

# Growing degree-day influences growth rate and length of maturity of Northwest Atlantic halibut (*Hippoglossus hippoglossus* L.) across the southern stock domain

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## Abstract

The NAFO divisions 3NOPs4VWX5Zc Atlantic halibut (*Hippoglossus hippoglossus* L.) stock is managed over a large spatial scale, spanning over 20° of longitude and 6° of latitude. Previous studies have shown that female halibut in the warmer southern area mature at sizes 10–20 cm smaller than female halibut in the colder north. Our goal was to examine the role of growing degree-day (GDD, the number of days X temperature °C above a minimum threshold) on growth rate and length at maturity (LM50%). Two separate datasets, associated with the stock-wide DFO-Industry Halibut Longline Survey, were used to estimate these life history traits. GDD had a significant effect on both growth rates and probability of maturity. Females grew faster and matured at a larger size than males. Female growth rate at a reference length of 90 cm corresponding to the southerly NAFO 4X was ~11.5 cm/year, significantly faster than in the northerly NAFO division 3N (8 cm/year). Male growth rate at 90 cm corresponding to NAFO divisions 4X and 4W were 7.2 and 7.5 cm/year, significantly faster than in NAFO divisions 3N and 3Ps (5.6 and 5.8 cm/year). Both sexes matured at smaller sizes in the southern areas with higher GDD. Females in the warmer southern divisions were more likely to mature ~10–28cm less than the more northerly divisions. However, the corresponding prediction intervals for NAFO divisions were very wide. On average, fish mature at a smaller size in 4WX, but we cannot predict length at maturity for any new observations in any division. We have identified large variation in life history traits across the stock domain associated with the thermal regime. Such variation in life history traits could be used to improve the assessment models and may also be indicative of stock structure that could be eroded if not addressed in the management of the fishery.

**Key words:** Northwest Atlantic halibut, growth rate, length at maturity, growing-degree day, stock structure

## Introduction

The definition of a stock unit is the foundation of a fish stock assessment, and often assumes that the unit captures uniform population dynamics (Cadrin *et al.*, 2013; Kerr *et al.*, 2016). Atlantic halibut (*Hippoglossus hippoglossus* L.) is a large, long-lived, cold-water, sexually dimorphic flatfish that can attain sizes up to 3 m in length, live up to 50 years, and ranges throughout the North Atlantic (Collette and Klein-Macphée, 2002). The management unit of NAFO Divisions 3NOPs4VWX5Zc Atlantic halibut extends about 20° of longitude (~2000 km) and 6° of latitude (~650 km), and includes three Northwest Atlantic Fishery Organization (NAFO) subareas, comprised of seven divisions and subdivisions (throughout this paper we will refer to both as ‘divisions’) (Fig. 1). This initial designation took place in 1988 and was based largely on the ecology of Pacific halibut (*Hippoglossus stenolepis*), which has been a focus of study by the International Pacific Halibut Commission (IPHC) since 1923. Over time, the Pacific halibut stock assessment has been refined as initial assumptions about, for example, constant growth and a highly migratory homogenous population, were overturned by new scientific evidence (Webster and Clark, 2013; Stewart and Martell, 2014; Nielsen and Seitz, 2017). On the Atlantic coast, halibut have received considerably less scientific attention, owing to the prioritization of the historically high value of Atlantic cod (*Gadus morhua*) and

other groundfish species (Neilson *et al.*, 1993). Atlantic halibut abundance and landings have been increasing steadily since the mid 2000s (Trzcinski and Bowen, 2016), resulting in a renewed interest, both commercial and scientific, in safe-guarding this valuable resource (den Heyer *et al.*, 2013; Seitz *et al.*, 2016; Shackell *et al.*, 2016; Boudreau *et al.*, 2017; Murphy *et al.*, 2017; French *et al.*, 2018; Le Bris *et al.*, 2018). Recent tagging analyses (den Heyer *et al.*, 2013; Seitz *et al.*, 2016; Kersula and Seitz, 2019) as well as the spatial and temporal structure of juvenile distribution, suggests that halibut exhibit more resident non-migratory behavior than previously assumed (Shackell *et al.*, 2016; Boudreau *et al.*, 2017; French *et al.*, 2018). It is timely to consider whether life history traits vary across the management unit and how results contribute to the management unit definition (Ying *et al.*, 2011; McBride, 2014; Lorenzen, 2016). In this study, we investigate variation in individual growth rate and length at maturity of halibut across the stock domain.

As has been observed across several taxa (Cappo *et al.*, 2013) including flatfish (Roff, 1982), individuals of the same species can grow more slowly and reach larger sizes at colder, higher latitudes than their smaller counterparts residing at warmer, lower latitudes. Sigourney *et al.* (2006) suggested that halibut may exhibit such a geographic gradient in length at maturity in the northwest Atlantic. The size at maturity for a population is often expressed

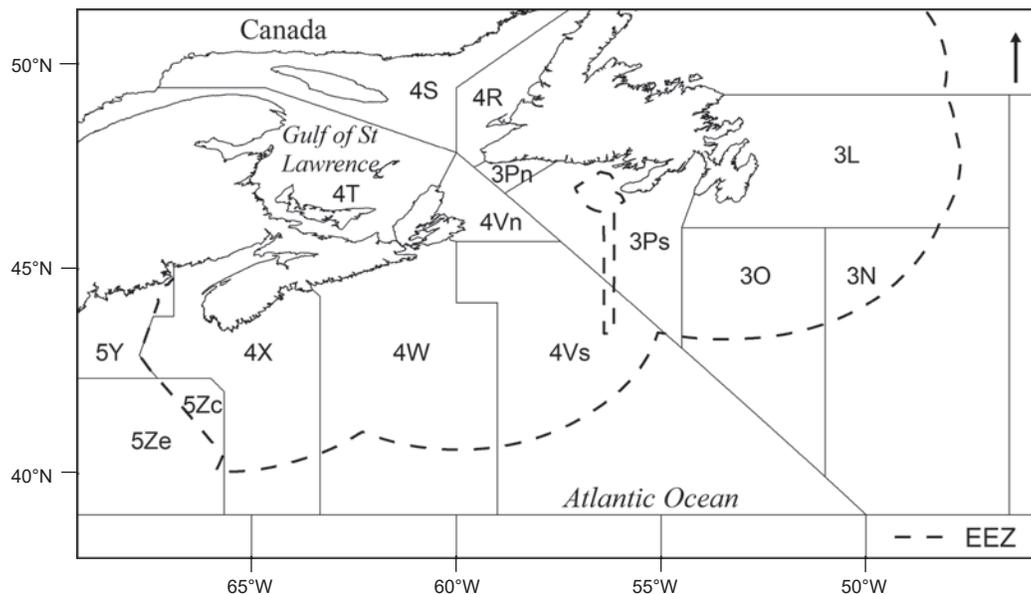


Fig. 1. Northwest Atlantic ocean showing NAFO divisions 3NOPs4VWX5Zc, the stock unit for Atlantic Halibut (DFO, 2015). Dashed line represents exclusive economic zone (EEZ). NAFO shapefile obtained from: <https://www.nafo.int/Data/GIS>, EEZ shapefile obtained from: <http://www.marineregions.org/gazetteer.php?p=details&id=8493>, and world map shapefile obtained from: [http://thematicmapping.org/downloads/world\\_borders.php](http://thematicmapping.org/downloads/world_borders.php).

as the value at which 50% of the sample is mature (LM50%). In the warmer southern divisions 4X5YZ (Fig. 1), Sigourney *et al.* (2006) estimated LM50% of male and female halibut to be 80 cm and 103 cm respectively. Whereas, in the colder northerly divisions two earlier studies estimated, male and female LM50% to be 77 cm and 119 cm (Trumble *et al.*, 1993), and 80 cm and 125 cm respectively (Bowering, 1986). Average annual bottom temperature on the southern edge of the stock domain can be  $\sim 7^{\circ}\text{C}$  warmer than on the northern edge. “Thermal time” (*sensu* Neuheimer and MacKenzie, 2014) is commonly referred to as growing degree-day (GDD) and is based on the concept that growth rate is dependent on temperature which affects physiological rates, and that the growth increment is dependent on the integral of suitable temperatures up to a given time or age (Neuheimer and Taggart, 2007). This concept of growth potential is borrowed from the agricultural field and has been used successfully to examine fish growth (*e.g.* Neuheimer and Taggart, 2007; Neuheimer *et al.*, 2008; Neuheimer and Gronkjaer, 2012). Here we estimate growth rate and LM50% using two separate datasets linked to the stock-wide DFO-Industry halibut survey, and test the hypothesis that spatial variation is correlated with GDD. To compare with older studies and investigate whether life history traits vary among NAFO divisions, we predict growth and LM50% for each division using the median GDD per NAFO division.

## Methods

### Data

#### Joint Industry-DFO Halibut Longline Survey

The data used to estimate growth and maturity were obtained from two different programs conducted during the joint Industry-DFO Halibut Longline Survey. The Longline Survey is a fixed station survey that occurs mainly from May to August in NAFO divisions 3NOPs4VWX at locations with high historical halibut catch rates (Zwanenburg and Wilson, 1999). Between 1998 and 2016, roughly 220 fixed stations were sampled per year. Data were collected by DFO-certified fisheries observers on commercial fishing boats which used a standardized fishing protocol, comprised of 1000 size 14–16 circle hooks, and 6–12 hour soak times. All survey participants are required to fish within license conditions, including the mandatory discarding of all halibut less than the minimum legal length of 81 cm. Special license conditions were issued to some boats in 2011 to allow undersized fish to be retained for biological sampling as it is only possible to assess sex and maturity from gonads. Maturity data, referred to herein as the Maturity Collection (MC) Program, were collected by the fisheries observers

on the Longline Survey trips. Growth data were derived from the Halibut All Sizes Tagging (HAST) Program (den Heyer *et al.*, 2012), which uses the Longline Survey as its platform for tag release.

#### Halibut All Sizes Tagging (HAST) Program

We derived growth data using data from the HAST Program in which halibut were double-tagged using t-bar anchor tags (den Heyer *et al.*, 2013). Data recorded by observers on the Longline Survey included release date, release length, and location. Sex, length, recapture date, recapture length, and location were reported at recapture. Recaptures were reported year round, with peak recaptures in the summer reflecting the seasonal distribution of fishing effort.

#### Maturity Collection (MC) Program

We derived maturity data from the MC program observer data collected on the Longline Survey. On the survey, DFO-certified fisheries observers recorded: location, depth, temperature, total catch, species by weight, individual weight, length, sex, and maturation state for all halibut caught on fixed station and commercial index sets. Maturity codes are assigned to each fish using a classification scheme that was updated in 2011 for the MC program, aimed to improve observers skills. In this study we only used data collected after 2010. Halibut maturity code definitions used by trained observers in the DFO-industry longline survey and commercial index are available upon request (C. den Heyer, pers. comm). Additionally, as a means to reducing uncertainty/inconsistencies that can be associated with the subjectivity of observer data, we conducted a further quality control analysis, and removed observers who showed signs of misclassification. Finally, we only included observers that had sampled in both NAFO divisions 3 and 4.

#### Growing degree-day (GDD) as an index of growing potential

GDD is the number of days multiplied by a daily temperature above a threshold, on an annual basis (units are denoted as  $^{\circ}\text{C}\cdot\text{day}$ ). GDD were calculated using output from the high resolution numerical ocean circulation model “BNAM” (BIO North Atlantic Model). This model has been used to study a number of physical and ecosystem related processes in the Northwest Atlantic Ocean (Brickman *et al.*, 2016, 2018; Wang *et al.*, 2016). The model simulation starts in 1990 and runs to the present year. The 2001–2015 timeframe was used in this study. Spatial GDD was computed for each year as the time integral of bottom temperature greater than  $3^{\circ}\text{C}$  over the 12 month period (Fig. S2). The lower threshold of  $3^{\circ}\text{C}$

was chosen as halibut occur more frequently above 3°C (Shackell *et al.*, 2016; French *et al.*, 2018). Within the HAST dataset, we estimated the average GDD value for each tagged fish by connecting the release and recapture locations using a vector, drawing a 0.25 decimal degree buffer around the vector and then calculating the average GDD value within the buffer. Within the MC dataset, we estimated the average GDD values for each fish within 0.25 decimal degree buffers that were drawn around each sample point.

## Analysis

### Model Approach

We wished to determine the effect of GDD and fish length on growth rate, and on length at maturity, for each sex across NAFO divisions. We are interested in comparing

life history trait estimates among NAFO divisions, to test the hypothesis that variation in GDD leads to variation in life history traits among NAFO divisions. Although the overlap is substantial, GDD varies among NAFO divisions with GDD in the northerly NAFO division 3N being lower than that in 4X (Fig. 2). To compare growth rate among NAFO divisions, we predicted growth rate at the median GDD per NAFO division. Because of the hierarchical structure in the MC data, we compared LM50% among NAFO divisions by resampling the MC data, and then aggregated predicted values by NAFO division. Differences among predicted values were evaluated with t-tests.

### Growth Model

Our goal was to predict growth rate using GDD and fish length for each sex. Using the HAST data, we selected all fish that were re-captured in the same NAFO division

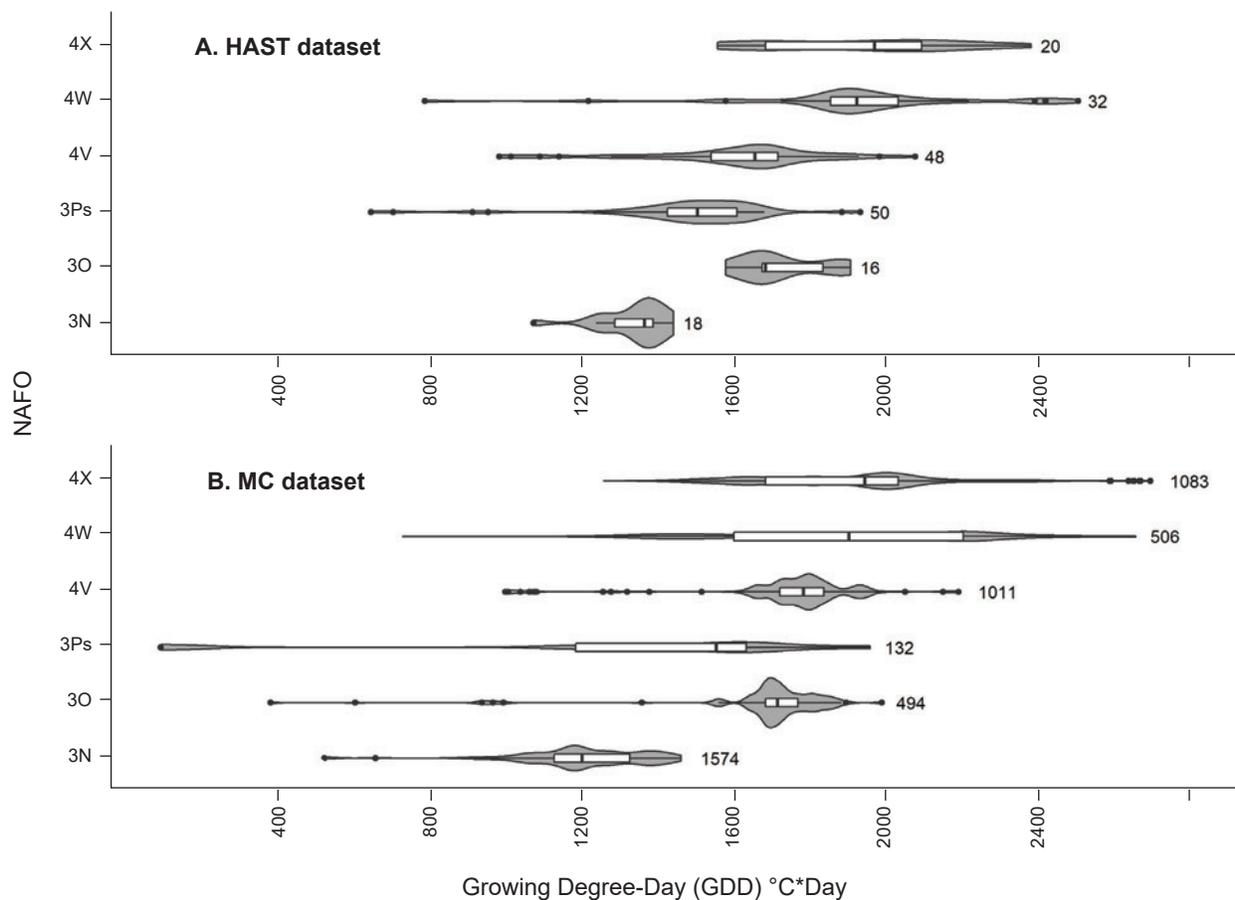


Fig. 2. Boxplots overlaying violin plots of annual Growing Degree-Day (GDD °C\*day) across NAFO divisions for (A) HAST dataset used to estimate growth rate and (B) MC dataset used to estimate LM50%. Sample sizes within each NAFO division/dataset are inset. Boxplot lines represent the lower and upper quartiles, the box represents the inner quartiles (25–75%) and the horizontal line is the median. Violin plots are complementary to the boxplots and show the probability distributions of the data.

where they were initially tagged and at liberty for >60 days. We assumed growth followed a von Bertalanffy function, and used the Gulland and Holt (1959) method where relative growth is a function of average length at recapture and length at release.

$$GR = a + b * Sex + c * Length + d * GDD \quad (1)$$

We used R statistical programming (R Core Team, 2018) to model Equation 1 (where GR is the length at recapture less the length at release per year for each sample, “*a*” is the intercept term, “*b*” is the coefficient corresponding to the effect of factor Sex, “*c*” is the coefficient specifying the effect of the covariate Length. Length is the average of length at release and length at recapture and “*d*” is the coefficient describing the effect of the covariate GDD. Our initial suite of models included an interaction term between the factor sex and the covariate length, to test whether the slope of growth rate on length differed between sexes. We assumed a Gamma distribution, and used generalized linear models specifying a log link. Models were evaluated based on Akaike’s Information Criterion (AIC), the model with significantly lower AIC was selected as the final model.

### Maturity Model

Our goal was to predict LM50% using GDD and length for each sex. Using the MC data, we used a generalized linear mixed model approach (Bates *et al.*, 2015). We set observers ( $n = 8$ ) as a random effect to address the variation in maturity assessment by observers. We used a logistic function to estimate LM50% (Equation 2).

$$p = \frac{e^{(a+b*length+c*GDD+d*Sex)}}{1 + e^{(a+b*length+c*GDD+d*Sex)}} \quad (2)$$

The response “*p*” is the proportion mature, “*a*” is the intercept, “*b*” is the coefficient describing relationship between length and the proportion “*p*” of mature fish, “*c*” is the coefficient describing relationship between GDD and “*p*”, and “*d*” is the coefficient describing the difference between the two sexes. We fit sequential models of increasing complexity, using a binomial error distribution. Models were evaluated based on Akaike’s Information Criterion (AIC), the model with significantly lower AIC was selected as the final model.

We simulated fixed and random effect parameter coefficients ( $n = 1000$ ) using the final model posterior distributions to create Bayes estimates of the median and confidence intervals using the R package “merTools” (Knowles and Frederick, 2016). Predicted values and intervals were also simulated ( $n = 1000$ ) from the model parameter distributions, from which we estimate length at

50% maturity (LM50%) and length ranges for each sex. The prediction intervals included residual variance of the model as well as fixed and random sources of uncertainty using a method recently developed by Knowles and Frederick (2016). The addition of residual variance greatly inflates the confidence intervals, and is rarely reported (Knowles and Frederick, 2016). However, we judged that it was important in this circumstance given the dynamic nature of observer derived data. Length ranges around the median LM50% were estimated as the length range where prediction intervals, around LM50%, corresponded to 50% mature.

## Results

### Growth (HAST) dataset summary

There were 97 females and 87 males, totaling 184 samples in the HAST dataset. Female average length ranged from 75.5 cm to 181.5 cm and a median length of 120 cm. The median GDD was 1623°C\*day. Male average length ranged from 68.5 cm to 150.5 cm and the median length was 94 cm. The median GDD was 1671°C\*day (Table S1, Fig. S1). Growth rate declined with length and increased with GDD in both sexes but there is considerable variation in all relationships (Fig. 3).

### Growth Rate Model

We first fit a model that included an interaction term between the factor sex and the covariate length, but the interaction term was not significant. Once the interaction was dropped from the model, all remaining terms were significant (Table 1). Annual growth rate declined with length, males grew more slowly than females and GDD had a significantly positive effect on both sexes. The model accounted for 19% of the variation in growth rate (McFadden’s pseudo- $R^2$ ) (Table 1).

### Maturity (MC) dataset summary

There were 3082 females and 1718 males, totaling 4800 samples in the MC dataset; 47% of the females samples were mature while 62% of the male samples were mature. The minimum female length ranged from 60 cm to 178 cm and the median length was 95 cm. The median GDD was 1555°C\*day. The minimum male length ranged from 68.5 cm to 150.5 cm and a median length of 94 cm. The median GDD was 1686°C\*day (Table S1, Fig. S1).

### Maturity Model

The model that best fit the data included a random intercept and a random slope for the observer effect (Table S2). The marginal (fixed effects alone) and conditional (fixed and

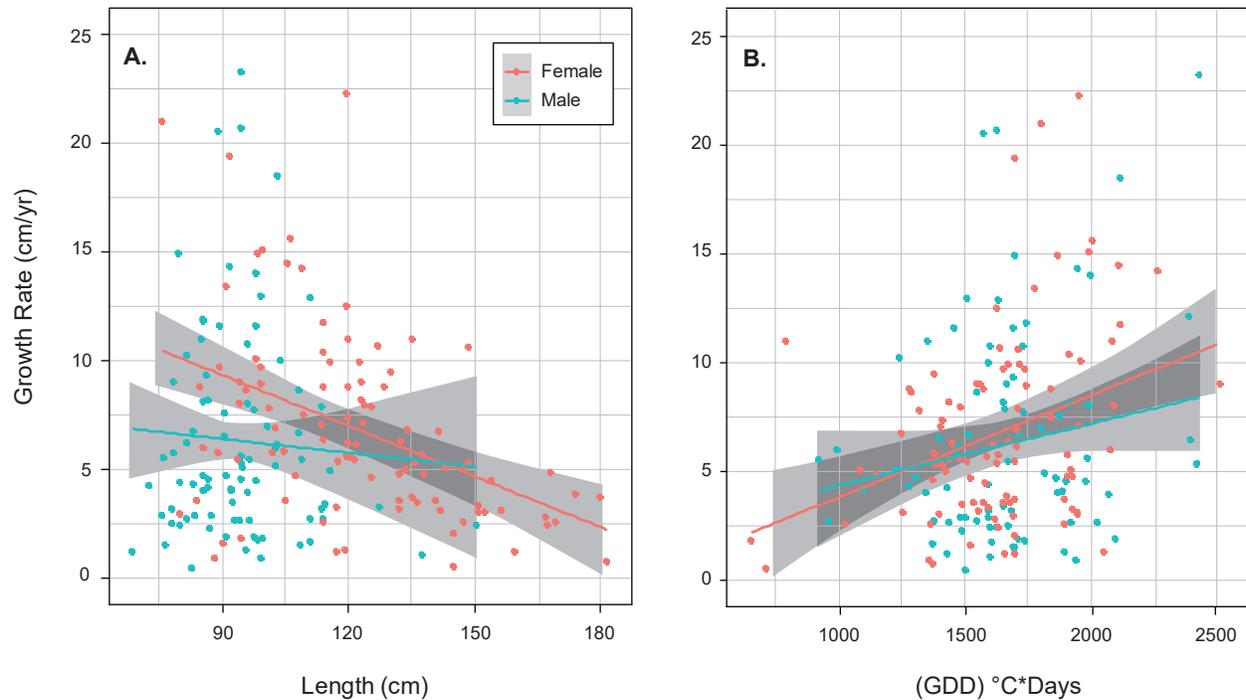


Fig. 3. Growth rate of males (blue) and females (red) as (A) a function of length (cm) and (B) growing degree-day (GDD °C\*day). Lines are the fitted linear model. The grey shading represents the 95% confidence intervals.

random effects)  $R^2$  values were 0.46 and 0.75 respectively ( $n = 4800$ ). Sex, length, and GDD had significant effects on maturity status (Table 2). Males were more likely to be mature at a smaller length than females. The fixed effect coefficient of fish length was relatively larger and positive, indicating that the likelihood of being mature was greater for larger fish. To a lesser effect, the likelihood of being mature was greater for fish associated with higher GDD (warmer, longer). To summarize, the likelihood of a fish being mature, in this data set, was greater for males, and at larger lengths and higher GDDs (Table 2, Fig. 4). The

associated simulated random effects coefficients show that the intercepts of 4 observers are similar, but that there are two observers that differ (estimate differs from 0). With respect to median effect of random slopes, there are four observers that differ from the others, resulting in significant (differing from 0) simulated slope estimates (Fig. 4). Accounting for residual variance and uncertainty in the random and fixed effects resulted in very wide prediction intervals in all divisions (Fig. 5) and reflects that the program that trains observers how to assign maturity codes needs substantial improvement.

Table 1. Model summary results of growth rate analysis. “\*\*\*\*” corresponds to significant level 0.001, “\*\*\*” 0.01 “\*” 0.05 “.” 0.1 “.”.  $n$  samples=184

Model term	estimate	std.error	statistic	p.value	
Female (Intercept)	2.4154	0.3976	6.0746	0.0001***	
Male	-0.3657	0.1140	-3.2067	0.0016**	
Length	-0.0112	0.0024	-4.7706	0.0001***	
GDD	0.0050	0.0015	3.3346	0.0010***	
null.deviance	deviance	df.null	df.residual	AIC	
	91.62	78.12	183.00	180.00	987.59

Table 2. Model summary results of maturity analysis. Generalized linear mixed effects model fit by maximum likelihood corresponding to “m3” in Table S2. “\*\*\*” corresponds to significant level 0.001, “\*\*” 0.01 “\*” 0.05 “.” 0.1 ‘. *n* samples= 4800, *n* observers= 8 (Final Model AIC = 4388.3).

Model terms	estimate	std.error	statistic	p.value
Female (Intercept)	-0.58	0.52	-1.1190	0.2630
Male	2.29	0.10	23.7740	< 2e-16 ***
Length	2.76	0.50	5.5670	2.59e-08 ***
GDD	0.77	0.05	14.4610	< 2e-16 ***
Error terms	Std.Dev.	Corr		
Observer (Intercept)	1.45			
Length (slope)	1.34	0.48		
Residual	1.00			

**Life history trait estimates among NAFO divisions**

Both sexes grew faster in the more southerly divisions (4WX). With rates of up to 3.4 cm faster per year, the female growth rate corresponding to NAFO division 4X was significantly faster than in NAFO division 3N (Fig 6A, Table S3). Male growth rates corresponding to NAFO divisions 4X and 4W were significantly faster than those in NAFO divisions 3N and 3Ps, with rate up to 2 cm faster per year (Fig 6A, Table S3).

Both sexes matured at smaller sizes in the more southerly divisions (4WX). However, there were no significant differences among regions within sex in LM50% due to such wide prediction intervals (Fig. 6B, Table S3). Across the stock domain, female LM50% ranged from 92–145 cm, and male LM50% range from 65–120 cm. The female LM50% median estimates in the warmer southern divisions 4X and 4W were ~10–28 cm less than the more northerly divisions. The male LM50% estimate in subdivision 4X was up to 9 cm less than in northerly subdivisions (Table S3).

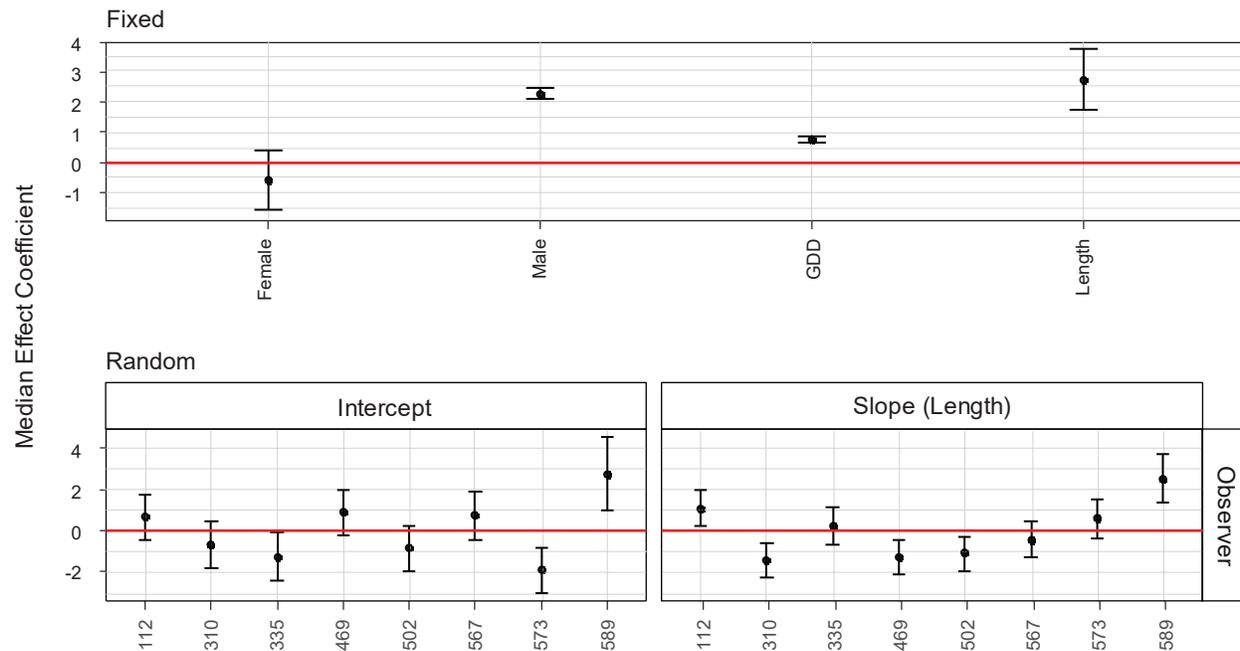


Fig. 4. Simulated median estimates (*n* = 1 000) of fixed (top) and random (bottom) effects parameters of final Maturity Status model derived from posterior distributions. Median estimates that overlap 0 are not significantly different from 0, or each other. Observer numbers are displayed on X axis.

## Discussion

Female halibut grew faster and matured at larger sizes than males reflecting the sexual dimorphism of the species (Kohler, 1967; Collette and Klein-Macphée, 2002; Sigourney *et al.*, 2006; Armsworthy and Campana, 2010; Beaty and Chen, 2017). Growth rate declined with length and increased with growing degree-day (GDD). Growth rates of both males and females were greater in the southern divisions (4X/4W) than in the northern divisions (3N/3Ps). Length at maturity (LM50%) was smaller for both sexes in the southern divisions than in the northern divisions but the distributions overlap considerably, partially reflecting the variation among observers in maturity status classification.

Studies that have estimated halibut length at maturity in this region were published a long time ago, and often without confidence intervals. Despite that, older studies can help shape expectations. Female LM50% estimates

in this study are consistent with other studies throughout the stock domain (Bowering 1986, Trumble *et al.*, 1993; Sigourney *et al.*, 2006). Sigourney *et al.* (2006) estimated female LM50% at 103 cm (CI 94–112 cm) in NAFO divisions 4X5YZ which is comparable to this study for female LM50% at 103 cm in 4X (CI 94–132 cm) and 98 cm in 4W (CI 90–130 cm). In an area corresponding to NAFO subarea 3, female LM50% was estimated as 119 cm (Trumble *et al.*, 1993) and 125 cm (Bowering, 1986), which corresponds to the larger female LM50% range estimated in this study (113–126 cm). Still, the variation observed in this study precludes us producing definitive LM50% estimate per division. We can state that, on average, fish mature at a smaller size in 4WX, but we cannot predict length at maturity for any new observations in any division. Given the large variation in the observer random effect, a much larger sampling program with many more trained observers would be needed to improve maturity estimates from at-sea evaluations of gonads. Directed sampling that spans the size composition in

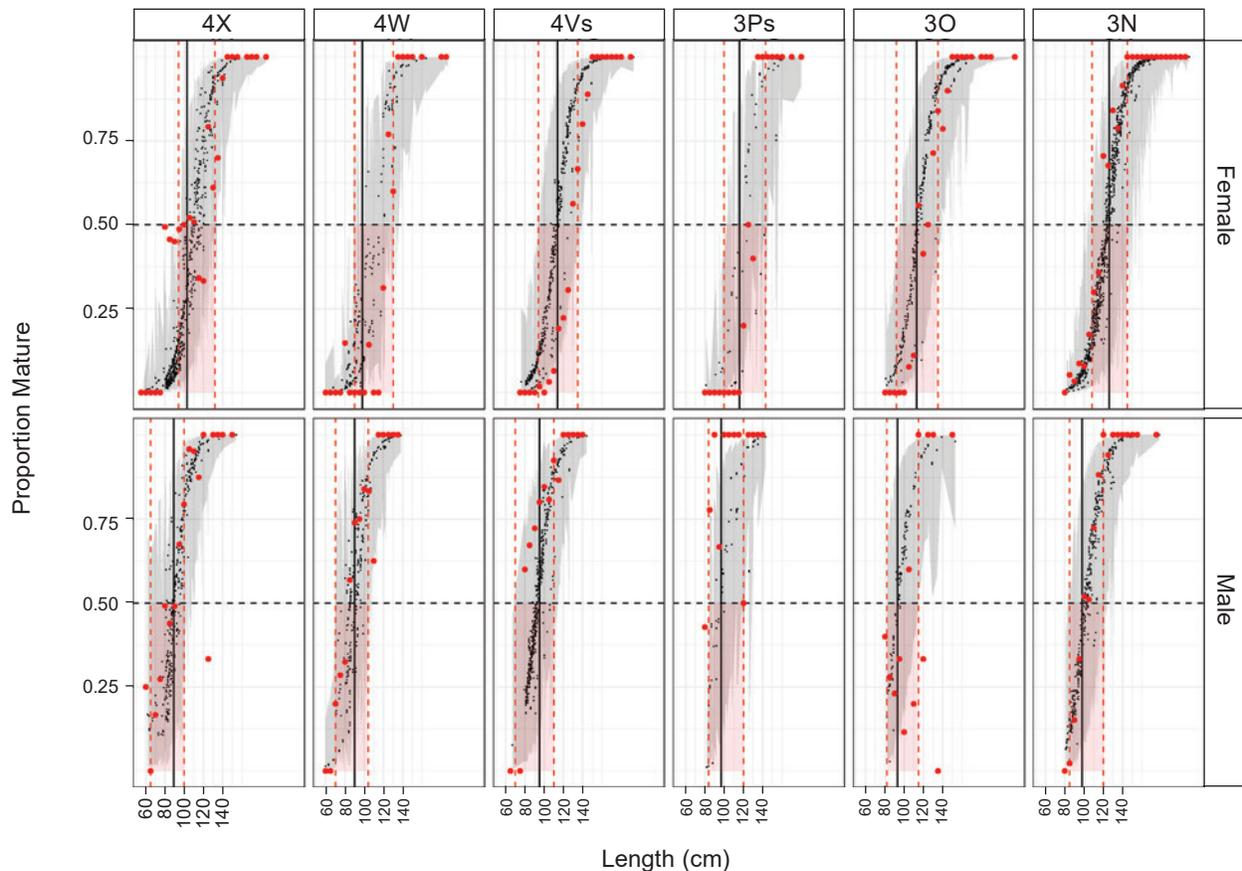


Fig. 5. Proportion Mature in each NAFO division for each sex. Model predictions (black points) and intervals generated by simulation ( $n = 1000$ ). Red points represent observed proportion mature. Horizontal dashed line shows proportion mature of 0.5, vertical solid black line is the LM50%. Pink shaded area refers to length range of LM50%, estimated as the lengths corresponding to the intersection when upper/lower prediction interval is  $\sim 0.5$ .

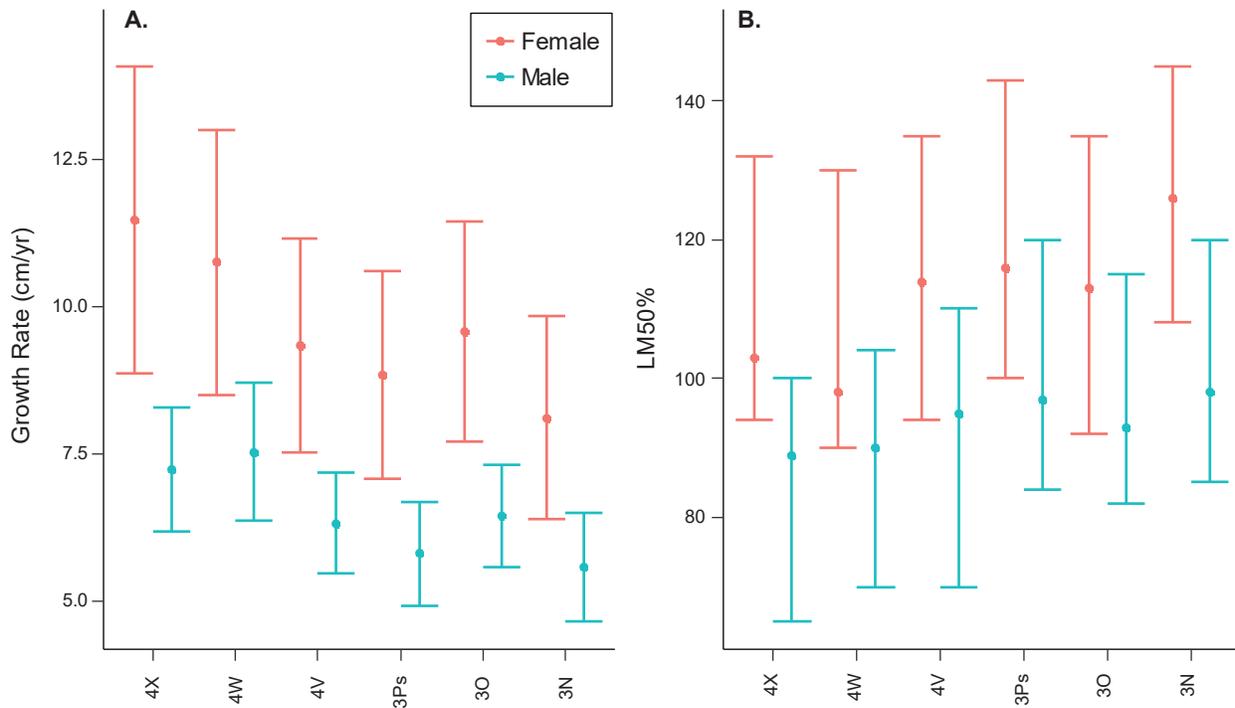


Fig. 6. Predicted (A) growth rate of males (blue) and females (red) at 90 cm and (B) Length at Maturity (LM50%) for each NAFO division.

each NAFO division for histological examinations, would provide improved estimates of size at maturity that would be more directly comparable to the historical data and allow for biologically important variation to be incorporated in stock assessment and management.

A unit stock assumes uniform population dynamics which in turn are affected by: age/size structure, spawning stock biomass (SSB), recruitment rates, reproductive potential, intrinsic population growth rate, and carrying capacity. Significant geographic variation within a unit stock in demographic rates will not only affect the stock assessment, but can also contribute to spatial variation in fishing mortality and the disappearance of high density areas (McBride 2014, Carson *et al.*, 2017). The current length-based, age-structured halibut assessment model (Cox *et al.*, 2016) includes a sex-specific growth curve based on otolith aging (Armsworthy and Campana, 2010). Spatial variability in the age-selectivity between the Scotian Shelf (4VWX) and the southern Grand Banks (3NOPs) is reflected by the ample variation in the length composition in the catches. Armsworthy and Campana (2010) acknowledged that the variance of both subarea growth curves were large and overlapped considerably, but at that time, their results represented the best available evidence and so the spatial variability in growth was not included in the assessment model. Here, we provide new information on spatial variation of life history traits.

Many stock assessments assume fixed growth and maturity rates, whereas, in reality, growth rates can vary, within and among years (Lorenzen, 2016). Indeed, variation introduced by observers was evident but we cannot discount the hypothesis that growth rates and length at maturity are naturally highly variable due to phenotypic plasticity. Increasingly, the plasticity of growth has motivated researchers to include “time-varying” productivity components in stock assessment models but again, the monitoring of these dynamic traits is costly and unavailable to us at this time. In the absence of a sound understanding of the spatial and temporal dynamics of life history traits, to safeguard the stock, additional precautionary strategies such as the protection of juvenile nurseries, should be employed (Lorenzen, 2016; Nielsen and Seitz, 2017; Kersula and Seitz, 2019). For now, our results represent the best available evidence and will be considered in the next halibut stock assessment.

Recently, we provided evidence to support the notion that the current stock unit definition is masking smaller-scale dynamics (Shackell *et al.*, 2016). This was further corroborated by other researchers who provided evidence that halibut in the eastern Gulf of Maine may be distinct from halibut in Canada (Seitz *et al.*, 2016; Kersula and Seitz, 2019) although there is mixing (Kanwit, 2007; Shackell *et al.*, 2016; Kersula and Seitz, 2019). We then identified persistent high density areas and estimated the

connectivity among them to be an order of magnitude smaller than the current stock unit domain (Boudreau *et al.*, 2017). Finally, we showed that the proportion of juvenile suitable habitat in each NAFO division is strongly related to historical (McCracken 1958) and current adult catch rates, supporting the “nursery size” hypothesis, which states that the amount of juvenile habitat is a proxy for adult production (French *et al.*, 2018). Here, we demonstrated statistical differences in growth rate between the most southerly and the most northerly divisions, but, despite the significant influence of GDD on size at maturity, there were no statistically significant differences in LM50% estimates for the NAFO divisions. Our current assessment framework can be improved by incorporating the current and historical evidence for spatial variation and plasticity in life history traits.

At present the indices of abundance and landings for this stock are increasing or near all-time recorded highs (Cox *et al.*, 2016; Trzcinski and Bowen, 2016; DFO, 2017). With the increase in abundance, we may see changes in life history traits such as growth and size at maturity that would impact the assessment. Monitoring programs will have to be designed to address spatial variability highlighted here. Further, the spatial variation in life history traits, highlighted herein and in Armsworthy and Campana (2010), may be linked to population structure. As the fishery expands, the failure to account for spatial structure could undermine the sustainability of the fishery and cost industry foregone yield. Careful review of all evidence, including genetics, life history variation and fisheries data is needed to evaluate the structure of this stock and ensure that management of the rapidly increasing commercial fishery is sustainable.

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