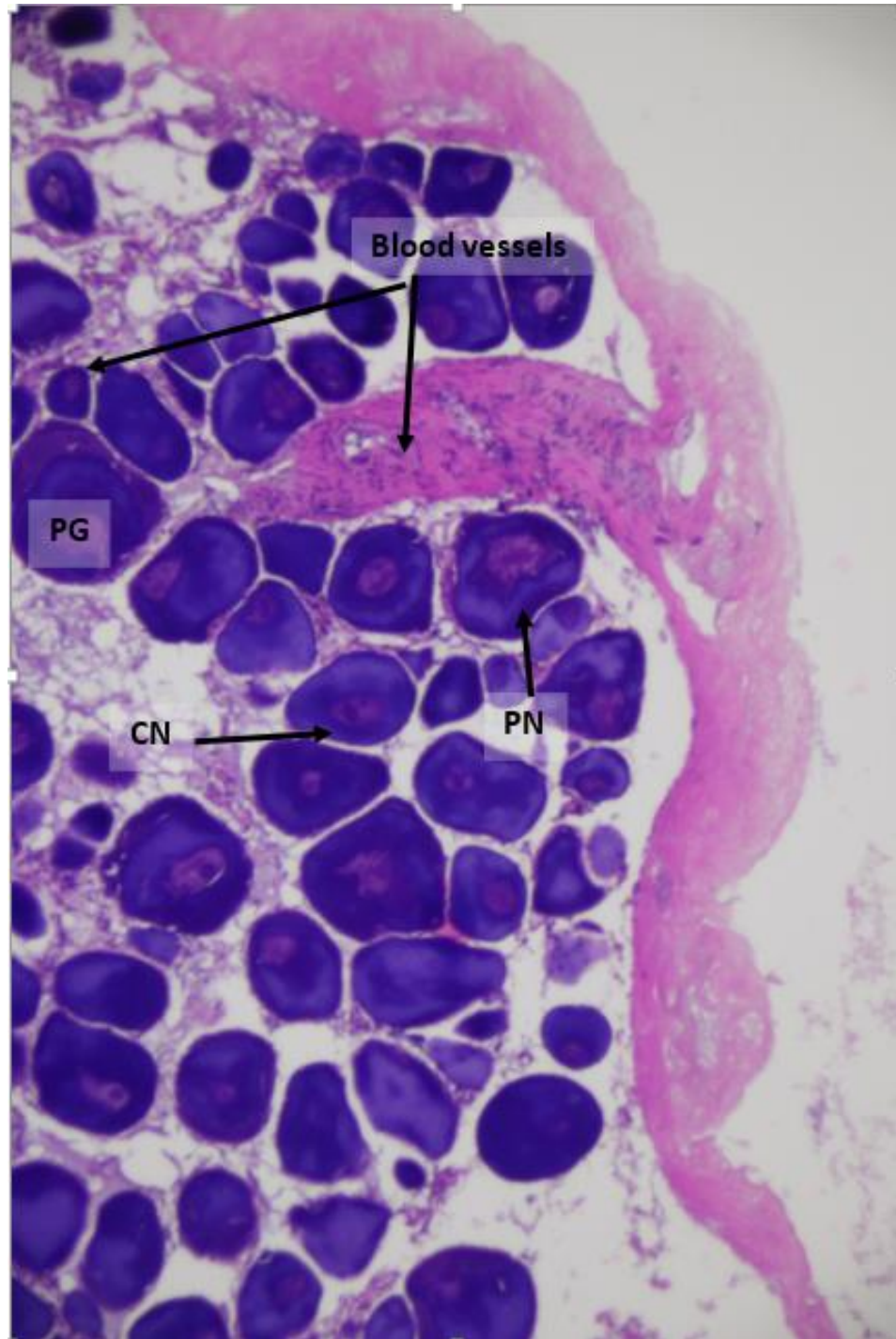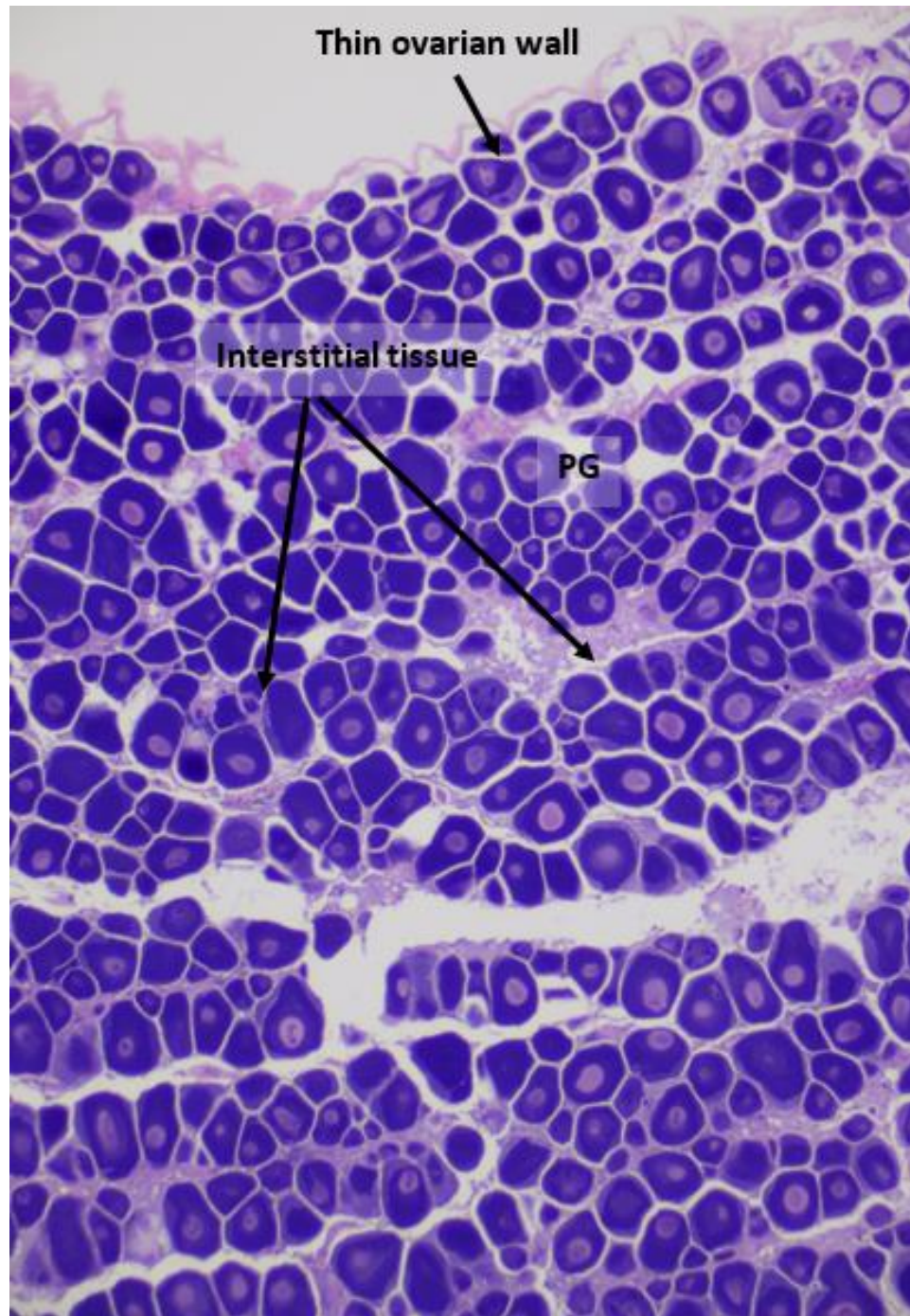
a thick ovarian wall.

Figure 2.3 Mature female histology image

Histology sample imaged at 20x magnification from a mature female Atlantic Chub Mackerel (35.3 cm TL) caught in October 2017.

Mature females were identified by the presence blood vessels, loosely packed primary growth oocytes (PG), diversity of PG size, and

a higher ration of PN to CN.

Figure 2.4 Immature female histology image

Histology sample imaged at 10x magnification from an immature female Atlantic Chub Mackerel (29.7 cm TL) caught in September 2016. Immature females were identified by the presence of small, tightly-packed primary growth oocytes (PG) with a small nucleus, a thin ovarian wall, and interstitial tissue.
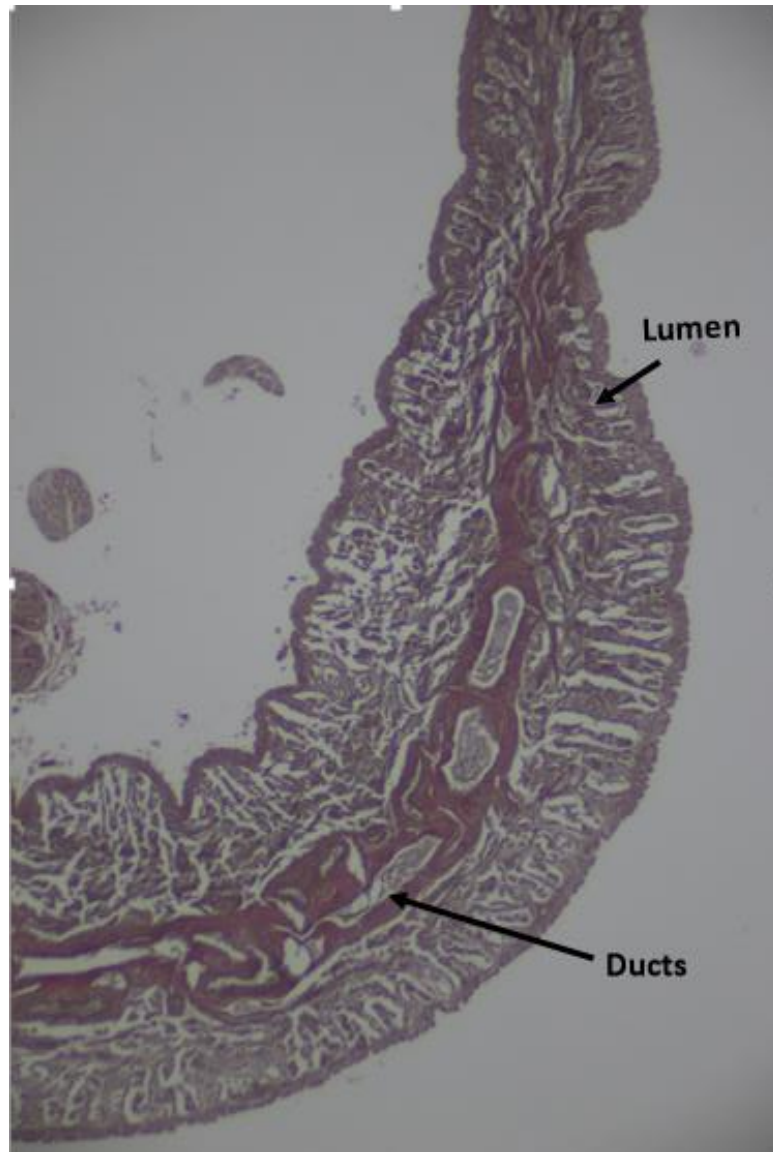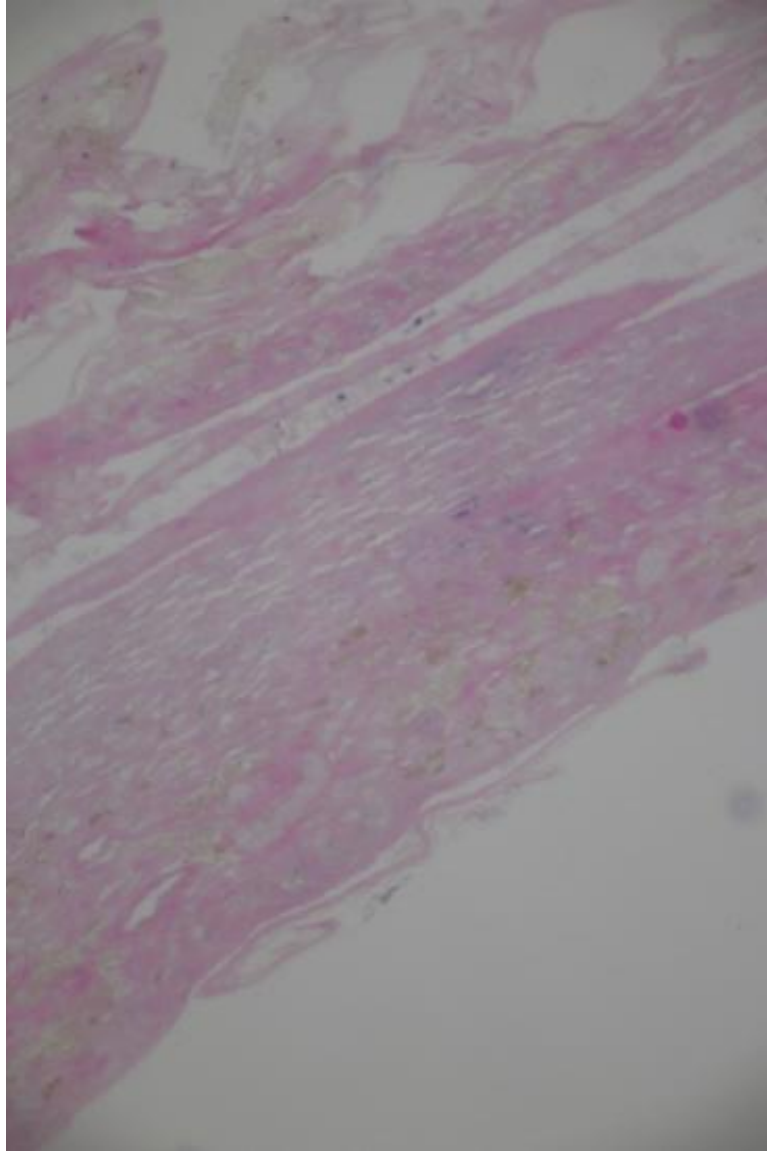
Figure 2.5 Male histology image

Histology sample imaged at 10x magnification from a male Atlantic Chub Mackerel (32.3 cm TL) caught in August 2016.

Figure 2.6 Non-gonadal tissue

Histology sample imaged at 10x magnification of non-gonadal tissue, mistaken for gonad tissue, from an Atlantic Chub Mackerel
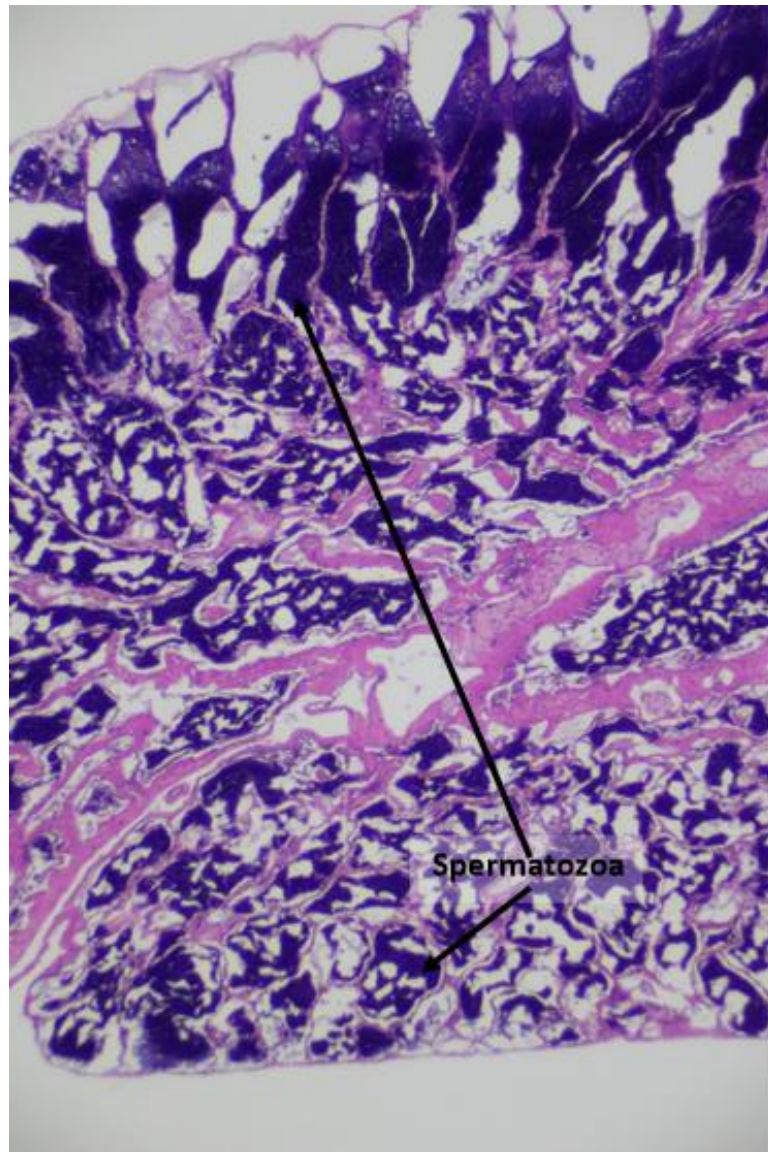
(29.4 cm TL) caught in September 2016.

Figure 2.7 Spawning capable male histology image

Histology sample imaged at 10x magnification from a spawning capable male Atlantic Chub Mackerel (35.0 cm TL) caught in

October 2017. Identified as spawning capable by the presence of spermatozoa in the lumens.
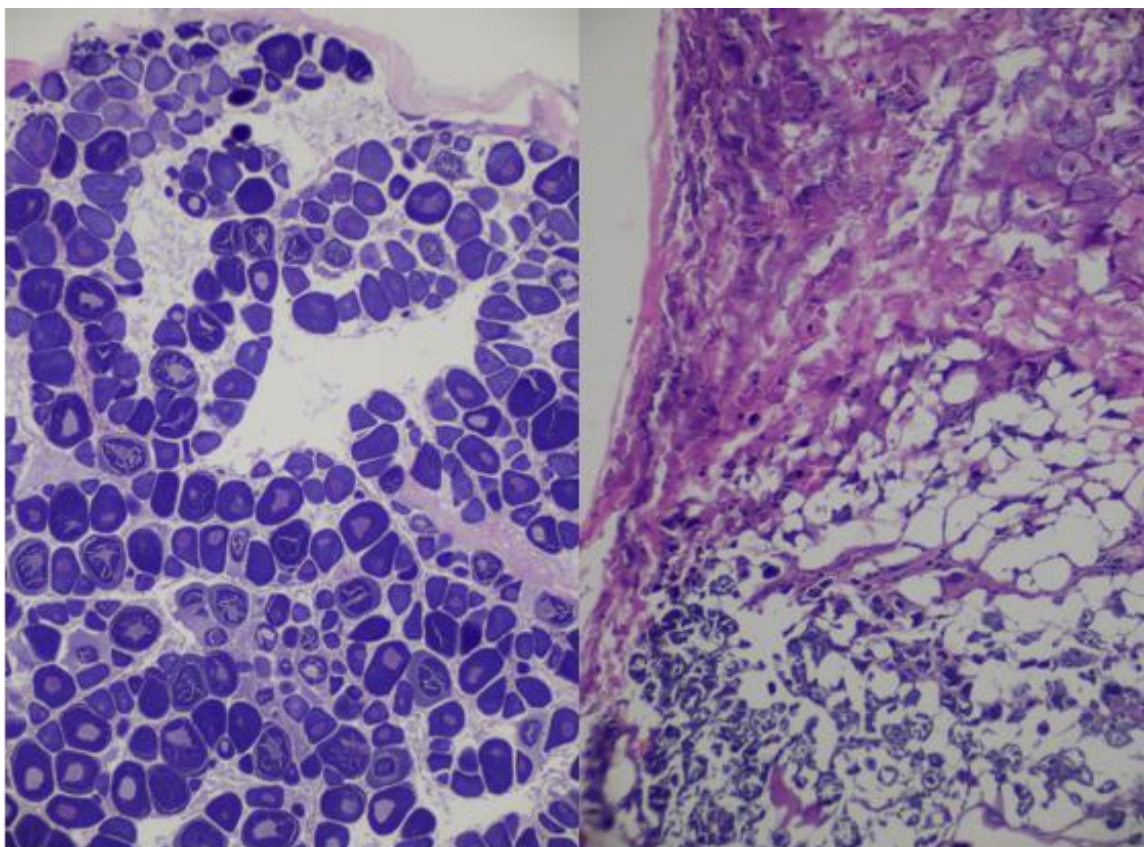
Figure 2.8 Comparison of fresh to frozen female gonad tissue

Histology sample imaged at 10x magnification from a mature female Atlantic Chub Mackerel (30.8 cm TL) caught July 2017. Frozen

tissue is shown on the right and the unfrozen tissue on the left for comparison.
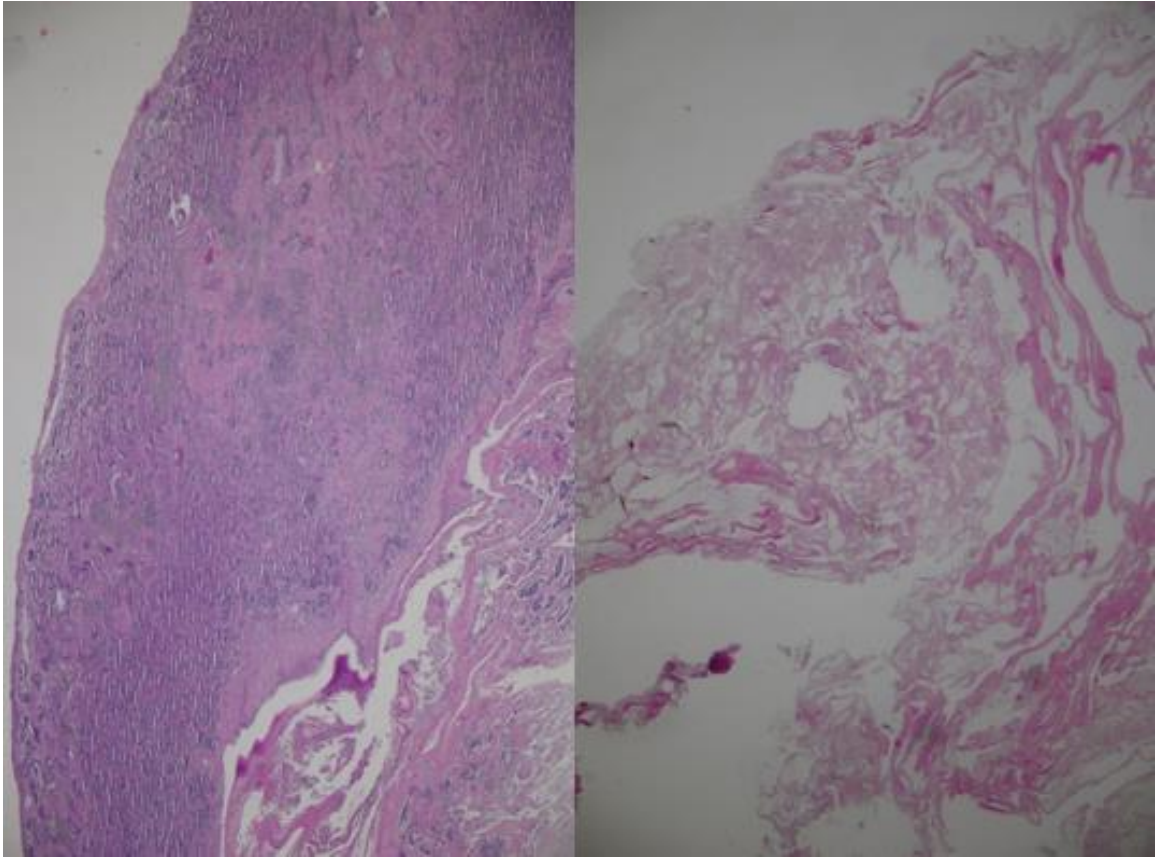
Figure 2.9 Comparison of fresh to frozen male gonad tissue

Histology sample imaged at 10x magnification from a male Atlantic Chub Mackerel (33.4 cm TL) caught July 2017. Frozen tissue is shown on the right and the unfrozen tissue on the left for comparison.
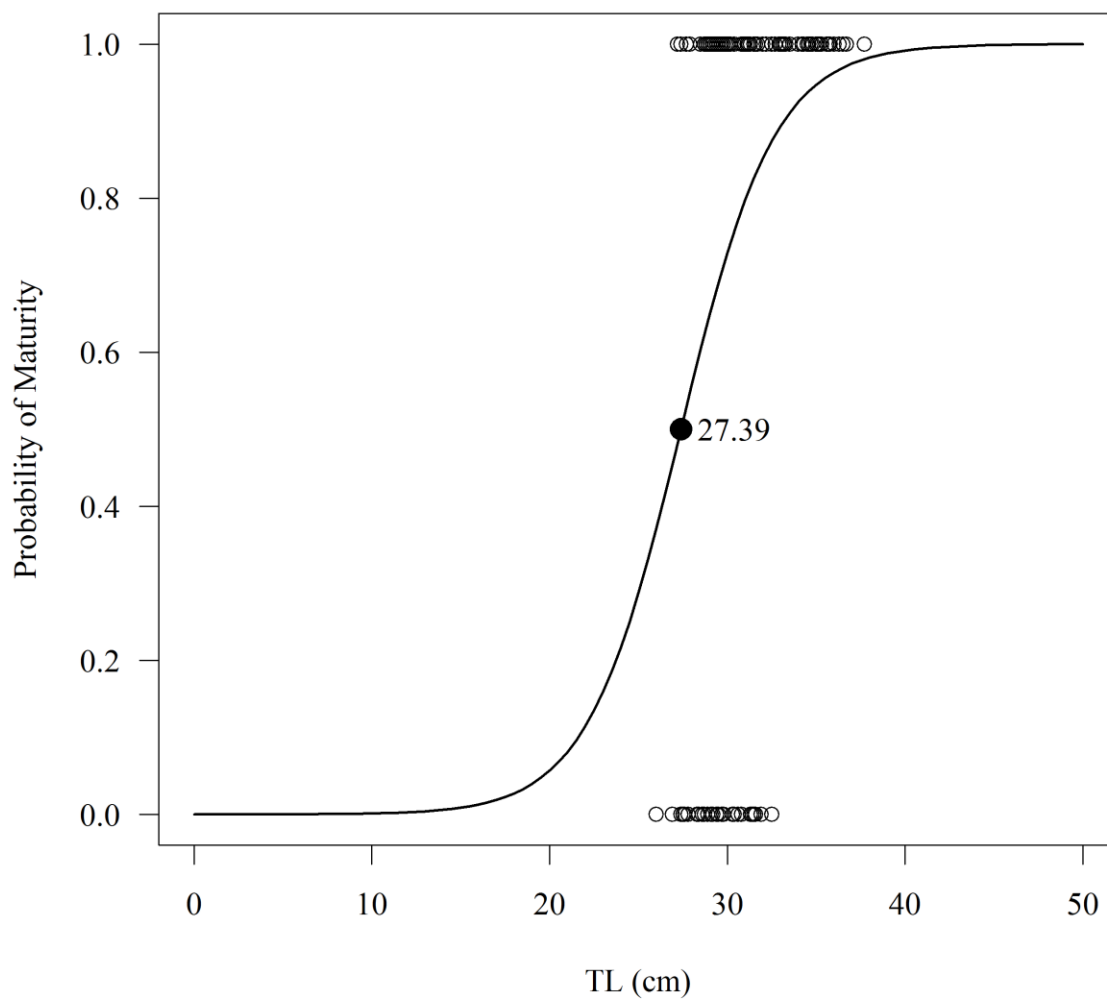
Figure 2.10 Female length-specific maturity

Logistic model describing the length-at-maturity for female Atlantic Chub Mackerel ($n = 151$) from the northwest Atlantic, where the inflection point L_{50} represents the mean parameter estimate for total length-at-50% maturity. Individuals were assigned a binomial maturity code indicating immature (0) or mature (1) status.
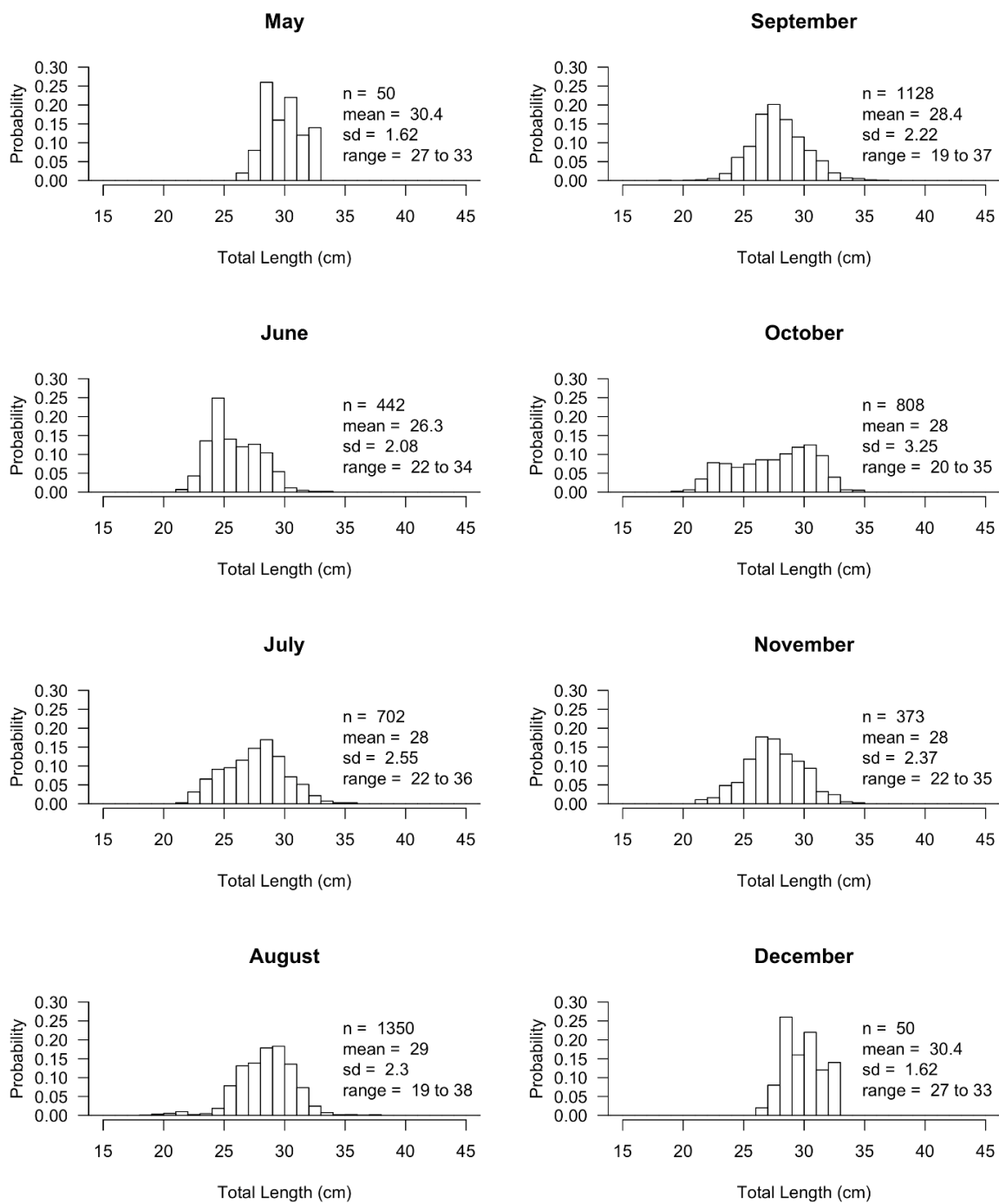
Figure 2.11 Length distribution of historical commercial catch

Historical commercial catch of Atlantic Chub Mackerel in the northwest Atlantic by month from 2007 to 2015.
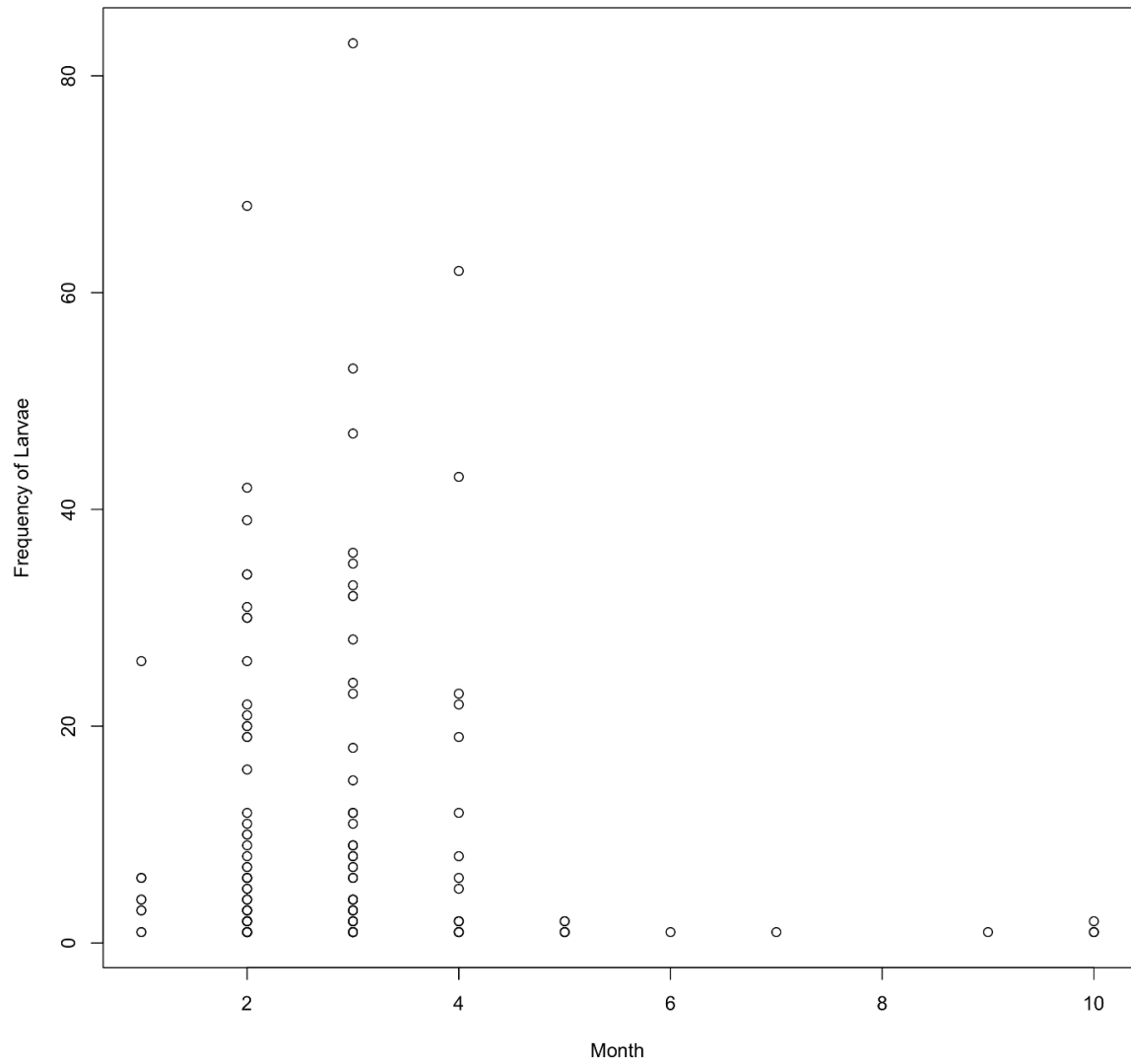
Figure 2.12 Frequency of larvae by month

Frequency of larval Atlantic Chub Mackerel by month collected from 20 years of surveys from 1983 to 2014. Data was collected by SEAMAP cruises in the northern Gulf of Mexico. 1,567 larval fish have been collected over all years sampled with lengths ranging from 1.2 to 35 mm BL.

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REFERENCES

Alba Jurado-Ruzafa. 2017. Age, growth and natural mortality of Atlantic chub mackerel *Scomber colias* Gmelin 1789 (Perciformes: *Scombridae*), from Mauritania (NW Africa) 1789(November).

Anderson, D., K. Burnham, and W. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. The journal of wildlife management:912–923.

Ballagh, A. C., D. Welch, A. J. Williams, A. Mapleston, A. Tobin, and N. Marton. 2011. Integrating methods for determining length-at-age to improve growth estimates for two large scombrids. Fishery Bulletin.

Bayhan, B. 2007. Growth characteristics of the chub mackerel (*Scomber japonicus* Houttuyn, 1782) in Izmir Bay (Aegean Sea, Turkiye). Journal of Animal Veterinary Advances (6):627–634.

Beamish, R. J., and G. A. Mcfarlane. 1983. The Forgotten Requirement for Age Validation in Fisheries Biology. Transactions of te American Fisheries Society 112(6):735–743.

Berrien, P. L. 1978. Eggs and Larvae Of *Scomber Scombrus* and *Scomber Japonicus* In Continental Shelf Waters. Fishery Bulletin 76(1):95–115.

Bertalanffy, L. Von. 1938. Human Biology a Quantitative Theory of Organic Growth (Inquireies on Growth Laws. II)*. Source: Human Biology 10174254(2):181–213. Wayne State University Press.

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri. 2011. A Standardized Terminology for Describing Reproductive Development in Fishes. Marine and Coastal Fisheries 3(1):52–70. Taylor & Francis

Group .

Burnham, K. P., and D. R. Anderson. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33(2):261–304. Sage PublicationsSage CA: Thousand Oaks, CA.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59(2):197–242.

Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries & Aquatic Sciences 58(1):30–38.

Carvalho, N., R. Perrotta, E. Isidro, and O. Cengiz. 2012. Age, Growth, Mortality and Reproduction of the Chub Mackerel (Scomber japonicus Houttuyn, 1782) from Saros Bay (Northern Aegean Sea, Turkey). Turkish Journal of Fisheries and Aquatic Sciences 12:799–809.

Carvalho, N., R. R. G. Perrotta, and E. Isidro. 2002. Age, Growth and Maturity in Chub Mackerel (Scomber japonicus Houttuyn, 1782) from the Azores. Life and Marine Sciences 19A:93–99.

Čikeš Keč, V., and B. Zorica. 2012. Length–weight relationship, age, growth and mortality of Atlantic chub mackerel *Scomber colias* in the Adriatic Sea. Journal of the Marine Biological Association of the United Kingdom 93(2):341–349. Cambridge University Press.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8(1):2–14.

Collette, B. B., and C. E. Nauen. 1983. FAO Species Catalogue Vol . 2 Scombrids of the
world an annotated and illustrated catalogue of Tunas, Mackerels, Bonitos and
related species know to date. Page FAO Fisheries Synopsis.

Cope, J. M., and A. E. Punt. 2007. Admitting ageing error when fitting growth curves: an
example using the von Bertalanffy growth function with random effects. Canadian
Journal of Fisheries and Aquatic Sciences 64(2):205–218. NRC Research Press
Ottawa, Canada .

Denney, N. H., S. Jennings, and J. D. Reynolds. 2002. Life-History Correlates of
Maximum Population Growth Rates in Marine Fishes. Source: Proceedings:
Biological Sciences 269(1506):2229–2237.

Dippold, D. A., R. T. Leaf, J. R. Hendon, and J. S. Franks. 2016. Estimation of the
Length-at-Age Relationship of Mississippi's Spotted Seatrout. Transactions of the
American Fisheries Society 145(2):295–304. Taylor & Francis.

Ellison, A. M. 1996. An Introduction to Bayesian Inference for Ecological Research and
Environmental Decision-Making. Ecological Society of America 6(4):1036–1046.

Essington, T. E., P. E. Moriarty, H. E. Froehlich, E. E. Hodgson, L. E. Koehn, K. L.
Oken, M. C. Siple, and C. C. Stawitz. 2015. Fishing amplifies forage fish population
collapses. Proceedings of the National Academy of Sciences of the United States of
America 112(21):6648–52. National Academy of Sciences.

Francis, R. I. C. C. 2016. Growth in age-structured stock assessment models. Fisheries
Research 180:77–86. Elsevier.

Froese, R. 2006. Cube law, condition factor and weight–length relationships: history,
meta-analysis and recommendations. Journal of applied ichthyology 22.4:241–253.

Gompertz, B. 1825. On the Nature of the Function Expressive of the Law of Human

Mortality, and on a New Mode of Determining the Value of Life Contingencies.

Source: Philosophical Transactions of the Royal Society of London 115:513–583.

Hernández, J. J. C., and A. T. S. Ortega. 2000. Synopsis of Biological Data on the Chub

Mackerel: *Scomber Japonicus* Houttuyn, 1782. FAO Fisheries Synopsis 157:77.

Houde, E. D. 1974. Effects of temperature and delayed feeding on growth and survival of

larvae of three species of subtropical marine fishes. Marine Biology 26(3):271–285.

ICES. 2006. ICES SGABC Report 2006 Report of the Study Group on Ageing Issues of

Baltic Cod (SGABC) International Council for the Exploration of the Sea Conseil

International pour l'Exploration de la Mer. ICES CM 45:16–1908.

ICES. 2015. ICES WKARCM Report 2015 Chub Mackerel (*Scomber colias*) (WARCM)

Report of the Workshop on Age Reading of Lisbon, Portugal.

Joana Vasconcelos, Manuel Afonso-dias, G. F., J. Vasconcelos, M. Afonso-dias, and G.

Faria. 2012. Atlantic chub mackerel (*Scomber colias*) spawning season, size and age

at first maturity in Madeira waters. Page Arquipélago: Ciências Biológicas E

Marinhas.

Juan-Jordá, M. J., I. Mosqueira, J. Freire, and N. K. Dulvy. 2013. Life in 3-D: life history

strategies in tunas, mackerels and bonitos. Reviews in Fish Biology and Fisheries

23(2):135–155. Springer Netherlands.

Kiparissis, S., G. Tserpes, and N. Tsimenidis. 2000. Aspects on the demography of Chub

Mackerel (*Scomber japonicus* Houttuyn, 1782) in the Hellenic Seas. Belgian Journal

of Zoology 130(1):3–7.

Lorenzo, J. M., and J. G. Pajuelo. 1996. Growth and reproductive biology of chub

mackerel *Scomber japonicus* off the Canary Islands. South African Journal of

Marine Science 17(1):275–280. Taylor & Francis Group.

Lorenzo, J. M., J. G. Pajuelo, and A. G. Ramos. 1995. Growth of chub mackerel *Scomber japonicus* (Pisces: *Scombridae*) off the Canary Islands. Sciemtoa Marina 59(3.4):287–291.

Lowerre-Barbieri, S. K., N. J. Brown-Peterson, H. Murua, J. Tomkiewicz, D. M. Wyanski, and F. Saborido-Rey. 2011a. Emerging Issues and Methodological Advances in Fisheries Reproductive Biology. Marine and Coastal Fisheries 3(1):32–51. Taylor & Francis Group .

Lowerre-Barbieri, S. K., K. Ganias, F. Saborido-Rey, H. Murua, and J. R. Hunter. 2011b. Reproductive Timing in Marine Fishes: Variability, Temporal Scales, and Methods. Marine and Coastal Fisheries 3(1):71–91. Taylor & Francis Group.

Lucio, P. 1997. Biological notes of Spanish mackerel (*Scomber japonicus*) in the Bay of Biscay from the Basque country catches.

Luna, L. G. 1968. Manual of histologic staining methods of the Armed Forces Institute of Pathology. Blakiston Division, McGraw-Hill.

Martin, W. R. 1949. The mechanics of environmental control of body form in fishes. The Ontario Fisheries Research Laboratory 70(58):1–91.

Martins, M., and S. Gordo. 1984. On the comparison of spanish mackerel (*Scomber japonicus* Houttuyn, 1782) from Corringe Bank and Peniche. ICES (50).

Martins, M. M. 1996. New biological data on growth and maturity of Spanish Mackerel (*Scomber japonicus*) off the Portuguese coast (ICES Division IX a). Page International Council for the Exploration of the Sea. Lisboa Portugal.

Martins, M. M. 2007. Growth variability in Atlantic mackerel (*Scomber scombrus*) and Spanish mackerel (*Scomber japonicus*) off Portugal. ICES Journal of Marine Science 64(9):1785–1790.

Mendes, B., P. Fonseca, and A. Campos. 2004. Weight-length relationships for 46 fish species of the Portuguese west coast. Journal of Applied Ichthyology 20(5):355–361. Blackwell Verlag GmbH.

Mid-Atlantic Fishery Management Council. 2015. Scoping Document for Council Action on Unmanaged Forage Species. Page 18.

Moutopoulos, D. K., and K. I. Stergiou. 2002. Length-weight and length-length relationships of fish species from the Aegean Sea (Greece). Journal of Applied Ichthyology 18(3):200–203.

Oravecz, Z., and C. Muth. 2017. Fitting growth curve models in the Bayesian framework. Psychonomic Bulletin & Review:1–21. Springer US.

van Overzee, H. M. J., and A. D. Rijnsdorp. 2015. Effects of fishing during the spawning period: implications for sustainable management. Reviews in Fish Biology and Fisheries 25(1):65–83. Springer International Publishing.

Pardo, S. A., A. B. Cooper, and N. K. Dulvy. 2013. Avoiding fishy growth curves. Methods in Ecology and Evolution:1–8.

Perrotta, R. G., N. Carvalho, and E. Isidro. 2005. Comparative Sudy on Growth of Chub Mackerel (*Scomber japonicus* Houttuyn, 1782) From Three Different Regions: NW Mediterranean, NE and SW Atlantic*.

Plummer, M. 2016. rjags: Bayesian Graphical Models using MCMC.

Powell, A. B., R. T. Cheshire, E. H. Laban, J. Colvocoresses, P. O'Donnell, and M.

Davidian. 2004. Growth, mortality, and hatchdate distributions of larval and juvenile

    spotted seatrout (*Cynoscion nebulosus*) in Florida Bay, Everglades National Park.

    Fishery Bulletin 102(1):142–155.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. Vienna,

    Austria.

Reeves, S. 2003. A simulation study of the implications of age-reading errors for stock

    assessment and management advice. ICES Journal of Marine Science 60(2):314–

    328. Oxford University Press.

Richardson, D. E., J. K. Llopiz, C. M. Guigand, and R. K. Cowen. 2010. Larval

    assemblages of large and medium-sized pelagic species in the Straits of Florida.

    Progress in Oceanography 86(1–2):8–20. Pergamon.

Ricker, W. E. 1975. Computation and interpretation of Biological Statistics of Fish

    Populations. Bulletin of the Fisheries Research Board of Canada 191:311–312.

Santos, M., M. Gaspar, P. Vasconcelos, and C. Monteiro. 2002. Weight–length

    relationships for 50 selected fish species of the Algarve coast (southern Portugal).

    Fisheries Research 59(1):289–295.

Sinovcic, G., M. Franicevic, B. Zorica, and V. Cikes-Kec. 2004. Length-weight and

    length-length relationships for 10 pelagic fish species from the Adriatic Sea

    (Croatia). Journal of Applied Ichthyology 20(2):156–158. Blackwell Verlag GmbH.

Thorson, J. T., and C. A. Simpfendorfer. 2009. Gear selectivity and sample size effects

    on growth curve selection in shark age and growth studies. Fisheries Research

    98(1):75–84.

Vasconcelos, J., M. A. Dias, and G. Faria. 2011. Age and growth of the Atlantic chub

mackerel *Scomber colias* Gmelin, 1789 off Madeira Island. Revista de Biología Marina y Oceanografía 1:27–34.

Velasco, E. M., J. Del Arbol, J. Baro, and I. Sobrino. 2011. Age and growth of the Spanish chub mackerel *Scomber colias* off southern Spain: a comparison between samples from the NE Atlantic and the SW Mediterranean. Revista de biología marina y oceanografía 46(1):27–34. Universidad de Valparaíso. Facultad de Ciencias del Mar.